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TABLE OF CONTENTS

Volume 109

INDEX TO NEW TAXA

Volume 109

(New taxa are indicated in *italics*; new combinations designated n.c.)

ARTHROPODA

Crustacea

Insecta

HEMICHORDATA

CHORDATA

Pisces

Amphibia

Mammalia

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New species of mammals from northern South America: Bats of the genera *Histiotus* Gervais and *Lasiurus* Gray (Chiroptera: Vespertilionidae)

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Abstract.—Two strikingly differentiated species of northern South American *Histiotus* and *Lasiurus* have been long known, but until now have remained undescribed and unnamed. The new *Histiotus* (*H. humboldti*) is a relict species, most like *H. montanus* Philippi & Landbeck, but differing from it and all other *Histiotus* in small size (forearm <47 mm, maxillary toothrow length <5.7 mm), fragile skull, and weak dentition. Isolated populations occur at medium elevations (1500–2200 m) in the Coast Range, in the Mérida Andes, and on Cerro Neblina in Venezuela, and in the Central and Western Andes and upper Cauca Valley in Colómbia. The new *Lasiurus* (*L. atratus*) is a Guayanan endemic known from Venezuela, Suriname, and French Guiana. Medium size (forearm 44–47 mm, max. toothrow l. 4.4–5.0 mm) and black wings relate it to *L. varius* Poeppig of Chile and *L. castaneus* Handley of Panamá and Costa Rica; but very bright black and white underparts; small antorbital fossa; obsolete lachrymal process, supraorbital ridge, and basial pits; and well-developed mastoid process distinguish it from both.

Mammals and their ectoparasites were collected in Venezuela between 1965 and 1968 by the Smithsonian Venezuelan Project, supported in part by a contract (DA-49-MD-2788) of the Medical Research and Development Command, Office of the Surgeon General, U.S. Army. Numerous papers have described the ectoparasites and mammals of the Project. Throughout these papers undescribed species of mammals have been referred to by alphabetical designations. Some of these have been named subsequently by Handley & Ferris (1972), Handley & Gordon (1980), Handley (1984, 1987). This paper provides formal descriptions for insect-eating bats of the genera *Histiotus* Gervais and *Lasiurus* Gray.

Material and Methods

Measurements.—All measurements used in this paper are in millimeters and follow the directions of Kalko & Handley (1994). Cranial measurements were taken with the assistance of a binocular microscope, with dial calipers reading to 0.1 mm.

Specimens are deposited in the following institutions: American Museum of Natural History, New York (AMNH); Estación Biológica de Rancho Grande, Maracay (EBRG); Field Museum of Natural History, Chicago (FMNH); National Museum of Natural History, Washington (USNM); Universidad Central de Venezuela, Caracas (UCV).

Systematics

A new species of Leaf-eared bat, genus *Histiotus* Gervais

One of the first bats netted by the Smithsonian Venezuelan Project at its inception in July 1965, at Los Venados in the Coast Range overlooking Caracas, was a species of *Histiotus*. This genus had not been found previously in Venezuela. In a few weeks we caught three more *Histiotus* at Los Venados and at the Hotel Humboldt higher up on the mountain. These represented a new species that I describe and name here.

This species has been mentioned in the literature as *Histiotus montanus colombiae* Thomas by Tamsitt & Valdivieso (1966) from Cauca, Colómbia, and as *Histiotus* sp. A by me (Handley 1976) from Distrito Federal, Venezuela, and by Gardner (1990) from Cerro Neblina, Venezuela.

Histiotus humboldti, new species
(Fig. 1, Table 1)

Synonymy.—

Histiotus montanus colombiae Tamsitt & Valdivieso, 1966:102 (not *Histiotus colombiae* Thomas, 1916).

Holotype.—USNM 370968, adult female (lactating); skin, skull, and skeleton; collected 24 July 1965 by Charles O. Handley, Jr. Original number, SVP 00092.

Type locality.—Los Venados, 4 km NNW Caracas, 10°32′N, 66°54′W, 1498 m, Distrito Federal, Venezuela. The holotype was caught 150 m west of park headquarters buildings in a mist net set across a Jeep trail in second-growth forest with thick underbrush. This area is classified as LOWER MONTANE humid forest (bh-MB) in the Holdridge system (Ewel and Madriz 1968).

Etymology.—This impressive bat is named in honor of the great naturalist Alexander von Humboldt who traveled widely in Venezuela in 1799 and 1800 and described many Venezuelan mammals (Hershkovitz 1987).

Distribution.—*Histiotus humboldti* has a fragmented range, with apparently isolated populations in southwestern Colómbia (on the lower eastern flanks of the Western Andes at El Tambo and Quisquio and near the head of the Cauca Valley at Popayán), in north-central Colómbia in the northern part of the Central Andes (La Ceja and Poblado), in the Mérida Andes in western Venezuela (near San Juan de Lagunillas), in the Coast Range in northern Venezuela (Los Venados and Pico Avila), and on Cerro Neblina in southern Venezuela. Elevational range, from 1498 m at Los Venados to 2217 m at La Ceja.

Ecology.—*Histiotus humboldti* is a montane species that occurs at medium elevations, lower than *H. montanus* usually is found at this latitude. Specimens from the Coast Range in northern Venezuela were taken in moist, second-growth, evergreen forest; fairly tall at Los Venados, low and very dense at Hotel Humboldt on Pico Avila. Three were taken in forest trails and one was netted in a livestock pen where trees remained, but underbrush had been cleared (Handley 1976). On Cerro Neblina *H. humboldti* was taken in scrubby tepuyan vegetation in open areas close to rocky sand hills (A. L. Gardner, pers. comm.).

Diagnosis.—*Histiotus humboldti* can be recognized as a *Histiotus* by its enormous ears, plain (unornamented) snout, *Eptesicus*-like skull, and vespertilionid dentition. It can be distinguished from other *Histiotus* by its small size, delicate rostrum, fragile zygomata, inflated braincase, and small, weak dentition.

Description.—Dorsal coloration bright tan to brown, darker where blackish hair bases show through; underparts buff with fuscous hair bases showing through. Ears very large (28–32); anterior lobe wide (4.3–5.5) and forming a point where it folds; tragus relatively short and broad (9–11 × 3.5–4.0); tibia and fingers relatively short (tib. 17.5–18.8, F2 39.1–40.6, F3 78.3–80.5, F4 62.6–65.6, F5 56.2–60.0). Skull (Fig. 1) fragile throughout; rostrum short (max. toothrow l. 5.3–5.6), narrow (max. br. 5.9–6.1), and shallow; facial profile sharply dished; lachrymal ridge strongly developed; supraorbital region bulges, but is not ledged; braincase and area of postorbital constriction notably inflated; zygoma fragile, but with a large postorbital process; pterygoid processes thin and delicate. Teeth small and

Fig. 1. Dorsal, ventral, and lateral views of the skull and lateral view of the mandible of *Histiotus humboldti*, USNM 560627, male, from Cerro Neblina, Amazonas, Venezuela. A. L. Gardner photograph. Scale 7:1.

Table 1.—Measurements (in millimeters) and mass (in grams) of adult *Histiotus humboldti.*

	USNM 370968* Los Venados Venezuela ♀	UCV J-03208 Cerro Neblina Venezuela ♀	FMNH 72340 La Ceja Colombia ♀	EBRG [US370967] Los Venados Venezuela ♂	USNM 370969 Pico Avila Venezuela ♂	USNM 370970 Pico Avila Venezuela ♂	USNM 560627 Cerro Neblina Venezuela ♂	FMNH 86719 Popoyán Colombia ♂
Total length	109	107	—	106	110	110	110	—
Tail vertebrae	50	50	—	52	48	47	51	—
Hind foot (dry)	9	11	10	9	10	9	11	11
Ear from notch	30	28	—	32	30	31	29	—
Forearm	45.7	46.8	46.8	45.5	45.7	45.5	46.9	46.0
Tibia	17.5	18.0	18.0	17.5	18.3	17.9	18.8	18.6
Calcar	26.3	23.0	—	26.1	22.8	—	23.8	—
Mass	—	11.5	—	—	—	—	9.5	—
Greatest length	16.4	16.5	—	16.0	16.3	16.4	16.9	—
Zygomatic breadth	9.6	9.8	—	9.2	9.5	9.5	9.4	—
Postorbital breadth	4.7	4.5	—	4.5	4.4	4.5	4.5	—
Braincase breadth	8.1	8.0	—	7.8	8.3	7.9	8.0	—
Braincase depth	5.8	5.8	—	5.6	5.6	5.8	6.2	—
Maxillary toothrow length	5.4	5.5	5.4	5.5	5.3	5.5	5.6	5.4
Postpalatal length	6.5	6.1	—	6.3	6.4	6.6	6.6	—
Maxillary breadth	6.0	6.0	5.9	6.0	5.9	6.1	6.0	6.1
Canine breadth	4.2	4.2	4.1	4.2	4.1	4.1	4.3	4.2

* Holotype.

weak, with low cusps; dental formula 2/3-1/1-1/2-3/3 × 2 = 32.

Comparisons.—*Histiotus humboldti* differs in almost every detail from *H. macrotis* Poeppig and *H. velatus* I. Geoffroy. It most resembles *H. montanus colombiae,* a taxon with which it is sympatric in some areas, but these species differ in many details. Coloration, both dorsally and ventrally, is similar in both species. Ears of *H. humboldti* are proportionally about the same size as those of *H. m. colombiae,* but the anterior lobe is wider and is more pointed than in any *H. montanus* (not as extreme as in *H. velatus,* however). The tragus is shorter and broader than in any other *Histiotus.* The tibia is shorter than in any *H. montanus* and finger proportions resemble *H. velatus* more than they do *H. m. colombiae.* In fact, in all finger measurements, *H. humboldti* is smaller or averages smaller than *H. m. colombiae.*

Skulls of *Histiotus montanus* and *H. macrotus* are similar to one another and quite different from *H. velatus,* but the skull of *H. humboldti* is so distinctive, that compared with it, the skulls of the other three species are relatively similar to one another. In that comparison the skull of *H. humboldti* looks as though it might even represent a different genus. In fact it bears a strong superficial resemblance to skulls of North American *Plecotus* E. Geoffroy, *Idionycteris* Anthony, and *Euderma* H. Allen. Compared with the other species of *Histiotus,* the skull of *H. humboldti* is more delicate throughout; braincase and postorbital are much more inflated; rostrum is much shallower and narrower; dishing of facial profile is much more pronounced; lachrymal ridge is more developed, but the supraorbital ledge is undeveloped; zygomata are less flaring and much more fragile; pterygoid processes are more fragile; teeth are relatively tiny, very weak, and have lower cusps. Its relatively delicate skull and weak dentition indicate that *Histiotus humboldti* must have a softer diet than the other species of *Histiotus.*

Remarks.—Linares (1973) reported a specimen of *Histiotus* in the Muséum National d'Histoire Naturelle, Paris (MNHN), collected in 1894 by Briceño Gabaldon, near Mérida, Venezuela. Linares regarded the specimen as quite different from Colómbian and Ecuadorean *H. montanus* because it had smaller canines and upper premolars, an enlarged postorbital process on the zygoma, and a dished facial profile. He thought some features of the specimen were reminiscent of *H. velatus*. However, because of scant material and inadequate knowledge of variation in *Histiotus*, he tentatively identified the specimen as *H. m. colombiae* (not typical).

Some characters that Linares ascribed to the Mérida specimen are characteristic of *Histiotus humboldti*. However, the suite of measurements of the Mérida specimen place it within the size range of *H. m. colombiae*, and show that it is apparently too large to be *H. humboldti*. I conclude that Linares was correct in identifying the Venezuelan specimen in MNHN as *H. montanus*.

Recently Jesús Molinari (pers. comm.) has taken *Histiotus humboldti* (confirmed by measurements and photographs of the skull) adjacent to an extensive island of xeric vegetation at Tierra Negra, 1550 m, ca. 12 km S San Juan de Lagunillas, Estado Mérida, Venezuela. Thus, in Venezuela, *Histiotus montanus* is known in the Mérida Andes, while *H. humboldti* appears to have a fragmented distribution at medium elevations in the Coast Range, in the Mérida Andes, and on a Guayanan tepui, peripheral to the range of *H. montanus*. A similar relationship is observed in Colómbia. This suggests to me that *H. humboldti* once had a more extensive, continuous range in the mountains of northern South America that has been overrun and fragmented by *H. montanus*.

Specimens examined.—Colombia: Antioquia: La Ceja, [ca. 2217 m], 2 alc. (FMNH); Poblado, [ca. 1600 m], 1 alc. (AMNH). Cauca: Popayán, 1750 m, 1 alc. (FMNH). Venezuela: Amazonas: Cerro Neblina, Camp II, 2.8 km NE Pico Phelps, 1820 m, 1 skin & skull (USNM), 1 skin & skull (UCV). Distrito Federal: Los Venados, 4 km NNW Caracas, 1498 m, 2 skin, skull & skeleton (USNM); Pico Avila, 5 km NNE Caracas, 2092–2101 m, 1 skin, skull & skeleton (USMN), 1 skin & skull (EBRG).

References to other specimens.—Colombia: Cauca: El Tambo, 1800 m, 1 skin & skull (Swedish Mus. Nat. Hist., Tamsitt & Valdivieso 1966); Quisquio, 1700 m, 1 skin & skull (Swedish Mus. Nat. Hist., Tamsitt & Valdivieso 1966). Published measurements (fa. 46.1, 47.2; max. toothrow l. 5.4, 5.6) (Tamsitt & Valdivieso 1966) agree with *Histiotus humboldti*.

A new species of Red Bat, genus *Lasiurus* Gray

In collections of the Field Museum of Natural History, I found a specimen (FMNH 93235) of a strikingly beautiful red bat representing an undescribed species. It was collected in Suriname in 1961 by Harry Beatty. A short time later, in the collections of the Universidad Central de Venezuela in Caracas. I discovered two more specimens of the same species that had been collected in Bolívar state in Venezuela in 1962 by Juhani Ojasti. None of these specimens has been mentioned in the literature, but recently a specimen from French Guiana has been reported by Brosset & Charles-Dominique (1990) and by Masson & Cosson (1992).

Lasiurus atratus, new species
(Fig. 2, Table 2)

Synonymy.—

Lasiurus spec.? Brosset & Charles-Dominique, 1990:543.

Lasiurus castaneus Masson & Cosson, 1992:476 (not *Lasiurus castaneus* Handley, 1960).

Holotype.—FMNH 93235, adult male, skin and skull, collected 10 Feb 1961 by Harry A. Beatty.

Type locality.—Kaiserberg Airstrip, Zuid

Fig. 2. Dorsal, ventral, and lateral views of the skull of the holotype of *Lasiurus atratus,* FMNH 93235, male, from Kaiserberg Airport, Zuid River, Suriname. Scott Steppan photograph. Scale 5.6:1.

River, Suriname. According to Stephens & Traylor (1985), this is a hilly region that had undisturbed lowland rainforest at the time of Beatty's visit. It is located about 03°07'N, 56°27'W, at an elevation of about 278 m.

Etymology.—The Latin *atratus,* dressed in black, refers to the black wing membranes, which lack the ornate finger outlines that characterize the common red bat (*Lasiurus blossevillii*) of South and Central America.

Distribution.—Known only from Saül in southern French Guiana, from the type lo-

Table 2.—Measurements (in millimeters) of adult *Lasiurus atratus*.

	Venezuela						Suriname	Fr. Guiana
	El Dorado		Imataca				Kaiserberg	Saül
	UCV 5409 ♀	UCV 5410 ♀	Ochoa 2587 ♀	Ochoa 2588 ♀	Ochoa 3183 ♂	Ochoa 506 ♂	FMNH 93235* ♂	Masson & Cosson (1992) ♂
Total length	112	116	—	—	—	—	—	—
Tail vertebrae	53	57	—	—	—	—	—	—
Hind foot (dry)	10	10	11	11	11	11	10	
Ear from notch	13	13	—	—	—	—	13	—
Forearm	46.9	46.8	47.6	46.0	45.9	45.1	46.1	45.3
Tibia	21.8	19.5	20.8	21.1	20.1	20.2	19.2	—
Calcar	14.1	13.6	16.5	16.5	13.9	14.9	12.7	—
Greatest length	13.2	13.0	12.9	12.7	12.5	12.6	13.0	12.9
Zygomatic breadth	9.9	10.2	9.9	9.6	9.3	10.0	9.4	9.6
Postorbital breadth	4.3	4.3	4.1	4.3	4.1	4.1	4.8	4.2
Braincase breadth	7.9	7.8	7.6	7.9	7.7	7.7	7.7	7.6
Braincase depth	6.4	6.2	6.1	6.1	6.0	6.2	6.5	6.5
Maxillary toothrow length	4.9	5.0	4.9	4.7	4.4	4.8	4.9	4.8
Postpalatal length	5.9	6.1	5.7	5.8	5.5	5.7	5.8	5.7
Maxillary breadth	6.5	6.8	6.8	6.5	6.1	6.8	6.4	6.6
Canine breadth	5.4	5.7	5.5	5.3	5.0	5.5	5.4	5.4

cality in southern Suriname, and from eastern Venezuela (Km. 55 on the highway southeast of El Dorado, and in the Imataca Forest, ca. 28 km E Tumeremo, Bolívar). Elevational range, 100 m in Bolívar to 278 m at Kaiserberg Airstrip. Probably *Lasiurus atratus* is a Guayanan endemic.

Ecology.—Localities in Suriname and Venezuela where this bat was collected in 1961 and 1962 were in undisturbed lowland rainforest, Tropical humid forest (bh-T) in the Holdridge classification (Ewel & Madriz 1968). The specimen from French Guiana was netted above a small stream on the border of heavy tropical humid forest and a cultivated clearing (Masson & Cosson 1992). Specimens taken in the Imataca Forest in Venezuela by José Ochoa, 1990–1992, and by Ochoa and Elisabeth Kalko in 1993, were netted over water-filled roadside ditches in secondary forest.

Diagnosis.—*Lasiurus atratus* is characterized by red dorsal coloration, black face, contrasting black and white chest, long black wings, medium size, small anteorbital pit, obsolete lachrymal process, slightly attenuated exoccipital process, well-developed mastoid process, small median anterior mesoterygoid process, obsolete basial pits, and relatively large molars.

Description.—A medium-sized *Lasiurus* (greatest length of skull 12.9–13.2) with long wings (forearm 45.3–46.9); dorsal coloration bright rufous red, without white or black hair tips; median buffy band of hairs much wider than black basal and red distal bands; face black; chin reddish; throat, chest, and belly contrasting black and white or brown and white (hairs white tipped, with successive black, pale or dark brown, and black bands); prominent white humeral spot; flanks buffy; wings black or blackish, lacking ornamental outlines around fingers and forearm; ears tan; interfemoral membrane furred to or near distal edge.

Skull (Fig. 2) with conventional shape of red bat group; rostrum broad (max. br. 6.1–6.8), but very short (max. toothrow l. 4.4–5.0) and shallow, sloping sharply downward anteriorly; facial profile straight; braincase large and globose, tilted up from palatal plane; sagittal crest low; lambdoidal crest weak and incomplete; mastoid process well-developed; exoccipital process triangular, with a somewhat attenuated tip; zygoma weak, straight on dorsal edge; anteorbital pit small; lachrymal process and supraorbital ridge obsolete; palate short (max. toothrow l. 4.4–5.0) and wide (max. br. 6.1–6.8); anterior median process of mesopterygoid fossa short and wide; basial pits poorly developed.

Dental formula 1/3-1/1-2/2-3/3 × 2 = 32; anterior upper premolar tiny, wedged between lingual borders of canine and P4; molars moderately large; M3 with fully developed second commissure.

Comparisons.—Three species of red bats occur in the Guayana Region. They are graded in size. *Lasiurus egregius* Peters is large (fa. 50.0, gr. l. 15.7), *L. atratus* is medium (fa. 45.3–46.9, gr. l. 12.9–13.2), and *L. blossevillii* Lesson & Gernot is small (fa. 36–41, gr. l. 11.5–11.9). In the red phase (the only phase known in *L. egregius* and *L. atratus*) dorsal coloration is similar in all three—bright rufous red, with a wide buffy median band on hairs. The face is black in *L. atratus*; reddish or dusky in the other species. Coloration of the underparts varies widely in the three species—all red like the dorsum in *L. egregius*; speckled brown or gray and buff, moderately differentiated from the dorsum in *L. blossevillii*; sharply differentiated black and white in *L. atratus.* Wings are ornate, with fingers and forearm outlined with reddish in *L. blossevillii*; plain black in *L. atratus* and *L. egregius.* With respect to cranial features, *L. atratus* shares characters with *L. egregius* and *L. blossevillii.* but it differs from both of these species in having the anteorbital pit small, the lachrymal process obsolete, and the supraorbital process poorly developed.

Like *Lasiurus atratus,* its geographically remote relatives, *L. castaneus* of Central America and *L. varius* of Chile, have black unornamented wings, but otherwise they are quite different from it. Both have shorter wings and strongly developed lachrymal and supraorbital processes and anteorbital pit. *L. castaneus* has totally different coloration—blackish underparts, dark dorsum, and narrow median band on dorsal hairs, as well as more elevated braincase, well-developed basial pits, and much reduced M3. Underparts of *L. varius* are uniform orange-buff, and it has much more robust molars; cranial characters relate it more closely to *L. blossevillii.*

Specimens examined.—Suriname: Nickarie: Kaiserberg Airstrip, Zuid River. [ca. 278 m], 1 skin and skull (FMNH). Venezuela: Bolívar: Km 55 on highway south of El Dorado, 100 m, 2 skins & skulls (UCV); Reserva Forestal Imataca (Unit 5), ca. 28 km E Tumeremo, 140–180 m, 1 skin & skull, 1 skin, skull & skeleton, 2 alcoholics with skulls, 7 alcoholics (collection of J. Ochoa), 2 alcoholics with skulls (USNM). Total 16.

References to other specimens.—French Guiana: 4 km N Saül, 03°40′N, 53°13′W (Masson & Cosson 1992). As described and measured by Masson and Cosson (1992), this specimen can be only *Lasiurus atratus* (see Table 2).

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Identity and taxonomic status of the Mexican garter snake *Thamnophis vicinus* Smith, 1942 (Reptilia: Serpentes: Natricidae)

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Abstract.—The nominal garter snake species *Thamnophis vicinus* is shown to be a localized color pattern morph of the wide-ranging *T. cyrtopsis collaris*; this morph is known to occur only in three populations in the Mexican state of Michoacán.

Thamnophis vicinus was originally described (Smith 1942) from the vicinity of Morelia, Michoacán, on the basis of ten specimens differing from *T. cyrtopsis* only in lacking a vertebral stripe and in having large dorsal spots arranged in three rows rather than four. Bogert & Oliver (1945), Milstead (1953), Duellman (1961), and Webb (1966) concluded that *T. vicinus* is merely a color pattern morph of *T. cyrtopsis* (specifically of *T. cyrtopsis collaris* in the current taxonomy) and not a distinct species. However, Webb (1978) reexamined most of the type series of *T. vicinus,* and six additional specimens from other areas in Michoacán that combined pattern features of *T. vicinus* and *T. cyrtopsis collaris.* He concluded that the taxonomic status of *T. vicinus* is uncertain; for that reason, he tentatively resurrected *T. vicinus* as a separate species.

Materials and Methods

Preserved specimens were borrowed from the: American Museum of Natural History (AMNH); California Academy of Sciences (CAS); private collection of E. A. Liner (EAL); Field Museum of Natural History (FMNH); University of Kansas Museum of Natural History (KU); Los Angeles County Museum of Natural History (LACM); Louisiana State University Museum of Natural Science (LSUMZ); Museum of Comparative Zoology, Harvard University (MCZ); Michigan State University Museum (MSU); Texas Cooperative Wildlife Collection, Texas A&M University (TCWC); Florida Museum of Natural History, University of Florida (UF); University of Illinois Museum of Natural History (UIMNH); University of Michigan Museum of Zoology (UMMZ); and Collection of Vertebrates, University of Texas at Arlington (UTA). Four standard characters (numbers of ventrals, subcaudals, and maxillary teeth; relative tail length) were recorded; the results are summarized in Table 1. Several aspects of color pattern also were noted and are detailed under Results and Discussion.

Specimens examined include: Colima, LSUMZ 7846; Durango, MSU 4434–36; Guanajuato, CAS 5848; Guerrero, LACM 130112; Hidalgo, MCZ 11432, UMMZ 99085; Jalisco, MSU 9801, 9803 (2 spec.); Michoacán, FMNH 37116–22, 39058–61, 100098 (holotype of *T. vicinus*), 126499–504, LACM 65252, MCZ 56019, 131014, UIMNH 23414, 23435, UMMZ 102510, 104699, 112537, 112541, 119409–12, 121546, UTA R-6050–52; Oaxaca, AMNH 97889, 103091, 103100, 107001, EAL 1797, LACM 130111–12, LSUMZ 7560, UF 11326–27; Querétaro, TCWC 53068; Sinaloa, CAS 24077, 24082, KU 40349, 78923, 83413, LACM 130113, MSU 567; Zacatecas, UMMZ 118433.

Table 1.—Variation in four meristic or mensural characters in *Thamophis cyrtopsis collaris* from Mexico. The Northern Sample includes specimens from northwestern Michoacán and from populations north of Michoacán; the "*vicinus*" Morph Sample includes specimens from populations in which any individuals exhibit a *T. vicinus* color pattern; and the Southern Sample includes specimens from Guerrero and Oaxaca. Ventral and subcaudal data are from Webb (pers. comm.) as well as specimens examined by the author. Values are given as mean ± standard deviation (range of variation) and sample size.

Character		Northern sample	"*vicinus*" morph sample	Southern sample
Ventrals	♂♂	158.1 ± 3.65 (152–166) 34	159.9 ± 2.95 (155–165) 11	152.8 ± 4.50 (149–158) 4
	♀♀	153.8 ± 3.59 (146–162) 50	153.1 ± 3.94 (147–159) 16	150.2 ± 3.17 (144–155) 19
Subcaudals	♂♂	97.8 ± 6.50 (86–109) 27	87.7 ± 2.06 (84–90) 7	89.7 ± 5.03 (85–95) 3
	♀♀	91.9 ± 5.93 (80–103) 28	79.9 ± 3.73 (74–88) 10	81.4 ± 2.56 (77–85) 14
Tail/Total Length (%)	♂♂	28.3 ± 1.12 (26.4–29.6) 8	25.5 ± 0.68 (24.7–26.7) 8	28.7 (28.7) 1
	♀♀	27.7 ± 1.60 (25.1–30.4) 7	24.7 ± 1.15 (22.7–27.0) 10	25.8 ± 0.83 (23.9–26.6) 9
Maxillary Teeth	♂♂	26.7 ± 0.76 (26–28) 7	27.5 ± 1.73 (25–29) 4	—
	♀♀	25.7 ± 0.82 (25–27) 10	26.5 ± 1.29 (25–28) 4	26.7 ± 0.76 (26–28) 7

Results and Discussion

I examined 30 specimens from throughout Michoacán that could be identified as either *T. vicinus* or *T. cyrtopsis collaris.* Partial or complete supression of the vertebral light stripe, accompanied by enlargement and frequent fusion of two or more sets of dark dorsal spots or blotches on at least the anterior portion of the body, occurs in specimens from three separate areas in Michoacán: near Morelia, in the northeast; at Tancítaro, in the west-central region; and in the Sierra de Coalcomán, in the southwest (Fig. 1). The *T. vicinus* dorsal pattern is by no means uniform in these areas. Most specimens from the vicinity of Morelia are preservative-darkened, hence details of pattern are sometimes difficult to discern. No indication of a vertebral stripe is evident on six specimens (FMNH 126499–500, 126504; MCZ 56019; UIMNH 23435; UMMZ 102510), but there appears to be one present on UIMNH 23414, as well as traces of a fragmented, indistinct one on FMNH 100098 (which, ironically, is the holotype of *T. vicinus*). In all examples, the anteriormost postnuchal spots are enlarged and fused to form transverse blotches that extend from the venter to the vertebral row and interrupt the lateral stripes. For a varying distance thereafter, the lateral blotches alternate with the dorsolateral spots, the latter being fused transversely across the back to form a single, vertebral row of blotches. This pattern (Fig. 2) contrasts with that usually attributed to *T. cyrtopsis collaris,* in which the vertebral light stripe is distinct, both it and the lateral stripes are uninterrupted, there are no transverse bands on the neck, and the dorsolateral spots are not fused across the back (Fig. 2).

The vertebral stripe is present on all eight specimens from the Sierra de Coalcomán, although it is relatively faint in all but one (UMMZ 104699). Six specimens from the vicinity of Dos Aguas (UMMZ 119411–12, 121546; UTA R-6050–52) have the characteristic *T. vicinus* blotch pattern anteriorly

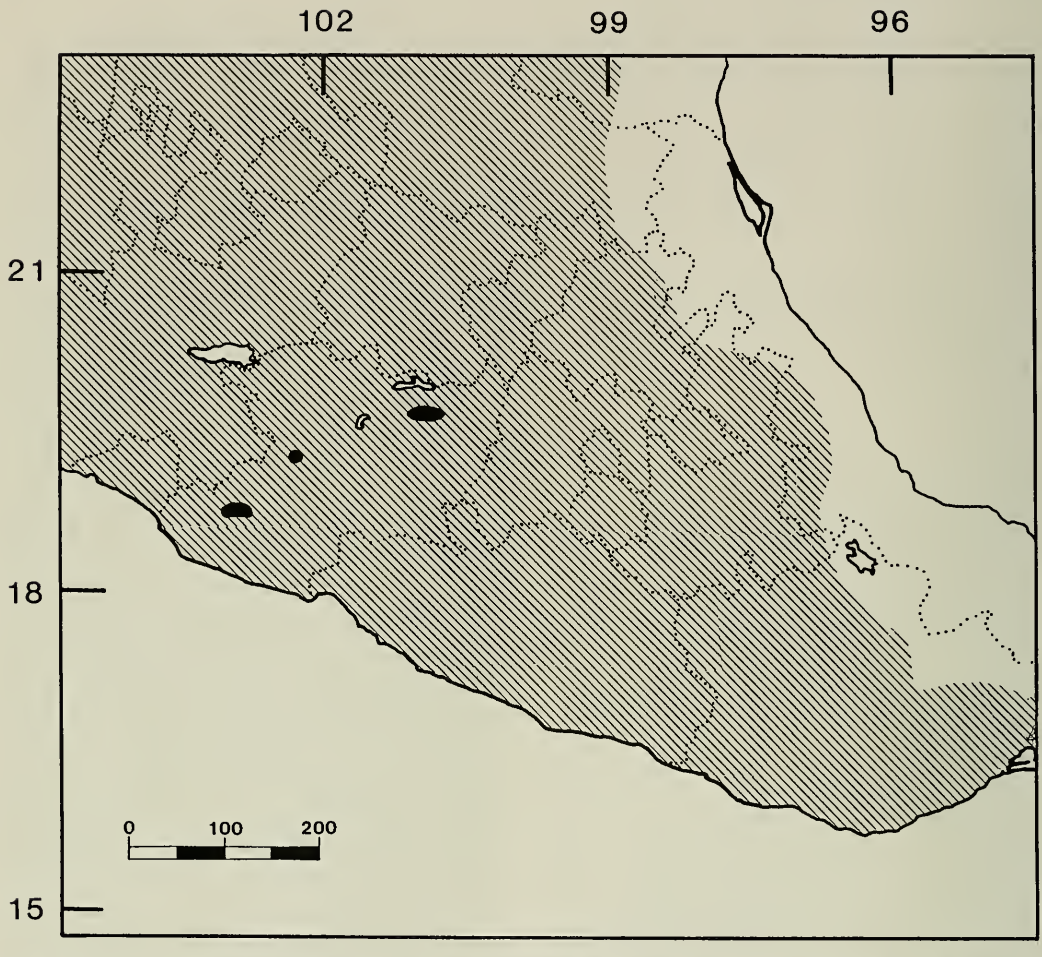

Fig. 1. Map of southwestern Mexico showing the range of *Thamnophis cyrtopsis* (diagonal lines) and the areas where animals having a dorsal pattern characteristic of the "*vicinus*" morph have been collected (black blotches).

(Fig. 3), whereas the two specimens (UMMZ 104699, 112537) from farther west (toward Coalcomán) have a *T. cyrtopsis collaris* blotch pattern on the neck (Fig. 3).

Finally, a series of 11 specimens (FMNH 37116–22, 39058–61) from Tancítaro, which lies about halfway between Morelia and the Sierra de Coalcomán, exhibit an array of dorsal patterns. All but one of the series (FMNH 37117) have a vertebral stripe, but it is faint in six of the specimens. In terms of the dorsal blotching, four specimens have a pattern more-or-less typical of *T. vicinus,* four are more characteristic of *T. cyrtopsis collaris,* and three appear to be intermediate (Fig. 4).

None of the authors who have discussed *T. vicinus* has suggested that it differs from *T. cyrtopsis collaris* in any respect other than color pattern, although Webb (1978, Table 1) showed that specimens referred to the former have a lower mean number of subcaudals than the latter. The specimens I examined from within the "range" of *T. vicinus* do, indeed, have fewer subcaudals (and a proportionally shorter tail) than specimens of *T. cyrtopsis collaris* from northwestern Michoacán (LACM 65252; MCZ 131014; UMMZ 119409–10) and farther

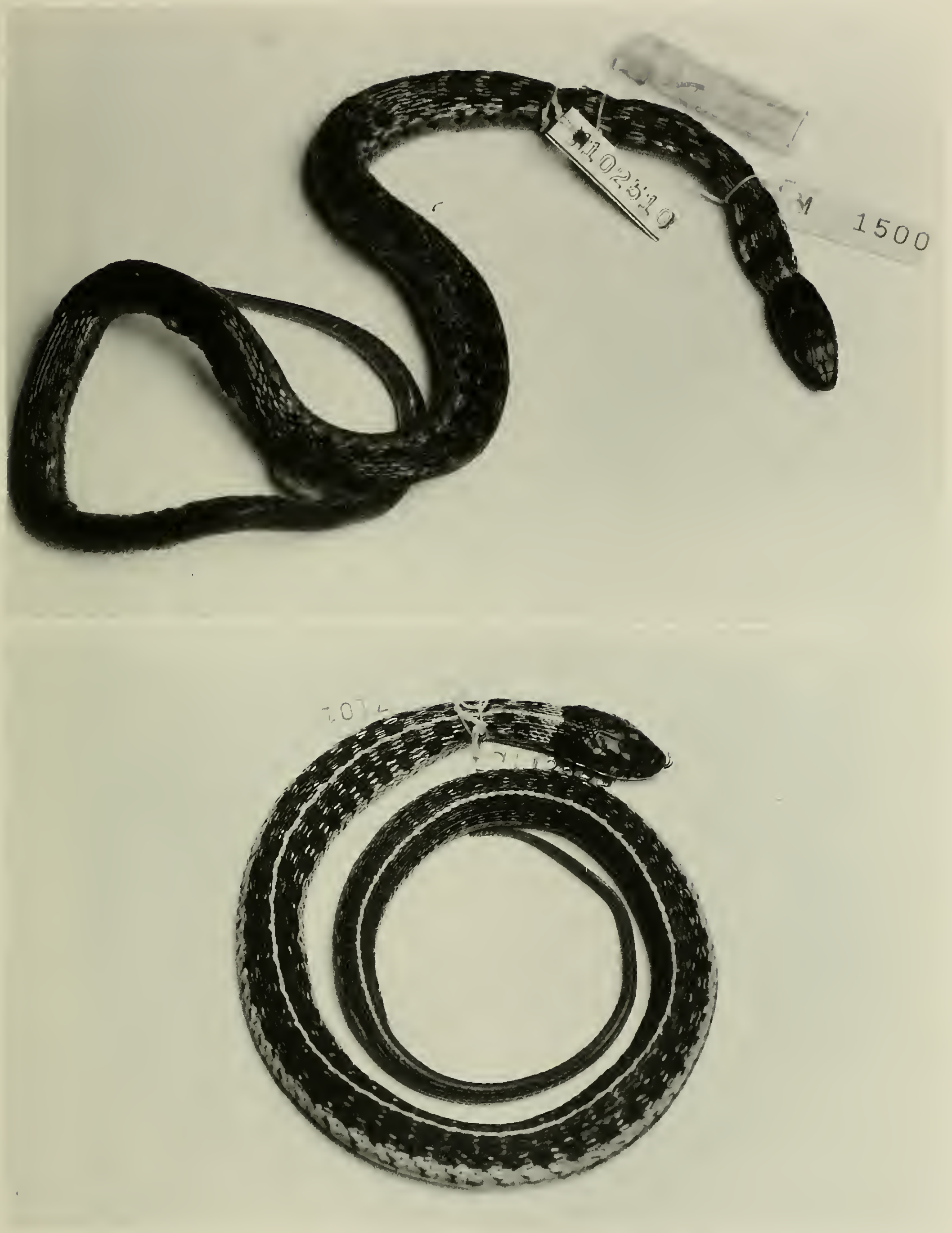

Fig. 2. Upper: Adult male *Thamnophis cyrtopsis collaris* (UMMZ 102510) from Pino Gordo (= 37 km by road W Ciudad Hidalgo), Michoacán, Mexico, showing a dorsal pattern characteristic of the "*vicinus*" morph. Lower: Subadult female *Thamnophis cyrtopsis collaris* (UMMZ 112541) from Uruapan Parque Nacional, Michoacán, Mexico, showing a dorsal pattern characteristic of the subspecies.

Fig. 3. Upper: Adult female *Thamnophis cyrtopsis collaris* (UMMZ 121546) from Dos Aguas, Michoacán, Mexico, showing a dorsal blotch pattern characteristic of the "*vicinus*" morph. Lower: Subadult male *Thamnophis cyrtopsis collaris* (UMMZ 104699) from the Cerro de los Havillos, near Coalcomán, Michoacán, Mexico, showing a dorsal pattern characteristic of the subspecies.

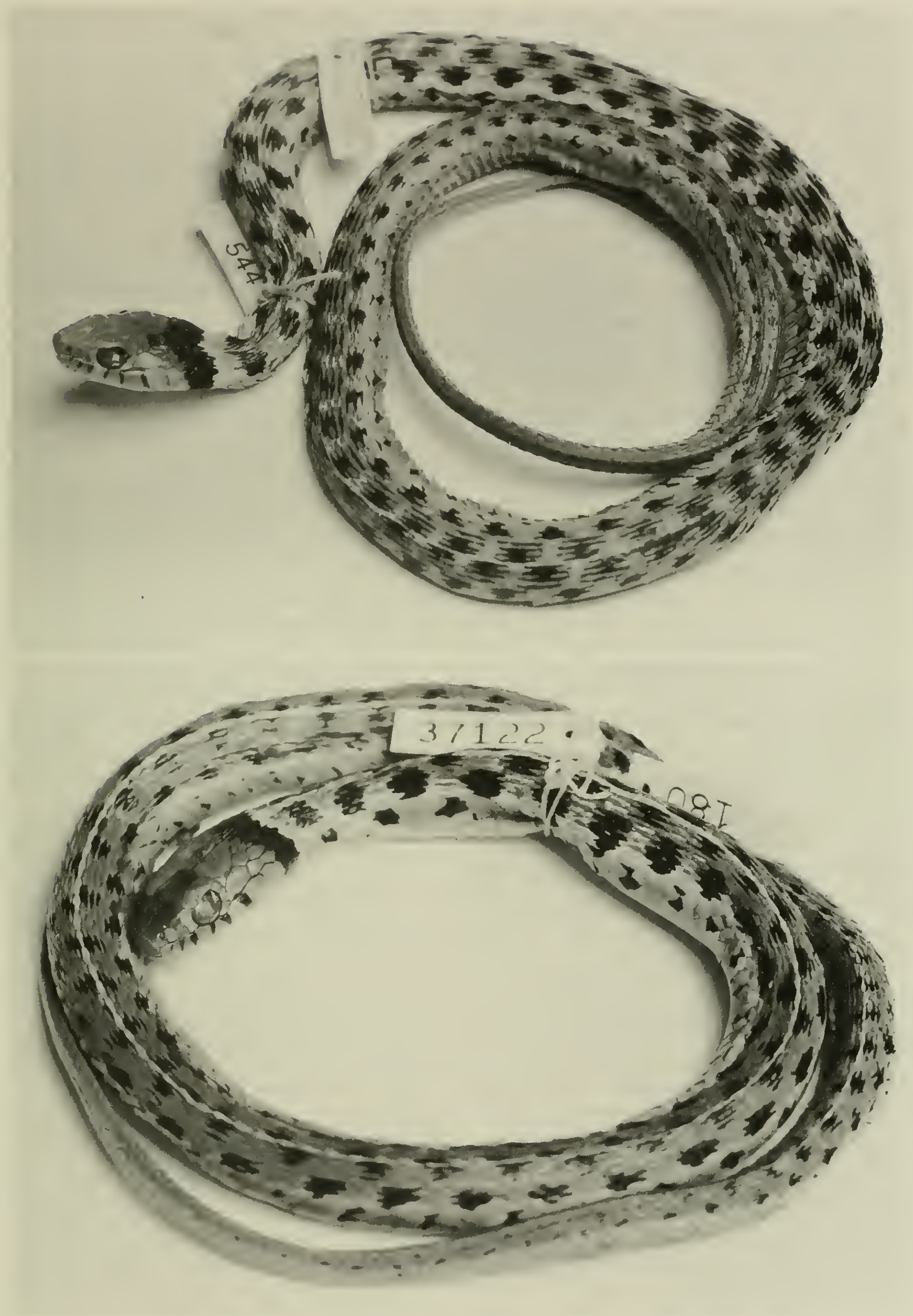

Fig. 4. Upper: Adult female *Thamnophis cyrtopsis collaris* (FMNH 39059) from Tancítaro, Michoacán, Mexico, showing a dorsal blotch pattern characteristic of the "*vicinus*" morph. Lower: Adult female *Thamnophis cyrtopsis collaris* (FMNH 37122) from Tancítaro, Michoacán, Mexico, showing a dorsal pattern characteristic of the subspecies.

north in the range of that subspecies, but the mean number of subcaudals is not significantly less than that of *T. cyrtopsis collaris* from Guerrero and Oaxaca to the south (Table 1). Interestingly, still farther south—in Chiapas and Guatemala—*T. cyrtopsis collaris* has subcaudal counts that approach those of the population north of Michoacán (Webb 1982).

Because *T. vicinus* does not differ mensurally or meristically from both geographically adjacent populations of *T. cyrtopsis collaris,* and differs only inconsistently in a few aspects of color pattern, it is apparent that *T. vicinus* represents nothing more than a variant pattern morph—and a junior synonym—of *T. cyrtopsis collaris.* Analogous situations are not uncommon in other species of *Thamnophis* (see Rossman et al. 1996).

Acknowledgments

I thank the curatorial staffs at the institutions mentioned under Materials and Methods for the loan of specimens in their care. I also am grateful to R. G. Webb for providing a set of his raw data on *T. cyrtopsis collaris,* M. Kleiner for photographic assistance, J. Boundy for making the map, and D. A. Good for constructive criticism of the manuscript.

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Review of the genus *Cociella* Whitley (Teleostei: Platycephalidae) with the description of three new species

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Abstract.—The genus *Cociella* Whitley is diagnosed as having vomerine teeth in two discrete patches, teeth in jaws not depressible, diagonal scale rows slanting downward above lateral line more numerous than lateral-line scales, lateral-line scale pores with a single canal opening to the exterior, iris lappet a simple lobe, side of head bicarinate, suborbital ridge bearing one spine under middle eye and one spine under rear margin of eye (additional spines may or may not be present posterior to eye), and upper preopercular spine distinctly longer than lower spines, bearing a small accessory spine on base. *Cociella punctata* (Cuvier) is removed from the synonymy *C. crocodilus* (Tilesius) and the occurence of possible intergrades between *C. punctata* and *C. crocodilus* is discussed. Young *C. punctata* appear to utilize the mangroves as nursury grounds. Three new species tentatively assigned to *Cociella* are described, *C. heemstrai* from off the west coast of southern Africa, *C. somaliensis* from off Oman and Somalia and *C. hutchinsi* from the Arafura Sea. A key to the species of *Cociella* is provided that primarily uses differences in arrangement of spines on the suborbital ridge, fin ray counts, number of gill rakers, and scale counts to separate the species.

The status of many nominal genera of the Platycephalidae remains unclear. Relatively little has been published in this regard since extensive revision of Japanese flatheads by Matsubara & Ochiai (1955). Matsubara & Ochai (1955) synonymized *Platycephalus punctatus* (Cuvier *in* Cuvier & Valenciennes, 1829) under *Platycephalus crocodilus* (Tilesius, 1812), restricting the genus *Cociella* to *C. crocodilus.* The genus *Cociella* is here regarded as containing *C. crocodilus, C. punctata,* and three new species described below. This paper attempts to clarify the limits *Cociella* and compares features between *Cociella* and *Ratabulus.*

The taxonomic significance of the pore morphology of the lateral-line scales in the Platycephalidae is well documented. Matsubara and Ochiai (1955) found that differences in pore structure of the scales were useful as generic characters in *Cociella, Onigocia, Platycephalus* and *Rogadius.* This was further corroborated by Hughes (1981, 1985) who, in addition to pore structure, also included other features of lateral-line scale morphology in a comprehensive study of the flatheads that utilized scanning electron microscopy. The configuration of lateral-line scale pores is also considered important here. For example, the scale pores of *Thysanophrys* have two canals to the exterior and are Y-shaped; those of *Onigocia* also have two canals to the exterior and resemble short, stubby Ts. Other flathead nominal genera with two canals include *Inegocia, Papillolabium, Rogadius, Sorsogona* and *Suggrundus.* On the basis of having two pore canals, and with the diagonal scale rows above the lateral line being equal or nearly so to the number of lateral-line scales, these genera are removed from consideration here.

A second group of genera has lateral line scale pores with one canal to the exterior: *Cociella; Elates; Grammoplites; Kumococius; Leviprora; Platycephalus;* and *Ratabulus.* To separate these from *Cociella,* it is necessary to use additional characters. The condition found in *Cociella* is given in parentheses. Vomerine teeth in a single patch is diagnostic for *Platycephalus* (two patches). A single elongate preopercular spine and six dorsal spines is unique to *Elates* (2–3 preopercular spines, 9 dorsal spines). Scale rows slanting downward above the lateral line closely approximate the number of lateral line scales in *Kumococius* and *Grammoplites* (scale rows are more numerous than lateral line scales). In *Leviprora,* the type of iris lappet (or umbraculum) on the upper surface of the eye is finger-like or cirrose (Matsubara & Ochiai 1955:5, Fig. 2F) and the two upper preopercular spines are subequal (iris lappet a simple lobe, upper propercular spine distinctly longest). *Ratabulus* shares many of the diagnostic features given here for *Cociella* but differs in having depressible teeth in the jaws, a greater number of spines on the suborbital ridge beneath the eye, more elongate lateral-line scales (Fig. 1A) and a smaller and more pointed iris lappet. Although there is some justification for placing *Cociella* in the synonymy of *Ratabulus,* such action would require additional evidence that is not available here.

Drawings of lateral line scales from the species of *Cociella, Ratabulus megacephalus* and *Kumococius rodericiensis* appear in Fig. 1A–G. These ctenoid scales are small, rather uniformly rectangular, have well-developed radii, and pores that open to the exterior through a single slender canal. The canal of *C. heemstrai* is somewhat shorter than the canals in other species of *Cociella.* In Fig. 1A, *Ratabulus megacephalus,* the pore and canal is quite similar to those of the other species shown but the scale is more slender and elongate. The scale from *Kumococius rodericiensis* (Fig. 1G) appears quite similar to those found in *Cociella* but the spine at the anterior margin of the pore is much more robust.

Methods.–Counts follow procedures described by Hubbs & Lagler (1958:19–24) with the following exceptions: number of diagonal scale rows slanting downward (and backward) starting with the row nearest the anteriormost lateral line scale and ending with row nearest the posterior lateral line scale; number of interpelvic scales are counted in a straight line between the pelvic bases. Measurements (in mm) were taken as follows: interorbital width is the least bony width between the eyes; orbit diameter is taken from the lower rear margin of the orbit to the base of the preocular spine; snout length is the distance from the tip of snout to rear base of the preocular spine; head length is taken from the tip of the snout to the rear margin of the head; and standard length is the stright line distance from the tip of snout to the rear margin of the hypural plate. Counts and measurements were routinely taken from the left side (unless damaged) while gill rakers were counted on the right side. The material examined was from the following institutions (abbreviations in parentheses): Academy of Natural Sciences of Philadelphia (ANSP); American Museum of Natural History, New York (AMNH); Australian Museum, Sydney (AMS); Bernice P. Bishop Museum, Honolulu (BPBM); California Academy of Sciences, San Francisco (CAS, SU); Commonwealth Science and Industrial Research Organization, Hobart (CSIRO); Field Museum of Natural History, Chicago (FMNH); Hebrew University, Jerusalem (HUJ); Hokkaido University, Hakodate (HUMZ); J. L. B. Smith Institute of Ichthyology, Grahamstown (RUSI); Kanudi Fisheries Research Station, Konedobu, Papua New Guinea (KFRS); Museum of Comparative Zoology, Harvard University (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); Museum für Naturkunde der Universitat-Humboldt, Berlin (ZMB); Museum of Zoology, University of Michigan, Ann Arbor (UMMZ); National Museum of

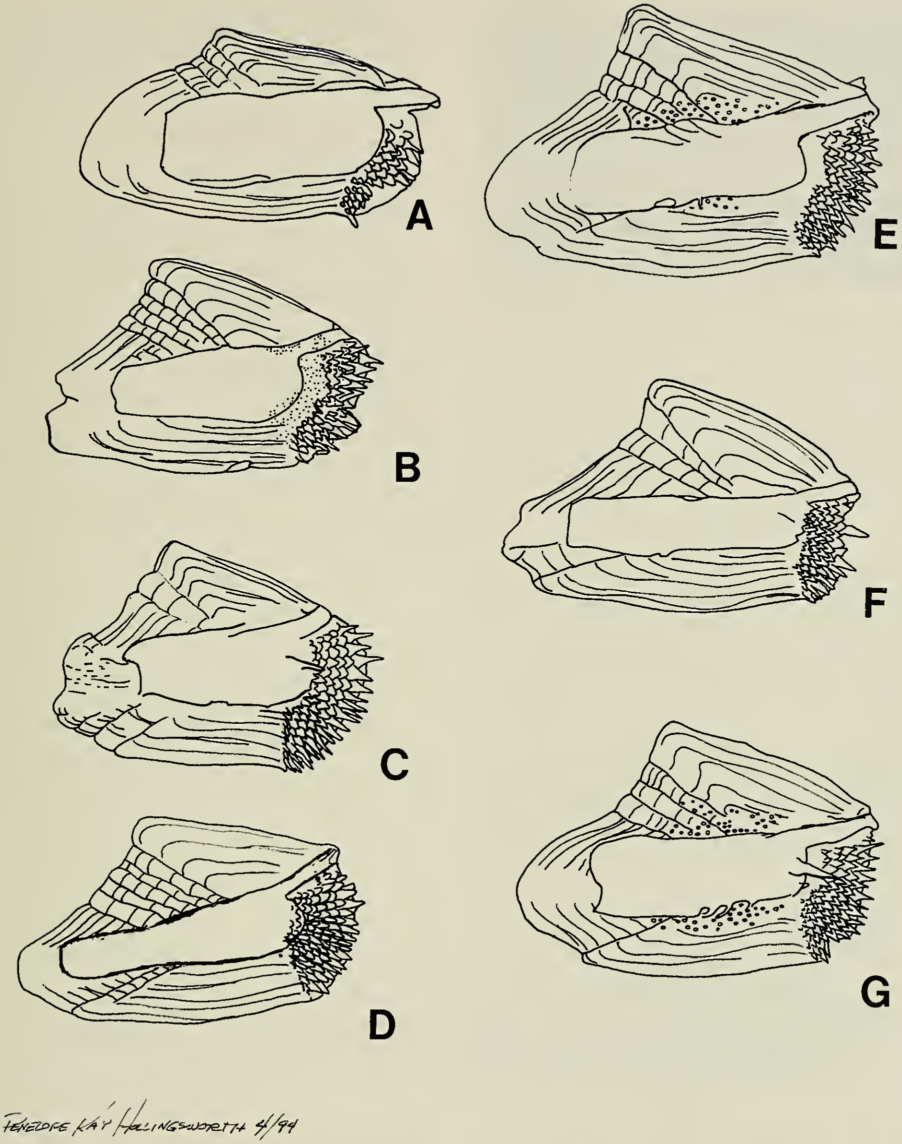

Fig. 1. Drawings of pored lateral line scales taken from right side (12th scale from front, scale length in parentheses) of species of *Cociella* and related flatheads: A, *Ratabulus megacephalus,* USNM 329510, 236 mm SL, (3 mm); B, *Cociella somaliensis,* USNM 326300, 216 mm SL, (3 mm); C, *Cociella heemstrai,* USNM 326629, 178 mm SL, (2.9 mm); D, *Cociella crocodilus,* USNM 329509, 261 mm SL, (3.6 mm); E, *Cociella hutchinsi,* USNM 327279, 240 mm SL, (4.3 mm); F, *Cociella punctata,* USNM 327189, 216 mm SL, (4.0 mm); G, *Kumococius rodericiensis,* WAM P26206, 180 mm SL, (4.0 mm).

Natural History, Washington D.C. (USNM); National Natuurhistorische Museum, Leiden (RMNH); Natural History Museum, London (BMNH); Natural History Museum, Los Angeles County (LACM); Naturhistorisches Museum, Vienna (NMW); Northern Territory Museum of Arts & Sciences, Darwin (NTM); Royal Ontario Museum, Toronto (ROM); South African Museum, Cape Town (SAM); Western Australian Museum, Perth (WAM); Zoölogische Museum, Universtiteit van Amsterdam

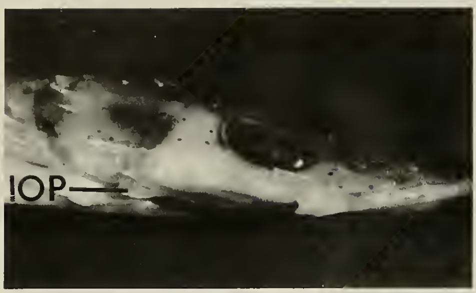

Fig. 2. Interopercular flap (IOP), right side of *Cociella punctata,* USNM 329292, 111 mm SL.

(ZMA); and Zoologisk Museum, Kobenhavns Universitet, Copenhagen (ZMUC).

Cociella Whitley, 1940

Cocius Jordan & Hubbs, 1925:286 (type species *Platycephalus crocodilus* Tilesius, 1812, by original designation).

Cociella Whitley, 1940:243 (substitute for *Cocius* Jordan & Hubbs, preoccupied).

Diagnosis.—A genus of platycephalid fishes characterized by the following: ocular papillae absent; iris lappet a simple lobe (Figs. 3, 7) or slightly bilobed (latter may be an artifact of preservation); anterior nostril with an elongate dermal flap posteriorly; interopercular flap present or absent; pelvic-fin rays I, 4+1; anteriormost 1 to 19 lateral-line scales bearing small spines; scale rows slanting downward above lateral line more numerous than lateral-line scales; lateral-line scale pores with a single opening to the exterior; suborbital ridge bearing one spine under middle of eye and one spine under rear margin of eye, additional spines may or may not be present posterior to the eye; a single preocular spine; preopercular spines 2 or 3, uppermost bearing a small accessory spine on base; side of head bicarinate; teeth villiform, caniniform or granular, in broad bands on tooth-bearing bones; and vomerine teeth in 2 discrete patches.

Key to the species of *Cociella*

1A. Dorsal-fin rays and anal-fin rays usually 11; total number of gill rakers on first arch 5–8 2

1B. Dorsal-fin rays and anal-fin rays usually 12; total number of gill rakers on first arch 9–18 4

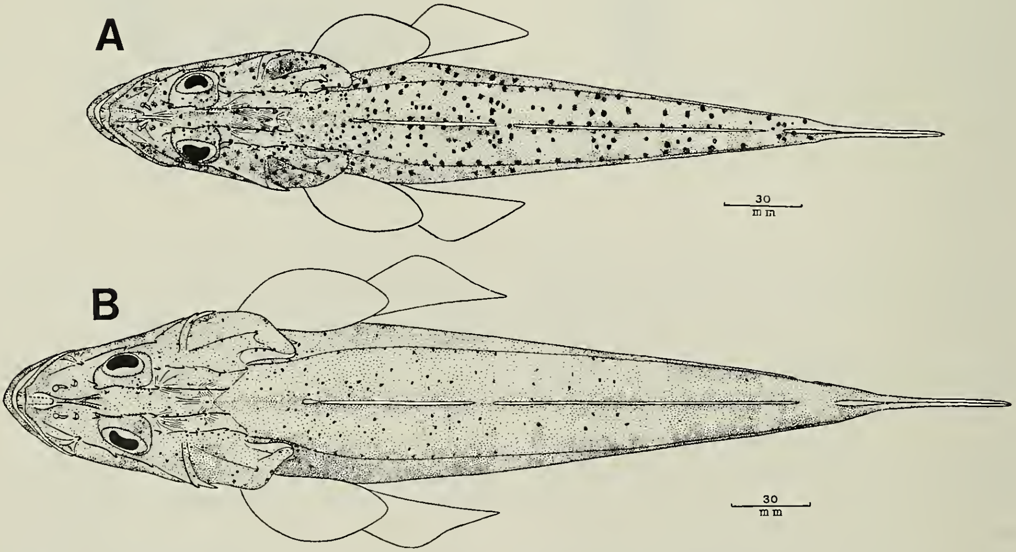

Fig. 3. Color pattern variation in *Cociella crocodilus* (After Matsubara & Ochiai, 1955): A, Pattern typical of *C. crocodilus.* Specimen from Kanaiwa, Japan, 285 mm SL; B, Pattern usually found in *C. punctata.* Specimen from the East China Sea, 340 mm SL.

2A. Suborbital ridge with 2 spines below eye, several spines behind eye; upper preopercular spine long, nearly reaching to opercular margin; preorbital spine slight or lacking .... *C. hutchinsi*, new species

2B. Suborbital ridge with 2 spines below eye, no spines behind eye; upper preopercular spine shorter, reaching about half-way to opercular margin; preorbital spine usually well developed ... 3

3A. Diagonal scale rows slanting downward above lateral line 74–91 ($\bar{X}$ = 80.6); total gill rakers usually 7 (6–8); interopercular flap absent .. *C. crocodilus.*

3B. Diagonal scale rows slanting downward above lateral line 60–76 ($\bar{X}$ = 67.1); total gill rakers 5–6, usually 6; interopercular flap present ... *C. punctata*

4A. Total gill rakers 9–11 ($\bar{X}$ = 10.0); interpelvic scale count 16–24 ($\bar{X}$ = 20.6); caudal fin dusky, with small dark spots on upper half ..*C. heemstrai*, new species

4B. Total gill rakers 12–18 ($\bar{X}$ = 15.1); interpelvic scale count 25–35 ($\bar{X}$ = 29.9); caudal fin light, with large dark spots and horizontal streaks throughout .. .. *C. somaliensis*, new species

Cociella crocodilus
(Tilesius, 1812)
Fig. 3A

Platycephalus crocodilus Tilesius, 1812, pl. 59, fig. 2 (original description, type locality, Nagasaki).—Cuvier *in* Cuv. & Val., 1829:256 (description taken from Tilesius).—Beaufort & Briggs, 1962: 159–161.—Burgess & Axelrod, 1971: 541, fig. 510.—Burgess & Axelrod, 1974:1006, fig. 302.

Platycephalus punctatus.—Günther, 1880: 66.

Platycephalus inermis (not *Silurus inermis* Houttuyn, 1878) Jordan & Evermann, 1903:361.

Thysanophrys crocodilus.—Jordan & Richardson, 1908:638–640, fig. 4.—Jordan & Metz, 1913:54, fig. 49.—Jordan et al., 1913:286, fig. 235.

Inegocia crocodilus.—Jordan & Thompson, 1914:279.

Cocius crocodilus.—Jordan & Hubbs, 1925:287.

Cociella crocodila.—Matsubara & Ochiai, 1955:87–89, figs. 32, 33 (in part).—Anonymous, 1975:214, pl. 208.—Masuda et al., 1975:342, pl. 146, figs. F, G.—Kyushin et al. (eds.), 1982:276, fig. 255.—Masuda et al. (eds.), 1984:322, pl. 289, figs. C, D.

Inegocia crocodila.—Tomiyama & Abe, 1963:69, fig. 201.

Material examined (63 specimens).—Japan: UMMZ 183219 (5, 140–174) Niigita. UMMZ 183220 (1, 181) Niigita. SU 23650 (1, 285) Naoetsu. UMMZ 183218 (2, 240–256) Namerikawa. UMMZ 183222 (1, 250) Namerikawa. FMNH 104717 (3, 142–204) Tokyo. FMNH 71864 (1, 193) Yokohama. MCZ 48821 (1, 140) Yenosima. MCZ 31160 (1, 126) Yenosima. UMMZ 198916 (1, 178) Toba. FMNH 58790 (1, 142) Toba. FMNH 57413 (5, 230–293) Osaka. USNM 151815 (1, 239) Kobe. NMW 11179 (2, 332–403) Kobe. ZMB 18778 (2, 251–258) Kobe. USNM 10734 (4, 192–216) Wakanoura. USNM 62317–18 (2, 112–175) Hiroshima & Onomichi. UMMZ 183215 (1, 218) northern Kyushu. CAS 120708 (2, 241) Nagasaki. SU 13362 (1, 350) Nagasaki. ZMUC P80233 (1, 146) Nagasaki. Korea, Pusan: UMMZ 183216 (5, 133–206). UMMZ 198900 (2, 159–172). USNM 143416 (2, 126–174). FMNH 55763 (1, 251). China: SU 31261 (1, 242). ZMA 112.715 (1, 339) near Chin-huang-tao. MCZ 13789 (1, 253) Shanghai. SU 32766 (1, 218) Ting-hai. USNM 130414 (1, 227) Ningpo. USNM 327194 (1, 245) northern East China Sea. HUMZ 108647 (1, 308) East China Sea. USNM 329509 (1, 261) Dongxiang. UMMZ 198909 (1, 88) Fukien. Taiwan: CAS 30012 (1, 231) Formosa Strait. CAS 15234 (1, 218) Formosa Strait. CAS 107973 (1, 171) Chilung. Hong Kong: ZMUC P80193-194 (2, 80–85).

Possible intergrades, C. crocodilus × C. punctata (5 specimens).—MNHN 05–222 (1, 170) Bay d'Along, Gulf of Tonkin. SU

Table 1.—Number of diagonal scale rows slanting downward above lateral line in the species of *Cociella.*

	53–55	56–58	59–61	62–64	65–67	68–70	71–73	74–76	77–79	80–82	83–85	86–88	89–91	*n*	$\bar{X}$
C. crocodilus								7	18	17	9	5	5	61	81.0
C. heemstrai	1	16	24	14	6	1								62	60.7
C. hutchinsi			6	14	5	1								26	62.9
C. punctata		2	1	16	29	34	23	6						111	67.9
C. somaliensis	2	12	11	7	2									34	59.9

14151 (1, 337) S.W. Kwangtung. HUMZ 109566 (1, 269) South China Sea, off Sarawak, Borneo. USNM 32924 (1, 394), Penghu Is., Taiwan. FMNH 47490 (1, 54) Singapore.

Description.—(Mean values appear in parentheses). Dorsal-fin rays I, VIII, 10–11 (10.9), usually 11; anal-fin rays 10–12 (11.0), usually 11; pectoral-fin rays 19–22 (20.3); pored lateral line scales 51–60 (54.3), the anteriormost 1–19 (8.2) scales bearing weak spines; number of diagonal scale rows above lateral line slanting downward 74–91 (81.0); diagonal scale count 14–20 (16.7); interpelvic scales 28–46 (34.4); total gill rakers on first arch 6–8 (7.1) and branched caudal rays 10–12 (11.3). Least interorbital width going into greatest diameter of orbit 2.3–4.3 (2.9). Nape, opercle and cheek behind eye covered with ctenoid scales; top of head and cheek below eye mostly naked, with a few embedded scales. Preorbital spine present; a pair of small nasal spines. Preopercular spines often two, sometimes three; uppermost longest, reaching about half-way to opercular margin. Infraorbital ridge usually smooth over anterior ¼ of eye, bearing 5–8 small spines posteriorly; suborbital ridge with one spine below middle of eye, a second spine below rear margin of eye, no spines behind eye. Lateral-line scale shown in Fig. 1D. Interopercular flap absent.

Color in alcohol.—Five or six dark bands usually crossing back. Dark spots on dorsum numerous anteriorly (on head, including upper surface of eye and on anterior trunk reaching below lateral line), more scattered and primarily above lateral line on posterior body. Spinous dorsal fin with broad dusky margin, clear area at base; second dorsal fin with dark spots on rays; anal-fin membranes dusky, rays pale; pectoral fin dusky below, with vertical rows of dark spots on upper half; pelvic fin dusky; caudal fin dusky, with a series of dark blotches or streaks that usually form a broad marginal band.

Remarks.—No type specimens are known for *Cociella crocodilus.* The species is based on an inconotype (Tilesius 1812: pl. 59, fig. 2) and a secondary description based on Tilesius given by Cuvier (*in* Cuvier & Valenciennes, 1829:256). A more complete description appears in Matsubara & Ochiai (1955:87–89). Several characters effectively separating *Cociella crocodilus* and *C. punctata* include differences in the number of diagonal scale rows slanting downward above the lateral line (Table 1), total numbers of gill rakers (Table 2) and presence or absence of a preopercular flap (Fig. 2). Most *C. crocodilus* have from 77 to 91 scale rows ($\bar{X}$ = 81) while most *C. punctata* have 56 to 73 scale rows ($\bar{X}$ = 67.9). Nearly all of *C. crocodilus* have 7 or 8 gill rakers ($\bar{X}$ = 7.1) while most *C. punctata* have 6 gill rakers or less ($\bar{X}$ = 6.0). The flap is absent in *C. crocodilus* but is usually well-developed in *C. punctata* (Fig. 2). This flap may be partially developed in young specimens and may be difficult to see in larger specimens that were poorly fixed or that have been preserved for many years.

Matsubara & Ochiai (1955) illustrated variation in color pattern between a specimen taken from off Kanaiwa, Ishikawa Prefecture, Japan (Fig. 3A) and one from the East China Sea (Fig. 3B). In general, large dark spots on the dorsum are typical for *C.*

Table 2.—Total number of gill rakers on the first arch in the species of *Cociella.*

	5	6	7	8	9	10	11	12	13	14	15	16	17	18	*n*	$\bar{X}$
C. crocodilus		1	45	6											52	7.1
C. heemstrai					14	36	13								63	10.0
C. hutchinsi		15	3												18	6.2
C. punctata	1	84	5												90	6.0
C. somaliensis								1	5	5	13	11	2	2	39	15.1

crocodilus (Fig. 3A), while *C. punctata* is characterized by having smaller and less prominent dark spots (Fig. 3B).

Intergrades.—Possible intergrades between *C. crocodilus* and *C. punctata* (Table 3) include three specimens from the northern South China Sea, one from off Sarawak, Borneo and one from Singapore (Fig. 4). Interopercular flaps present in some specimens from this area appear to be less strongly developed than is typical for *C. punctata.* A zone of intergradation may extend into the East China Sea and other areas surrounding the South China Sea and it is possible that a few specimens identified by me as *C. crocodilus* or *C. punctata* are actually intergrades. This could account for some of the overlap in characters for the two species as shown in Tables 1 and 2. Additional specimens from the South China Sea are needed to clarify relationships between the two species. If integration is occurring between *C. crocodilus* and *C. punctata,* it must be very limited as both species appear to be maintaining separate character states.

Distribution.—This species is found along the coast of China, Taiwan, Korea and southern Japan (Fig. 4). Limited data indicate that it is taken by trawling at depths from 50 to 90 m and attains a maximum size of about 400 mm SL.

Cociella punctata
(Cuvier *in* Cuvier & Valenciennes, 1829)
Figs. 2, 3B

Platycephalus punctatus Cuvier *in* Cuvier & Valenciennes, 1829: 243 (original description, type locality, Ceylon, Vanikoro Is.).—Günther, 1860:180.—Sauvage, 1875:307, pl. 36, figs. 5, 5a.—Day, 1876: 277, pl. LX, fig. 3.

Platycephalus malabaricus Cuvier *in* Cuvier & Valenciennes, 1829:245 (original description, type locality, Mahé).—Günther, 1860 (in part): 181.

Platycephalus quoyi Bleeker, 1856–1857: 206 (original description, type locality, Ternate and Amboina).

Platycephalus fasciatus Günther, 1872:397 (original description, type locality, Manila Bay).

Thysanophrys quoyi.—Fowler, 1927:289.—Herre, 1953:582.

Platycephalus crocodilus.—Barnard, 1927: 933 (in part).—Smith, 1950:178 (in part).—Beaufort & Briggs, 1962:161–162 (in part).—Fourmanoir, 1957:277 (in part)—Jones & Kumaran, 1980:644, fig. 550.

Suggrundus hunti Fowler, 1937:244, figs. 249, 250 (original description, type locality, Rayong, Siam).

Grammoplites jacksoni Fowler, 1944:175, figs. 25, 26 (original description, type locality, New Hebrides).

Cocius crocodilus.—Herre, 1953:578.

Thysanophrys punctatus.—Munro, 1955: 253, fig. 736 (fig. is *C. crocodilus,* after Jordan et al., 1913).

Cociella quoyi.—Munro, 1967:528–529, fig. 993.

Cociella crocodila.—Matsubara & Ochiai, 1955:87–89, figs. 32, 33 (in part).—Gloerfelt-Tarp & Kailola, 1984:121, figs. A, B.—Dor, 1984:89–90.—Knapp, 1984: no pagination (fig. is *C. crocodilus,* after Jordan et al., 1913).—Bianchi, 1985a:30 (fig. is *C. crocodilus,* after Jordan et al.,

Table 3.—Possible intergrades between *Cociella crocodilus* and *C. punctata.*

Character	Northern South China Sea			Borneo	Singapore
	MNHN 05-222	SU 14515	USNM 329294	HUMZ 109566	FMNH 47490
Number of scale rows above lateral line	74	76	71	73	71
Total gill rakers on first arch	7	6	6	6	7 (left), 6 (right)
Development of interopercular flap	Present, both sides	Present, both sides	Absent on left, trace on right	Absent on left, trace on right	Absent
Color pattern	?	?	Like Fig. 3A	Like Fig. 3B	?

1913).—Bianchi, 1985b:28 (fig. is *C. crocodilus,* after Jordan et al., 1913).—Knapp, 1986:483, fig. 155.1.—Baranes & Golani, 1993:305, pl. 7, fig. 23.

Material examined (123 specimens).—Syntypes: MNHN 6836 (1, 187) Voyage of Perón; MNHN 6851 (1, 209) Trincomalee, Ceylon; MNHN 5852 (1, 193) Vanikoro I. Taiwan: RUSI 38443 (1, 223) Tachi. Okinawa: USNM 75448 (1, 127) Naha. Philippines: BMNH 1872.10.18.117 (1, 190) Manila. SU 39846 (1, 55) Manila. SU 9598 (1, 107) Cavite. SU 39021 (1, 122) Nasugbu. USNM 99762 (1, 210) Leyte I. SU39020 (1, 203) Iloilo. SU 27219 (1, 170) Culion. SU 27218 (1, 190) Dumaguete. SU 29758 (1, 103) Dumaguete. CAS 81318 (6, 37–124) Dumaguete. USNM 329287 (1, 45) Dumaguete. USNM 329511 (1, 42) near Dumaguete. USNM 329512 (1, 79) near Dumaguete. SU 29756 (1, 141) Jolo I. Palau Islands: CAS 81319 (1, 97) Koror I. CAS 83122 (1, 130) Koror I. CAS 83121 (1, 182) Nardueis I. USNM 329288 (1, 243) Nardueis I. CAS 81320 (1, 208) Babelthuap I. USNM 329292 (2, 102–111) Babelthuap I. South Pacific: AMS I.17482-006 (1, 78) Guadacanal I. (1, 26) New Hebrides Is. Papua New Guinea: KFRS F.5629.01 (2, 190–210) Port Moresby. CSIRO 1517 (2, 156–161) Port Moresby. Indonesia: SU 13756 (1, 330) Manokwari. USNM 327189 (3, 62–216) Semei I. USNM 327289 ((4, 70–146) Misoöl I. USNM 325917 (5, 45–99) Kepuluan Aru, Borear I. WAM 27697.001 (1, 145) Tanimbar I. BPBM 19433 (1, 100) Ambon I. RMNH 5915 (3, 128–182) Ambon & Ternate Is. ZMA 112.697 (2, 135–136) Obi Is. USNM 264806 (1, 72) Bali. USNM 264805 (1, 100) Bali. USNM 264794 (1, 194) Bali. BMNH 1984.1.1.65 (1, 270) Bali. NTM S.11127-042 (1, 116) Bali. NTM S.10733.014 (1, 195) Bali. Gulf of Thailand: CAS 81316 (1, 73) Ko Chang I. CAS 81317 (1, 227) Bangkok fish market. USNM 32928 (1, 157) Prachuap Kiri Khan. ANSP 62861 (1, 150) Siracha. ANSP 68247 (1, 75) Rayong. Singapore:

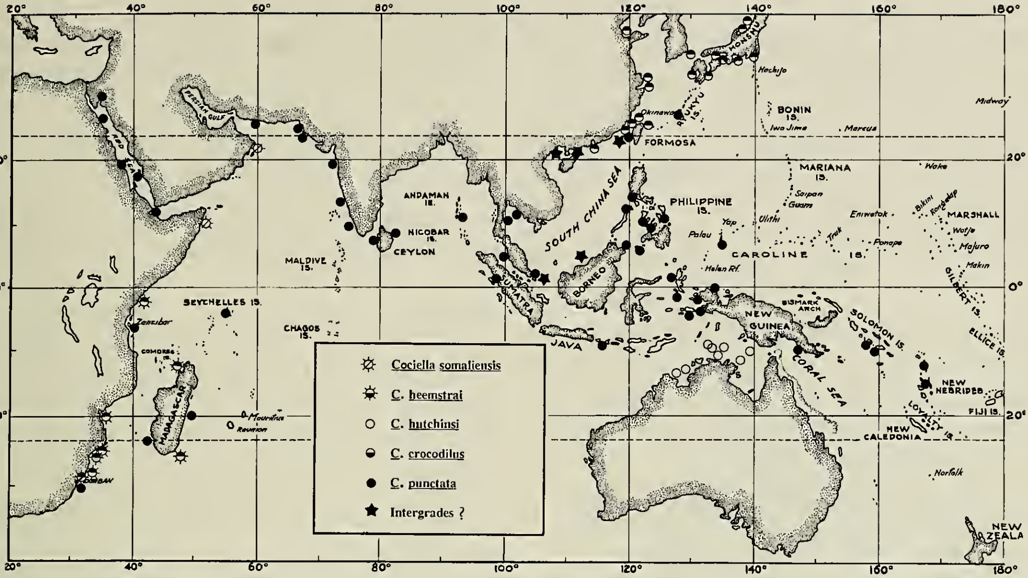

Fig. 4. Distribution of *Cociella crocodilus, C. heemstrai, C. hutchinsi, C. punctata,* and *C. somaliensis.*

SU 30809 (2, 61–76). NMW 11171 (2, 146). Malaysia: SU 27794 (1, 174) Sandakan. ZMUC P80196 (1, 210) Malacca. ZMUC P80195 (1, 109) Penang. ZMUC P80191 (2, 104–153) Penang. AMS B.5024 (1, 167) Penang. Ceylon: ROM 1878 (1, 130). USNM 327285 (1, 355) Colombo. India: SU 37202 (1, ?) Andaman Is., Port Blair. USNM 327288 (1, 227) Cochin. USNM 329285 (1, 209) Cochin. SU 41735 (2, 136–142) Calicut. AMS B.8128 (1, 205) Malabar. MCZ 4287 (1, 151) Carnara. NMW 11720 (2, 155–232) Bombay. ANSP 101419 (1, 180) Bombay. USNM 327284 (1, 288) near Bombay. Pakistan: LACM 38126 (1, 222) Karachi. USNM 327286 (1, 267) near Karachi. AMS B.8130 (1, 241) Sind. Iran: USNM 327283 (1, 358) Gulf of Oman. Western Indian Ocean: USNM 326291 (1, 200) Zanzibar. MNHN 6848 (1, 220) Mahé. AMNH 88086 (1, 170) Madagascar. USNM 327287 (1, 346) Madagascar. MNHN 1994.505 (1, 275) Madagascar. SU 31387 (3, 118–175) Durban. ANSP 55103 (2, 87–160) Durban. BMNH 1921.3.1.51 (1, 151) Durban. Gulf of Aden: Uncataloged, J. M. Rose 296-004 (1, 180) Djibouti. Red Sea: NMW 11718 (1, 170) Ghalefca. RMNH 15955 (2, 197–219) Kamaran. NMW 11719 (1, 162) Kamaran. BPBM 20382 (1, 195) Suakin. NMW 11167 (1, 164) Quseir. USNM 326280 (8, 129–185) Hurghada. HUJ 14019 (2, 303–320) Gulf of Aqaba.

Description. (Mean values appear in parentheses).—Dorsal-fin rays IX or I, VIII, 10–12 (11.0); anal-fin rays 11–12 (11.0); pectoral-fin rays 19–22 (20.6), usually 20 or 21; pored lateral line scales 50–56 (53.7) usually 53 or 54, anteriormost 1–16 (5.5) bearing small spines; number of diagonal scale rows above the lateral line slanting downward 56–76 (67.9); diagonal scale count 10–17 (13.7); interpelvic scales 21–41 (29.1); total gill rakers on first arch 5–7 (6.0); branched caudal rays 10–26 (11.3). Least interorbital width going into greatest diameter of orbit 1.8–6.0 (3.5). Nape covered with ctenoid scales; top of head, opercle and cheek bear embedded scales. Preorbital spine present; a pair of small nasal spines. Preopercular spines usually three, sometimes two; uppermost longest, reaching about half-way to opercular margin. Infraorbital ridge usually smooth over anterior ½ of eye, bearing 5–8 (small spines

Table 4.—Young stages of *Cociella punctata* associated with mangrove habitat.

Locality	SL (mm)	Depth of capture (m)	Bottom type
Thailand, CAS 81316	73	0–0.9	rocky, sand, mud
Philippines, USNM 329511	42	0–1.0	sand
Philippines, USNM 329512	79	0–0.5	sand, silt
Guadalcanal, AMS I.17482-006	78	?	?
Palau, USNM 329292	102–111	0–0.9	mud, sand, gravel, cobbles
Indonesia, USNM 329517	45–98	0–1.0	?

posteriorly); suborbital ridge with one spine below middle of eye, a second spine below rear margin of eye, no spines behind eye. Lateral-line scale shown in Fig. 1F. Interopercular flap present.

Color in alcohol.—Five or six dark bands usually crossing back. Numerous small dark spots on dorsum reaching below lateral line, more widely scattered posteriorly. Spinous dorsal fin with broad marginal dark band, clear area at base; second dorsal fin with dark spots on rays; anal fin interradial membranes dusky, rays pale; pectoral fin dusky on lower half, spotted above (fin entirely spotted in some specimens from western Indian Ocean); pelvic fin dusky; caudal fin variable (entirely dusky in a few), usually with a broad dark marginal band or series of dark spots and horizontal streaks, basal area more or less pale.

Remarks.—Young specimens of *Cociella punctata* appear to be closely associated with mangrove habitat (Table 4). The smallest typically have a broad dark saddle across the back in the area of the spinous dorsal-fin and a narrow saddle near the rear of the soft dorsal-fin (Fig. 5). In juvenile to adult *C. punctata,* five or six dark bands may cross the back (Fig. 3B) or in some, the bands may become obscure. A similar pattern is also found in juvenile to adult *C. crocodilus.*

One specimen of *C. punctata* (USNM 326291) from Zanzibar was found by East African Marine Fisheries Organization biologists in the stomach contents of a Chwaka sole (species unknown, recorded as 370 mm in total length).

Distribution.—This species is known from the Red Sea to South Africa, to Taiwan, Indonesia and to the New Hebrides (Fig. 4). As it is common off Port Moresby, Papua New Guinea, I would expect *C. punctata* to be found in northern Australian waters but, to my knowledge, none have been taken to date. Perhaps competition from some of Australia's endemic platycephalids has prevented *C. punctata* from becoming established. It is frequently taken at shallow depths by seines or with ichthyocide and it has been taken by trawl at depths from 23–250 m. Two large specimens (303,

Fig. 5. Young *Cociella punctata* from mangroves, USNM 329511, 42 mm SL; Negros, Philippines.

320 mm SL) were taken in a trap at 300 m in the Gulf of Aqaba (Baranes & Golani 1993:305).

Cociella heemstrai, new species
Figs. 6, 7

Platycephalus malabaricus (non Cuvier).—Gilchrist & Thompson, 1909:253.—Fowler, 1925:255.
Platycephalus tentaculatus (non Ruppell).—Fowler, 1925:255.
Platycephalus crocodilus (non Tilesius).—Barnard, 1927:933 (in part).—Fowler, 1934:488 (part).—Smith, 1950:378 (in part).—Fourmanoir, 1957:274 (in part).
Cociella sp.—Knapp, 1986:483.

Material examined.—Holotype, USNM 326281 (formerly RUSI 13761) (172 mm SL) Kenya, 02°38′S, 40°28′E, R/V *Fridtjof Nansen,* otter trawl, 280 m, 17 Dec 1980, Phillip C. Heemstra.

Paratypes (68): Natal: SAM 10514 (2, 232–245) Durban Bay. SAM 11877 (1, 203) Durban Bay. RUSI 1510 (2, 118–157) Durban. BMNH 1919.4.1.33 (1, 109) Durban. ANSP 54935 (2, 63–136) Durban; 1931. SU 69736 (1, 118) Durban. SAM 10035 (1, 216) Natal. RUSI 16492 (2, 135–138) Natal; 1914–20. ANSP 77600 (1, 235) Tugela R. N of Durban. SAM 11876 (3, 167–231) South Head, Tugela R., N of Durban; 21 Jan 1901. RUSI 36880 (3, 86–198) Tugela Bank, N of Durban. RUSI 1510 (2, 118–157) Durban. Mozambique: RUSI 10516 (1, 122) Inhaca Island near Lourenço Marques; Aug 1948. USNM 326296 (1, 178) Polana near Lourenço Marques; Feb 1969. RMNH 25144 (1, 172) Lourenço Marques; 5 Jul 1965. SAM 10822 (1, 215) Lourenço Marques; Jun 1920. SAM 26023 (1, 200) Lourenço Marques; Jun 1920. ANSP 77598 (1, 183) Delagoa Bay. USNM 326297 (1, 175) Delagoa Bay; 6 Feb 1969. USNM 326295 (2, 192–210) Delagoa Bay; 10 Feb 1969. SAM 16725 (1, 202) Delagoa Bay. BMNH 1922.2.9.29 (1, 175) Delagoa Bay. RUSI 39859 (5, 152–206) Maputo Bay (Delagoa Bay); 28 May 1992. USNM

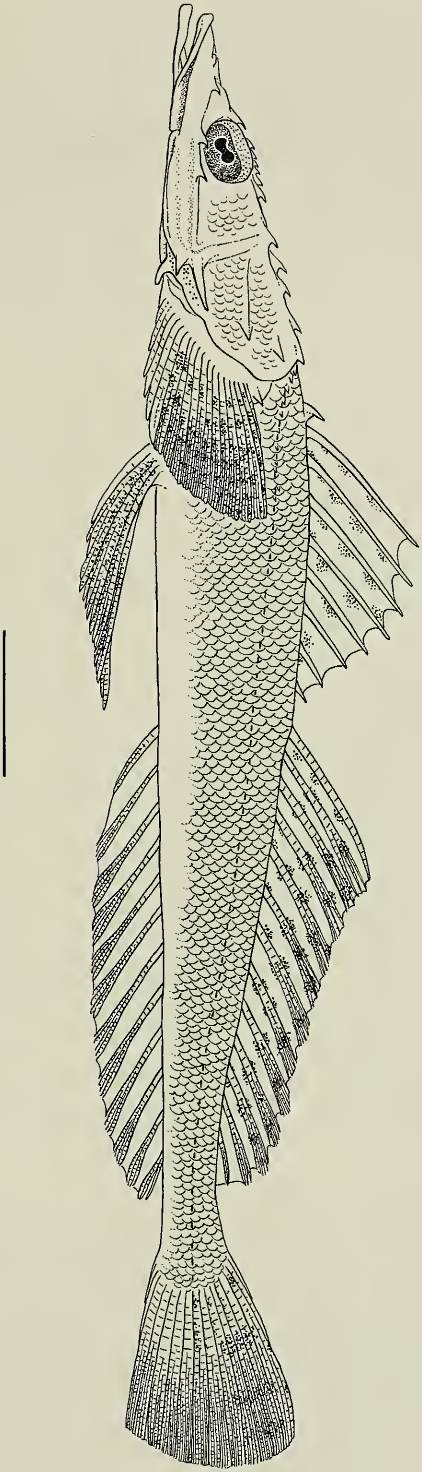

Fig. 6. Holotype of *Cociella heemstrai,* USNM 326281, 172 mm SL; Kenya.

Fig. 7. Paratype of *Cociella heemstrai,* USNM 303749, 180 mm SL; Mozambique Channel.

326294 (11, 83–144) Delagoa Bay, west side; 14 Feb 1969. USNM 326293 (8, 111–177) near Beira; 9 Oct 1964. Madagascar: MNHN B.2887 (4, 100–140) Nosy Be. USNM 326292 (3, 79–166) Northwest coast, Baie D'Amboro; 12 Feb 1964. USNM 303749 (4, 140–180) 12°42′12″S, 48°43′06″E; 11 Nov 1988. MNHN 1994.504 (1, 227) 25°03′S, 47°07′E; 12 Mar 1969.

Diagnosis.—This species is distinguished from others in the genus *Cociella* in having 9–11 gill rakers on the first arch (Table 2) and interpelvic scale count of 16–24 ($\bar{X}$ = 20.6). It is further distinguished by the following combination of characters: second dorsal fin and anal fin with 12 rays; ratio of snout length divided by interorbital width ranging from 2.5–4.4 ($\bar{X}$ = 3.4); only two spines on suborbital ridge below and behind eye; and interopercular flap present.

Description.—(Values for holotype given in parentheses). Dorsal-fin rays I, VIII or IX (I, VIII), 11–12 (12), usually 12; anal-fin rays 11–13 (12), usually 12; pectoral-fin rays 19–22 (20), usually 20 or 21; pored lateral line scales 52–55 (53), the anterior 3–19 (10) scales bearing weak spines; scale rows above lateral line slanting downward and backward 55–69 (64); diagonal scales 9–15 (12); interpelvic scales 16–24 (20); total gill rakers on first arch 9–11 (9), branched caudal rays 11–14 (11), usually 11 or 12. Measurements for the holotype and paratypes appear in Table 5. Least interorbital width going into greatest diameter of orbit 1.8–3.4 times (2.2), usually less than 2 times in specimens over 215 mm SL. Nape, opercle and cheek behind eye covered with ctenoid scales; top of head and cheek below eye mostly naked, with a few embedded scales. Preorbital spine single; a pair of small, reclining nasal spines usually present; infraorbital ridge smooth anteriorly, bearing 5–7 spines over posterior half of eye; suborbital ridge with one spine below middle of eye and a second spine near rear margin of eye; upper preopercular spine reaching nearly to opercular margin. Lateral-line scale shown in Fig. 1C. A narrow, elongate interopercular flap present.

Table 5.—Proportional measurements of *Cociella heemstrai* expressed in thousandths of standard length. Number of specimens given in parentheses after range.

Character	Holotype	Paratypes	
		Range	$\bar{X}$
Standard length (mm)	172.0	63.0–245.0 (62)	149.1
Head length	319.8	301.5–355.0 (62)	333.1
Snout length	95.9	79.8–111.8 (62)	98.6
Orbit diameter (greatest)	66.9	60.2–82.9 (62)	73.4
Interorbital width (least)	30.8	24.0–35.9 (62)	29.6
First dorsal spine length	22.1	15.0–36.7 (45)	24.5
Second dorsal spine length	130.2	94.7–166.5 (42)	124.3

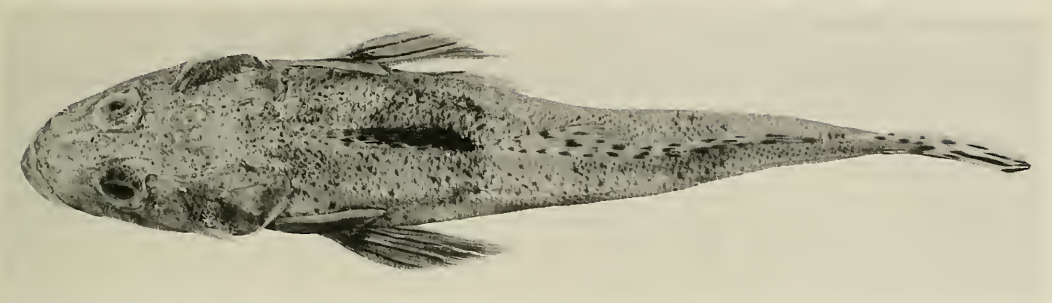

Fig. 8. Holotype of *Cociella somaliensis,* USNM 326300, 216 mm SL; Somalia.

Color in alcohol.—Dorsum grayish or brownish, sometimes with a few small dark spots. Spinous dorsal-fin dusky, with a few large dark spots. Soft dorsal-fin bearing numerous large dark spots. Pelvic fin dusky. Pectoral and caudal fins dusky below, with small dark spots near upper margin.

Color in life.—Specimens taken from Richards Bay and the Tugela Shelf off Natal were observed to have a bright yellow horizontal bar in the middle of the caudal fin. Live specimens seen at the Durban Aquarium had dark bands over the back and 4 or 5 pairs of white spots along the dorsum. The coloration pattern was somewhat similar to that exhibited by live specimens of *Platycephalus indicus* of similar size.

Distribution.—Cociella heemstrai is known from Durban, South Africa to Mombasa, Kenya and Madagascar (Fig. 4). Common in trawl catches at depths to 280 m., it is also taken by seining in shallow estuaries such as Durban Bay.

Etymology.—Named in honor of Phillip C. Heemstra, J. L. B. Smith Institute of Ichthyology, who, over the years, has contributed many specimens of flatheads to my studies.

Cociella somaliensis, new species

Fig. 8

Material examined.—Holotype, USNM 326300 (216 mm SL) Western Indian Ocean, Somalia, S of Ras Hafun, M/V *Beinta* Cruise 19, Sta. 13A, 10°13′N, 51°00′18″E, trawl, 30 m, 8 Feb 1987, Greg Small.

Paratypes (38): Somalia: USNM 326299 (8, 199–280) same data as holotype. USNM 302847 (3, 228–290) 10°20′54″N, 51°15′06″E; 8 Feb 1987. USNM 302846 (1, 271 same data as USNM 302847. USNM 326298 (20, 198–272) 10°07′24″N, 51°31′12″E; 6 Feb 1987. BMNH 1993.11.5.1–3 (3, 252–236) same data as USNM 326298. MNHN 1993-0265 (1, 213) same data as USNM 326298. MNHN 1993-0266 (1, 236) same data as USNM 326298. Oman: USNM 326301 (1, 273) 21°28′N, 59°28′E; 4 Dec 1963.

Diagnosis.—A species tentatively assigned to *Cociella* Whitley, it is distinguished from other members of the genus in having 12–18 gill rakers on the first arch (Table 2) and the ratio of snout length divided by interorbital width ranging from 2.0–2.5 ($\bar{X}$ = 2.2). It is further distinguished by the following combination of characters: an interpelvic scale count of 25–35 ($\bar{X}$ = 29.9); second dorsal fin and anal fin each with 12 rays; only two spines on suborbital ridge below and behind eye; and interopercular flap present.

Description. (Values for holotype given in parentheses).—Dorsal-fin rays I, VIII, 12; anal-fin rays 11–13 (12), usually 12; pectoral-fin rays 19–22 (20), usually 20 or 21; pored lateral line scales 52–55 (53), anterior 6–15 (9) scales bearing weak spines; diagonal scale rows above lateral line slanting downward 54–66 (54); diagonal scale count 10–14 (13); interpelvic scales 25–35

Table 6.—Proportional measurements of *Cociella somaliensis* expressed in thousandths of standard length. Number of specimens given in parentheses after range.

Character	Holotype	Paratypes	
		Range	$\bar{X}$
Standard length (mm)	216.0	199.0–290.0 (38)	241.4
Head length	318.1	296.9–328.0 (38)	310.6
Snout length	85.6	84.4–93.8 (38)	88.2
Orbit diameter (greatest)	65.7	55.4–67.4 (38)	62.5
Interorbital width (least)	38.0	36.4–44.7 (38)	39.6
First dorsal spine length	24.1	13.7–28.3 (31)	20.6
Second dorsal spine length	145.8	119.6–162.0 (33)	146.5

(30); total gill rakers on first arch 12–18 (17); branched caudal-fin rays 11–12 (11), usually 11. Measurements for holotype and paratypes appear in Table 6. Least interorbital width going into greatest diameter of orbit 1.3–1.8 (1.7) times. Nape, opercle and cheek behind eye covered with ctenoid scales; top of head and cheek below eye mostly naked, with a few embedded scales. Single preocular and preorbital spine; nasal spines usually absent; infraorbital ridge smooth anteriorly, bearing 5–7 small spines over rear half of eye; suborbital ridge with one spine below middle of eye and a second spine near rear margin of eye; upper preopercular spine curved slightly upward, reaching nearly to or slightly beyond opercular margin. Lateral-line scale shown in Fig. 1B. A narrow, elongate interopercular flap present.

Color in alcohol.—Dorsum light tan, usually with small scattered dark spots. Spinous dorsal-fin dusky, with large dark spots. Soft dorsal-fin pale, with large dark spots. Pectoral and pelvic fins dusky. Anal fin with pale rays, interradial membrane slightly dusky. Caudal fin pale, with bold dark spots and elongate bars throughout.

Distribution.—This species is found off Somalia and Oman (Fig. 4). It has been taken in the trawl catch at depths from 30–49 m.

Etymology.—Named for the country of Somalia, off whose shores all but one of the known specimens were captured.

Cociella hutchinsi, new species
Fig. 9

?*Platycephalus malabaricus* (non Cuvier).—Günther; 1880:41.

Suggrundus sp. 1.—Gloerfelt-Tarp & Kailola; 1984:123, color fig.—Sainsbury, Kailola & Leyland; 1985:120, color fig.

Material examined.—Holotype, CSIRO 1865 (206 mm SL) Australia, Arafura Sea, 09°16′S, 135°00′E; FRV *Soela*, trawl, 113 m, 27 Jun 1981. Paratypes (26): Arafura

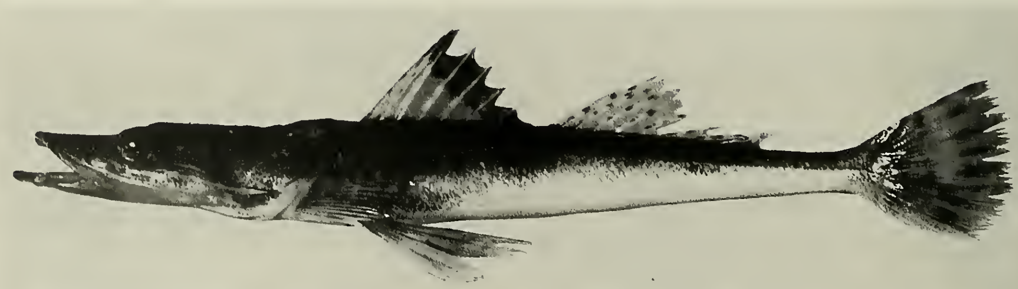

Fig. 9. Holotype of *Cociella hutchinsi*, CSIRO 1865, 206 mm SL; Arafura Sea (after Sainsbury et al. 1984).

Table 7.—Proportional measurements of *Cociella hutchinsi* expressed in thousandths of standard length. Number of specimens given in parentheses after range.

Character	Holotype	Paratypes	
		Range	$\bar{X}$
Standard length (mm)	206.0	142.0–261.0 (23)	203.4
Head length	363.1	351.4–393.8 (23)	373.5
Snout length	109.7	107.1–126.3 (23)	114.1
Orbit diameter (greatest)	77.7	76.2–90.3 (23)	82.4
Interorbital width (least)	20.4	17.6–25.1 (23)	20.8
First dorsal spine length	14.6	10.6–20.4 (21)	15.4
Second dorsal spine length	112.6*	110.0–142.9 (22)	128.7

* Indicates broken.

Sea: BMNH 1879.5.14.222 (1, 192) 9°59′S, 139°42′E; 10 Sep 1874. AMS I.27847-020 (4, 148–259) 10°02′S, 133°58′E; 17 Nov 1980. AMS I.21846-002 (2, 254–261) 09°38′S, 134°02′E; 17 Nov 1980. NTM S.11898-008 (1, 235) 10°18′S, 136°30′E; 24 Apr 1986. NTM S.12266-010 (1, 226) 10°20′S, 134°23′E; 13 Jun 1987. NTM S.11957-005 (2, 175–230) 10°18′S, 134°08′E; 16 Oct 1986. NTM S.11613-017 (2, 173–218) 10°15′S, 136°20′E; 10 Mar 1985. USNM 327179 (formerly NTM S.11621-002) (1, 240) 10°08′S, 136°48′E; 17 Mar 1985. Timor Sea: CSIRO 2739 (1, 177) 13°46–48′S, 128°13–14′E; 28 Jun 1980. CSIRO 2740 (1, 175) same data as CSIRO 2739. CSIRO 2741 (1, 165) same data as CSIRO 2739. USNM 327190 (3, 159–165) same data as CSIRO 2739. WAM P30716-001 (4, 142–184) 13°43.5′S, 128°38.6′E; 26 Dec 1969. USNM 326279 (2, 198–216) 12°04′S, 127°14–16′E; 29 Jun 1979.

Diagnosis.—This species is distinguished from other members of the genus *Cociella* in having 3–4 spines on the suborbital ridge under eye. It is further distinguished by the following combination of characters: second dorsal fin and anal fin with 11 rays; 6–7 gill rakers on the first arch (Table 2); interpelvic scales 23–34 ($\bar{X}$ = 28.1); interopercular flap absent; and ratio of snout length divided by interorbital width ranging from 4.6 to 6.7 ($\bar{X}$ = 5.6).

Description.—(Values for holotype given in parentheses). Dorsal-fin rays I, VII, I-I, VIII (I, VIII), 11; anal-fin rays 11; pectoral-fin rays 20–23 (22), usually 21 or 22; pored lateral line scales 51–55 (54), the anteriormost 2–8 (6) scales bearing weak spines; diagonal scale rows above lateral line slanting downward 59–68 (63); diagonal scale count 11–14 (12); interpelvic scales 23–34 (24); total gill rakers on first arch 6–7 (6); branched caudal-fin rays 11–12 (12). Measurements for the holotype and paratypes appear in Table 7. Least interorbital width going into greatest diameter of orbit 3.2–5.0 (3.8). Nape, opercle and cheek behind eye covered with ctenoid scales, top of head and cheek below eye mostly naked, with few embedded scales. Preorbital spine slight or lacking, a pair of small nasal spines present. Infraorbital ridge usually smooth over anterior ¼ of eye, bearing 7–10 small spines posteriorly; suborbital ridge with one spine below middle of eye, a second spine below rear margin of eye and 3–4 spines behind eye; upper preopercular spine reaching nearly to opercular margin. Lateral-line scale shown in Fig. 1E). Interopercular flap absent.

Color in alcohol.—Dorsum brownish; venter white with brownish stippling, sparse on breast, more evident posteriorly. Spinous dorsal fin dusky, with a broad submarginal black band. Soft dorsal fin pale, with small brownish spots on rays. Anal fin pale, rays white. Pectoral fin dusky brown, with traces of vertical dark bands, lower margin white. Pelvic fin with whitish base, stippled with brown, with well-developed submarginal dark band. Caudal fin dusky, sometimes with a series of streaks forming-submarginal dark band.

Distribution.—This is species is known from the Timor and Arafura Seas of Australia. It has been taken by trawling at depths from 39–108 m.

Etymology.—Named in honor of J. Barry Hutchins, Western Australian Museum, who has provided substantial assistance to the author's studies of Australian flatheads.

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New locality records of freshwater decapods from México (Crustacea: Atyidae, Cambaridae, and Palaemonidae)

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Abstract.—Collections in the Mexican states of Nayarit, Nuevo León, Tamaulipas, San Luis Potosí and Veracruz, provided significant new distribution records or data for seven freshwater decapods species. Information on each species is presented, including restricted synonymy, previously known distribution, new localities, and notes on the significance of the new data.

Villalobos-Hiriart et al. (1993) reported that Mexican freshwater decapods comprised about 132 species. Of these, many are known only from the type locality and, in several cases, knowledge on habitat is scarce or non-existent. Rapid changes in habitat conditions, introduction of non-native species, and decline in abundance of some elements of the original crustacean decapod fauna in northern México (see Contreras-Balderas 1991; Rodríguez-Almaraz & Campos 1994) prompted us to update the diversity, ranges, and habitat of the 22 species reported from that region. Collections in selected freshwater habitats in the states of Nayarit, Nuevo León, Tamaulipas, San Luis Potosí, and Veracruz produced significant new distribution data for seven freshwater decapods species one Atyidae, one Cambaridae and five Palaemonidae). Abbreviations used are: UANL, Arthropoda Collection, Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León; UABC, Invertebrate Collection, Facultad de Ciencias, Universidad Autónoma de Baja California; IBUNAM-EM, Crustacean Collection, Instituto de Biología, Universidad Nacional Autónoma de México. For each species listed, a restricted synonymy is provided and includes original description or redescription, changes in generic assignment, and known distribution.

Family Atyidae

Potimirim mexicana (De Saussure, 1857)

Potimirim mexicana.—Villalobos-Figueroa, 1959:295–313, pl. VI, figs. 29–38, pl. VII, figs. 39–50, pl. VIII, figs. 51–54, pl. IX, figs. 55, 56, map. 2, 3.—1982:217, 223.—Hart, 1961:67, 76.—Smalley, 1963: 177, 179, 181.—Villalobos-Hiriart et al., 1993:281.

Known distribution.—México. This species is found near the sea in the hydrological system of the Gulf of México slope, from Río Soto la Marina basin, Tamaulipas, to Río Grijalva basin, Tabasco, and rivers emptying in Laguna del Carmen, Campeche. Central America. Honduras, Costa Rica. Antilles. Cuba, Jamaica and Puerto Rico (Villalobos-Figueroa 1982).

Material examined.—21 females, Estero de Canalá, Guayabitos, Nayarit, 21°05′N, 105°15′W, 1 Jun 1995 (UANL). 8 males, 13 females, Camino a las Varas, Nayarit, 21°10′N, 105°14′W, 2 Jun 1995. 4 males, Río Coy (Río Choy) [Río Pánuco basin], 28 km south of Valles city, San Luis Potosí, 21°51′N, 98°56′W, 27 Aug 1994 (UANL). 3 males (topotypes, IBUNAM-EM uncat.),

M. A. Quevedo Park, Playa Norte, Veracruz, Veracruz, 19°14′N, 96°08′W, 1958.

Remarks.—Our specimens agree with Villalobos-Figueroa's (1959) description except that we found up to 15 uncinuli on the appendix interna and, like in *P. potimirim* (Müller), a plumose seta close to it. Even so, morphometric and shape features recorded by Villalobos-Figueroa allow easy separation of these two species. This record represents the farthest inland finding of *P. mexicana* in the Gulf of México slope, approximately 250 km upstream in the Rio Panuco-Rio Coy basin, and is the first report of this species in the Mexican Pacific slope.

Family Cambaridae
Procambarus roberti
Villalobos-Figueroa & Hobbs, 1974

Procambarus (*Pennides*) *roberti* Villalobos-Figueroa & Hobbs, 1974:8, fig. 2.—Hobbs, 1989:74.

Known distribution and habitat.—Ditch from La Media Luna, 4.8 miles (7.7 km) south of Río Verde (on highway to Pedro Montoya) and 2.5 miles (4 km) west on dirt road to Mina El Refugio, San Luis Potosí (type locality). In streams.

Material examined.—1 male I, 3 females, 6 juvenile males, 7 juvenile females, El Venado, San Luis Potosí (151 northwest of San Luis Potosí city and 105 km southwest of Matehuala city, San Luis Potosí), 22°58′N, 101°04′W, Feb 1994 (UANL).

Remarks.—The habitat of *Procambarus roberti* at El Venado is a spring-pool of approximately 20 m^2 with clear water and a rocky bottom. Only scarce grasses were observed in the margin of the pool amongst which the crayfishes were collected. Ostracods of the genus *Darwinula* and *Cypronodopsis* were in the sediment of the bottle where the crayfishes were fixed; however, the entocytherid symbiont, *Ankylocythere barbouri* Villalobos-Figueroa & Hobbs, 1974, was not found. It is not clear how *P. roberti* moved 160 km northwest from La Media Luna to El Venado since no superficial aquatic drainage system connects these localities. An hypogean dispersion or human introduction are two possible explanations.

Family Palaemonidae
Macrobrachium acanthurus
(Wiegmann, 1836)

Palaemon acanthurus Wiegmann, 1836: 150.

Macrobrachium acanthurus, Hedgpeth, 1949:30, figs. 1a, 2, 5.—Holthuis, 1952: 45–53, pl. 8, 9, figs. a, b.—Villalobos-Figueroa, 1982:217, 224.—Williams, 1984:66–68, figs. 44, 45.—Markham et al., 1990:419.

Known distribution and habitat.—From North Carolina, U.S.A. to Brazil (Holthuis 1952; Williams 1984). In México it ranges from southern Tamaulipas to Quintana Roo (Markham et al. 1990). The species lives in fresh or sometimes brackish water, and generally is not found far inland (Holthuis 1952).

Material examined.—3 males, Río Ramos [San Juan basin], municipality of Allende, Nuevo León, 25°16′N, 100°00′W, 15 Apr 1992 (UANL).

Remarks.—This is the first record of *M. acanthurus* in the state of Nuevo León and represents the farthest inland finding of this species in México, approximately 360 km upstream in the Río Bravo-Río San Juan basin.

Macrobrachium hobbsi
Nates-Rodriguez & Villalobos-Hiriart, 1990

Macrobrachium hobbsi Nates-Rodriguez & Villalobos-Hiriart, 1990:7, Fig. 3.—Villalobos-Hiriart et al., 1993:285.

Know distribution.—Los Tuxtlas area, southern Veracruz; Arriaga and Tonalá, Chiapas; Río Ostuta, Oaxaca, and Río Murga near Petatlán, Guerrero; presumably to

Nayarit (Nates-Rodriguez & Villalobos-Hiriart 1990; Villalobos-Hiriart 1993).

Material examined.—4 males, 1 female, 20 juveniles, Río Coy (=Río Choy), 28 km south of Ciudad Valles, San Luis Potosí, Apr, Jun 1994 (UANL); 1 male, 1 female, Río Huichihuayán, 70 km south of Ciudad Valles, San Luis Potosí, 21°32′N, 98°56′W, Apr 1994 (UANL); 7 juveniles, small pool, km 160 on the highway Tuxpam-Tampico, (30 km south of Pánuco [Ozuluama]), Veracruz, 21°51′N, 97°48′W, Nov 1993 (UANL); 3 juveniles, small pool, km 240 on highway Poza Rica-Tuxpam, Veracruz, 20°45′N, 97°31′W, Nov 1993 (UANL).

Remarks.—The presence of *M. hobbsi* in northern Veracruz and San Luis Potosí represents a northern range extension of approximately 850 km. It is remarkable that juveniles of *M. hobbsi* were found in the same habitat with *Palaemonetes mexicanus* Strenth, at Río Coy, San Luis Potosí. This does not agree with Strenth's (1976) conclusion that juveniles of *Macrobrachium* competitively exclude *Palaemonetes.*

Macrobrachium olfersi
(Wiegmann, 1836)

Palaemon olfersii Wiegmann, 1836:150.
Macrobrachium olfersi.—Holthuis, 1952: 95–103, pl. 24, pl. 25, figs. a, b.—Hedgpeth, 1949:35, figs. 1d, 4, 5.—Villalobos-Figueroa, 1967:167–171.—Villalobos-Hiriart, 1993:285.

Known distribution.—Western Atlantic slope. Lower Cape Fear River near Southport, North Carolina; Florida; Louisiana; Texas; and southern Veracruz, México to Santa Catarina, Brazil (Holthuis 1952). Eastern Pacific slope. From Chiapas to Nayarit, México (Villalobos-Hiriart et al. 1993).

Material examined.—1 male, 3 juveniles, Río Limón, 8 km north of Ciudad Mante, Tamaulipas, 22°49′N, 98°56′W, 12 Jun 1994 (UANL).

Remarks.—The identification of *M. olfersi* was possible by comparing the adult male above noted with the description and figures provided by Holthius (1952). The shrimps were collected in a shallow water area (15 cm depth) of the Río Limón, amongst aquatic vegetation. This records represent the farthest inland finding of this species in México, approximately 205 km upstream in the Rio Guayalejo-Rio Limón basin.

Palaemonetes kadiakensis Rathbun, 1902

Palaemonetes kadiakensis Rathbun, 1902: 93.—Strenth, 1976:2.—1994:91.
Palaemonetes (*Palaemonetes*) *kadiakensis,* Holthuis, 1949:92.—1952:212, pl. 51, figs. k–n, pl. 52, figs. a, b.—Smalley, 1964: 231.—Flemming, 1969:444.—Villalobos-Figueroa & Hobbs, 1974:15, fig. 8b.

Known distribution.—This species is widespread in fresh-water habitats of Central U.S.A., including the shores of lakes Ontario, Erie, and Michigan, the Mississippi basin, and the basin of several rivers emptying east and west of the Mississippi river in the Gulf of México (Holthuis 1952). The only Mexican record is that of Creaser (1932) for the state of Nuevo León, northeast México (Strenth 1976).

Material examined.—4 males, 5 females (1 ovigerous), Río Sabinas Hidalgo, Vallecillos, Nuevo León, 26°39′N, 99°59′W, 20 Apr 1979 (UANL). Tamaulipas: 21 males, 15 females, 13 Mar 1981 (UABC); 1 male, 3 ovigerous females, 22 Oct 1981; 1 male, 4 ovigerous females, 22 Nov 1981; 1 male, 6 females, 30 Jun 1982, Río Alamo, Cd. Mier, 26°25′34″N, 99°06′41″W; 1 male, 4 females (2 ovigerous), 23 Oct 1983, Presa Falcón, Miguel Alemán, 26°39′N, 99°12′W; 1 male, 2 females, 30 Mar 1983; 1 male, 4 females, 14 Mar 1987; Río Bravo, Matamoros 25°50′N, 97°24′W (UANL).

Remarks.—Based on the present record we believe that the material reported by Creaser (1932) from Nuevo León came from the Río Alamo-Río Salado basin (northern Nuevo León), which empties into the Río Bravo del Norte (Rio Grande) in the state of Tamaulipas. Previous collecting efforts in Central Nuevo León (Río San Juan basin) failed to produce specimens of *P. kadiakensis.*

The material of the Río Alamo (13 Mar 1981) was collected in shallow (<1 m depth) and clear-greenish water, the bottom was muddy and the aquatic vegetation included *Chara* sp. Additional information on the habitat is noted in Ruíz-Campos et al. (1985).

Palaemonetes mexicanus Strenth, 1976

Palaemonetes mexicanus Strenth, 1976:7, fig. 3.—1994:291.

Known distribution and habitat.—Small spring-fed river, 15 miles (24 km) west of Ciudad Valles, San Luis Potosí (type locality).

Material examined.—7 males, 20 females (5 ovigerous), Río Coy, 28 km south of Ciudad Valles, San Luis-Potosí, Apr, Jun 1994 (UANL).

Remarks.—This is apparently the first record of *P. mexicanus* since its original description by Strenth (1976). The new locality is about 50 km southeast of the type locality. Hobbs & Hobbs (1989) reported *P. mexicanus* to Mante river (Ciudad Mante, Tamaulipas); however, Strenth (1994) pointed out that Hobbs & Hobbs' specimens are of *P. hobbsi* Strenth, 1994.

Five ovigerous females (cl. 11.4–18.5 mm) were carrying 13 to 31 eggs having a diameter of 0.89–1.12 mm ($\bar{X}$ = 0.99) by 1.15–1.4 mm ($\bar{X}$ = 1.25).

Acknowledgments

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Neocrangon zacae (Chace, 1937) synonymized with *N. resima* (Rathbun, 1902), and compared with *N. communis* (Rathbun, 1899) (Decapoda: Caridea: Crangonidae)

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Abstract.—Features previously used to distinguish between *Neocrangon zacae* and *N. resima* overlap greatly. The rostrum can be low and narrow, slightly elevated and deep, or high with a plate with or without teeth. The width of the hand of the first pereopod also varies, as does the distal width of the antennal scale. Similar variability exists in the shape of the rostrum of *N. communis,* but this species has a prominent carina on the fifth abdominal somite and has broader hands of the first pereopod and a more horizontal dactyl. Usually, adult *N. resima* are smaller than *N. communis. Neocrangon zacae* is considered to be a junior synonym of *N. resima.* A redescription of *Neocrangon resima* is presented.

Crangonid shrimp of the genus *Neocrangon* Zarenkov, 1965, are characterized as follows: two median carapace spines, without submedian spines between the middorsal line and hepatic spine, the branchiostegal spine not very strong or flared sideways, the gastric region not depressed below the general level of the carapace, one or two spines at the distal end of the merus of first pereopod, second pereopods subchelate and subequal in length to other pereopods, fourth and fifth pereopods with normal dactyls; not broadened; lateral surface of the abdomen not sculptured. Four species have been reported from the northeastern Pacific: *N. communis* (Rathbun, 1899), *N. resima* (Rathbun, 1902), *N. abyssorum* (Rathbun, 1902) and *N. zacae* (Chace, 1937). Of these, *N. abyssorum* is the most distinct, having enlarged eyes, a bent antennular peduncle, a long and narrow rostrum and a thin exoskeleton. It generally occurs on the lower continental slope, but has been reported as shallow as 97 m (Butler 1980).

Colleagues conducting environmental impact surveys had difficulty distinguishing between *N. communis, N. resima* and *N. zacae. Neocrangon resima* has been recognized by its elevated rostrum with a ventral plate (Rathbun 1904:fig. 65). However, Rathbun noted that the development of the rostrum seemed to be dependent on age, with specimens smaller than 20 mm not showing this feature. Schmitt (1921) quoted Rathbun as stating that the rostrum of *N. communis* also could be variable, with some specimens regenerating a narrow rostrum with an elevated tip. The illustration of the rostrum given by Schmitt (1921:fig. 64) shows a bilobed rostrum with a small tooth, while that by Green & Butler (1988) shows a rostrum ending in a vertical plate. The rostrum of *N. zacae* was described as ascending at a slight angle "which varies somewhat" (Chace 1937).

The hands of the first pereopod of *N. resima* were reported by Schmitt (1921) to be shorter and with a more longitudinal margin than in *N. communis.* The hands of the first pereopod of *N. zacae* were said by Chace (1937) to have a "longer palm" than those of *N. resima,* as well as a more longitudinal dactyl. However, Green & Butler (1988) did not indicate any difference between the proportions of the palm of their specimen of *N. resima* and that of any other species.

Schmitt quoted Rathbun as saying that *N. resima* had a "slight" median carina on the fifth abdominal somite while *N. communis* had a "blunt" carina. Green & Butler (1988) illustrated a specimen of *N. resima* with a "moderate" median dorsal carina, but noted that the carapace and abdominal sulci bore a short pubescence, as Butler (1980) reported for *N. communis. Neocrangon zacae* lacked a carina on the fifth abdominal somite (Chace 1937).

The ranges and habitats of the three species have been reported to overlap in the eastern Pacific. According to Butler (1980), *N. communis* ranges from the Bering Sea to San Diego, California at 16–1537 m on mud. Green & Butler (1988) reported *N. resima* from mud or mixed mud and sand bottoms from Alice Arm, British Columbia to San Domingo Point, Baja California; Schmitt (1921) reported the depth range as 28–487 m. *Neocrangon zacae* has been reported from Monterey Bay, California to north of Gorgona Island, Colombia (although most reports come from California, U.S.A. and Baja California, Mexico) at depths from shore to 572 m. It has been reported from muddy or rocky bottoms. In southern California and Baja California, *N. zacae* usually was collected at shallower depths than *N. communis* (Wicksten 1980). *Neocrangon communis* and *N. resima* have been reported to be collected at the same trawling station (Schmitt 1921; Green & Butler 1988).

Considering the overlap in range, depth and morphological features reported for *N. communis, N. zacae* and *N. resima.* I examined specimens to determine what consistent differences could be found between them. Comparison of these specimens indicate that only two of these species are distinct.

Materials and Methods

I examined 179 specimens identified as *N. communis, N. resima* or *N. zacae* from Santa Monica Bay and Monterey Bay, California and Cook Inlet and the northeastern Gulf of Alaska. One hundred fifty two specimens from Santa Monica Bay were loaned by Ann Dalkey of the Hyperion Treatment Plant, Los Angeles County Environmental Monitoring Division; the specimens from Monterey Bay and Alaska were loaned by the California Academy of Sciences (CAS 014038, 020155, 020163 and 020155). I also examined the six syntypes of *N. resima,* collected off San Diego, California, from the National Museum of Natural History, Smithsonian Institution (USNM 25246).

For each specimen, I noted total length, shape (low, deep, with plate, with or without teeth) and elevation of the rostrum, presence or absence of a noticeable dorsal carina of the fifth abdominal somite, and shape of the hand of the first pereopod. These data were tabulated and compared with the original descriptions of the species.

Results

The most striking difference among the shrimp examined was that all specimens from the Gulf of Alaska and Cook Inlet had a pronounced and blunt dorsal carina on the dorsal surface of the fifth abdominal somite (Fig. 1f). None of those from California had more than a vague trace of a dorsal carina (Fig. 1c). The Alaskan specimens were larger, ranging from 37.1–61.1 mm in total length. The specimens from California ranged from 19.5–50.6 mm in total length, but most individuals (59) were between 35–40 mm long.

The shape of the rostrum was low and narrow in 87 specimens from California and 13 Alaskan specimens, elevated but without a plate in 52 specimens from California and eight from Alaska, and elevated and with a plate in 14 specimens from Santa Monica Bay, three from Monterey

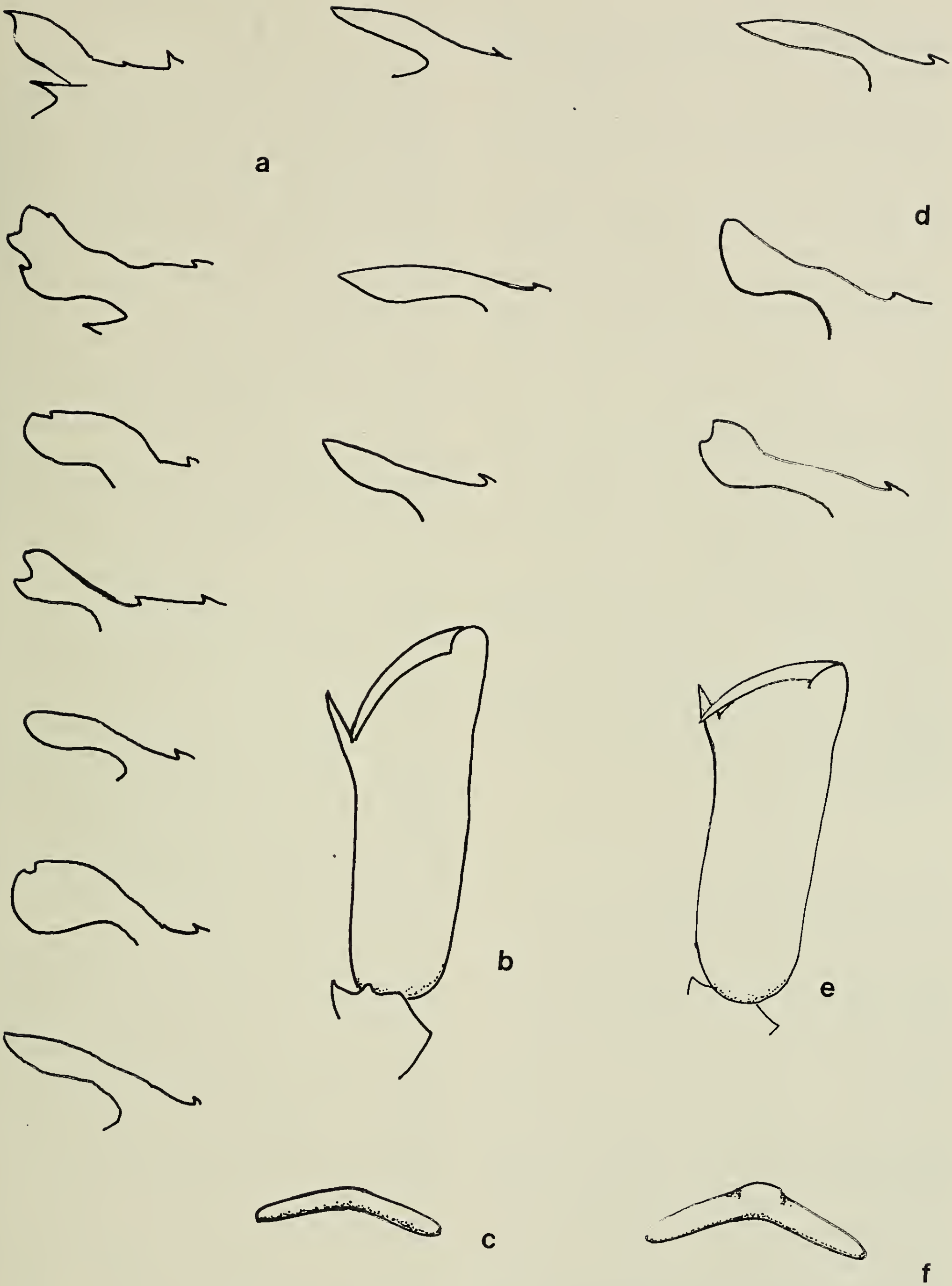

Fig. 1. *Neocrangon resima* (Rathbun, 1902). a, 10 shapes of the rostrum; b, subchela of first pereopod; c, dorsal surface of fifth abdominal somite in frontal view. *Neocrangon communis.* d, three shapes of the rostrum; e, subchela of first pereopod; f, dorsal surface of fifth abdominal somite in frontal view.

Bay and one from Alaska. In other specimens, the rostrum was broken off. In the collection from Santa Monica Bay, specimens with an elevated rostrum with a plate comprised about 9% of the total collection.

Some of the shapes of the rostrum are shown in Fig. 1a and 1d. It was difficult to determine the difference between "elevated and deep" and "elevated with a plate"; moreover, the number of teeth (if any) also varied. Most of the rostra did not have teeth except for a pointed apex. Among the syntypes of *N. resima,* the shape of the rostrum varied: two had a very low rostrum, one had a short but upraised rostrum and three had a moderately upraised rostrum. It is noteworthy that none of the syntypes had a raised rostrum with a plate, as illustrated by Rathbun (1904:fig. 65b).

Most of the specimens from Alaska had a broader hand and also a more horizontal dactyl of the first pereopod than those from California (Fig. 1e). In general, the specimens from California had a more elongated hand with a more vertical dactyl (Fig. 1b), similar to that illustrated by Chace (1937: fig. 9d) for *N. zacae.*

Discussion

In comparing the syntypes of *N. resima,* the other specimens and the descriptions, the presence or absence of a carina on the dorsal surface of the fifth abdominal somite was the most reliable distinguishing feature for recognition of species. Such a carina is present in *N. communis. Neocrangon communis* also may have a broader hand of the first pereopod, about 2.7–3× long as wide, although some specimens may have a hand as much as 3.7× long as wide (Butler 1980). The hand has a dactyl that closes somewhat horizontally. The specimens from Alaska could be confidently identified as *N. communis.* The specimen illustrated by Green & Butler (1988) as *N. resima* probably also belongs to *N. communis.* Except for the variation in the shape of the rostrum, the specimens fit well the description of *N. communis* given by Butler (1980, as *Crangon communis*).

The shape of the rostrum is unreliable as a diagnostic character of species of *Neocrangon.* Among the specimens from Monterey Bay and Santa Monica Bay, it varied from low to high, shallow to deep, and with or without a plate, which sometimes had teeth. Variation also occurred among the syntypes of *N. resima* and the specimens of *N. communis.*

Rathbun (1904) stated that the development of the rostral plate was dependent on age, "specimens 20 mm long show no evidence of it." However, in two specimens with a total length of 22–28 mm, there was an elevated rostrum; another had a rostrum with a well-developed plate. Because my samples contained only one specimen less than 20 mm long, it is difficult to say whether or not the development is related to age or size. The smallest specimen, 19.5 mm long, had a low rostrum without a plate.

The features of the fifth abdominal somite and first pereopod are indistinguishable between *N. resima* and *N. zacae.* The ranges as reported for the two species, their habitat and depth also overlap. In the absence of any other distinguishing features, *Neocrangon zacae* (Chace, 1937) must be considered to be a junior synonym of *N. resima* (Rathbun, 1902). It is unfortunate that the species was illustrated in Rathbun's work from an atypical specimen having a raised rostrum and a ventral plate, for this shape of the rostrum occurs in less than 10% of the population. A redescription of *N. resima,* including new information on variability within the species, follows.

Neocrangon resima (Rathbun, 1902)

Crangon resima Rathbun, 1902: 889.—Rathbun 1904:124, fig. 65.
Crago resima.—Schmitt 1921:96, fig. 64.
Crago zacae Chace, 1937:136, text-fig. 9.
Neocrangon zacae.—Kuris & Carlton 1977:554.—Wicksten 1980:39.

Neocrangon resima.—Kuris & Carlton 1977:554.

Redescription. (Modified from Chace 1937).—Rostrum usually narrow, with pronounced dorsal sulcus and blunt apex, variable in length, not reaching end of cornea of eye to exceeding entire eye. Rostrum ascending, usually at slight angle but as much as 45° in some specimens; ventral plate, with or without teeth, may be present.

Carapace about 0.25× length of abdomen. Gastric region not depressed below general outline of carapace. Two spines in dorsal midline, posterior one longer and arising in front of middle of carapace. Strong hepatic spine in line with anterior dorsal spine. Anterior margin with antennal and branchiostegal spines.

Eye large and black.

Abdominal somites with few small setae along ventral surface but without obvious pubescence. Somites 1 and 2 with elevated posterior portions, elevations preceded by broad, shallow transverse sulci. Somites 1–4 without carinae. Pleura of first to third somites with rounded or squared margins, fourth pleuron with minute posteroventral spine, fifth pleuron with posterolateral point. Fifth somite occasionally with obscure median carina. Sixth somite approximately 1.6× length of fifth, bearing pair dorsal longitudinal carinae separated by median sulcus and bounded by shallower lateral sulci. Telson longer than sixth somite, with slight median sulcus, bearing 2 pairs dorso-lateral spines, apex blunt.

Antennular peduncle with 3 segments, second 2–3× length of third, stylocerite short. Antennular flagella exceeding antennal scale. Basicerite of antenna with lateral spine. Spine of antennal scale exceeding blade, antennal scale about 3.5× long as wide.

Third maxilliped long and slender, extending slightly beyond antennular flagella, exopod with lash. First pereopod subchelate, merus with spine at outer angle of distal end, palm of subchela 3–3.3× long as wide, dactyl closing obliquely. Second pereopods slender, shorter than first, chelate. Third pereopods slender, extending well beyond third maxillipeds, fourth and fifth pereopods shorter; all with simple, slender dactyls. Uropods equal to or exceeding length of telson.

Color in life translucent, mottled finely with greenish-brown and scarlet on dorsal and lateral surfaces; ventral surface white, antennae banded with scarlet and white, uropods and telson mottled.

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Daldorfia Rathbun, 1904 (Crustacea: Decapoda) from the Neogene of Japan

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Abstract.—*Daldorfia nagashimai,* new species, is described from the Higashimorogata Formation (Upper Miocene - Lower Pliocene), Miyazaki Group of Miyazaki Prefecture, Japan. This species is characterized by a large carapace with irregular, large, granulose tubercles dorsally and without a deep, eroded area behind a longitudinally hexagonal mesogastric lobe. Another specimen representing a second unnamed species is recorded from the Aoso Formation (Upper Miocene) of Miyagi Prefecture, Japan. These species represent the first records of Neogene decapod crustaceans from Japan and extend the geologic range of the genus *Daldorfia* to the Late Miocene age.

The subfamily Parthenopinae is a small group including eight Recent genera, *Daira* de Haan, 1833, *Dairoides* Stebbing, 1920, *Daldorfia* Rathbun, 1904, *Leiolambrus* A. Milne Edwards, 1878, *Parthenope* Weber, 1795, *Solenolambrus* Stimpson, 1871, *Thyrolambrus* Rathbun, 1894, and *Tutankhamen* Rathbun, 1925. The fossil record of *Parthenope* Weber, 1795, is robust in Cenozoic deposits throughout the world (Glaessner 1969). *Daira* is recorded from the Eocene-Miocene of Europe, the Pliocene of Fiji, and the Miocene of Japan (Glaessner 1969; Müller 1984; Müller & Collins 1991; Karasawa 1993). The only known fossil *Leiolambrus* was described from the Upper Eocene Bartonian of England (Quayle & Collins 1981) and *Tutankhamen* also has been reported from the Oligocene Gambier Limestone of Australia (Jenkins 1985). The fossil records of the other four Recent genera are unknown throughout the world, but the extinct, *Mesolambrus declinatus* Müller & Collins, 1991, similar to *Thyrolambrus* Rathbun, 1894, was described from the Szépvölgy Formation (Upper Eocene) of Hungary; Glaessner (1969) recognised the Upper Eocene, *Phrynolambrus* Bittner, 1893 as the junior synonym of the subgenus *Pseudolambrus* Paulson, 1875, in *Parthenope,* but subsequently Guinot (1979) separated *Phrynolambrus* from *Pseudolambrus* and suggested that *Phrynolambrus* has a close affinity with *Daira* and *Dairoides.*

The purpose of this paper is to describe a new species and a related, but unnamed species of *Daldorfia* from the Neogene deposits of Japan. The materials were collected from a road cut (Loc. MYZ-4 of Karasawa 1993, 31°56′48″N, 131°16′46″E) at Akatani, Uranona, Takaoka-cho, Higashimorogata-gun, Miyazaki Prefecture (Fig. 1A). Siltstone of the Aya Member of the Higashimorogata Formation, Miyazaki Group (Upper Miocene to Upper Pleistocene) is exposed at this locality (Tomida 1991; Karasawa 1993). This formation is assigned to Zones N.17b–18 (latest Miocene-earliest Pliocene) of Blow's scale of planktonic foraminifera (Suzuki 1987). *Daldorfia nagashimai,* new species, is based upon the holotype and two paratype specimens included within calcareous nodules. Karasawa (1993) reported two species of crabs from this locality. The decapod as-

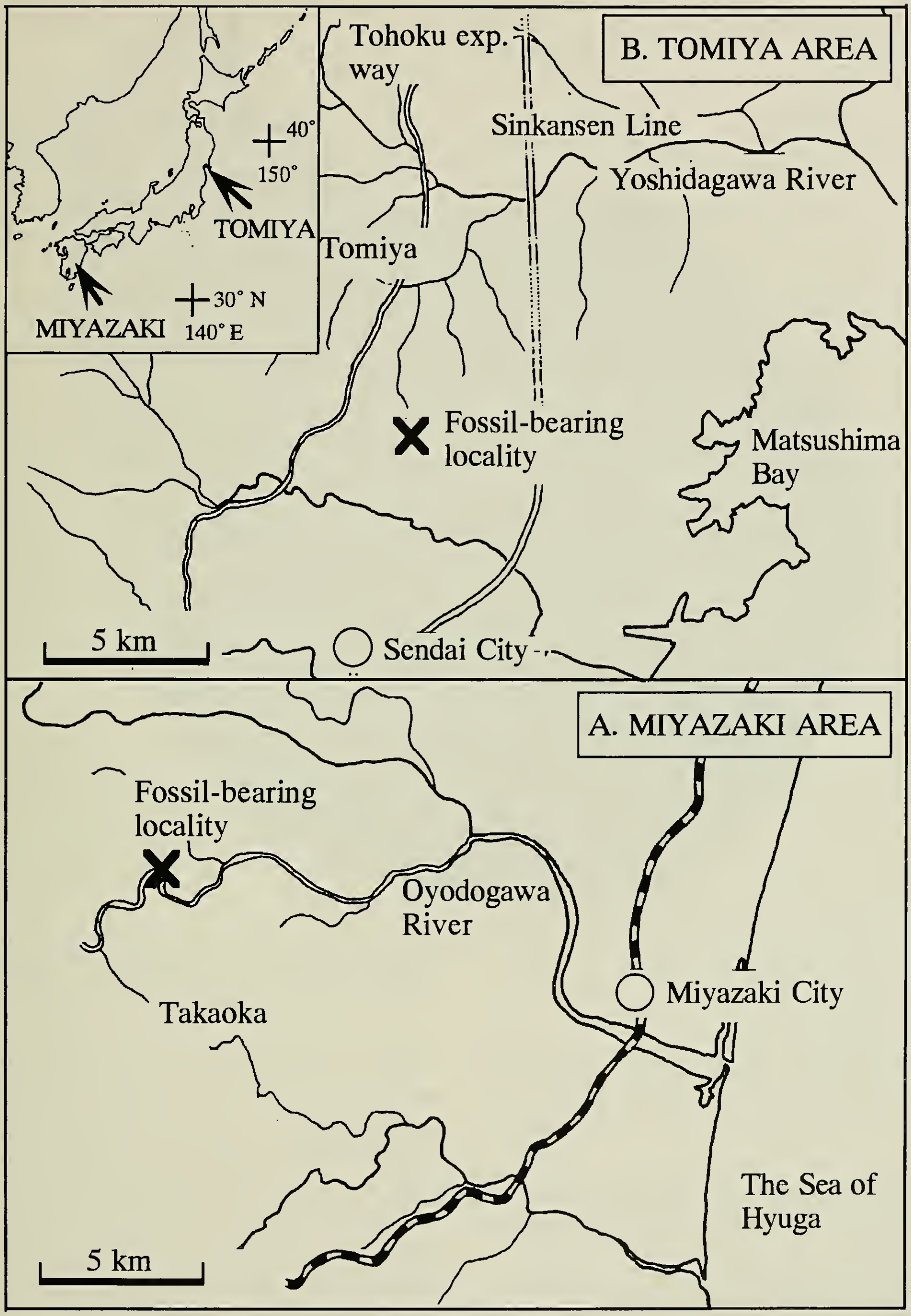

Fig. 1. Map of Japan showing the fossil-bearing localities.

semblage is dominated by *Carcinoplax prisca* Imaizumi. Two specimens of *Linuparus* sp. aff. *L. trigonus* (von Siebold) have been found also. Tomida (1991) reported some molluscs, *Perotrochus* sp., *Bathybembix* sp., *Hindsia* sp. and *Acila submirabilis* Makiyama from the locality. Decapods collected from the locality suggest an environment within the lower sublittoral zone on a muddy to sandy bottom (Karasawa 1993).

A large manus of the second species, *Daldorfia* sp., was obtained from the Aoso Formation at the exposed road-cut south of Matsugai, Tomiya Town, Miyagi Prefecture (38°20′22″N, 140°55′56″E) (Fig. 1B). The Aoso Formation consists mainly of cross-laminated, poorly consolidated coarse-grained sandstone with remarkable key beds of tuff layer (K7) intercalated within the lower part and a pumiceous tuff layer underlying the conglomerate bed (K8) in the middle part of the Formation (Kitamura et al. 1983). The decapod fossil was obtained from this lithology beneath the K8 beds. Fujiwara (1992) discussed the Late Miocene molluscan assemblages of the region. He discriminated the *Serripes-Miya* and *Glycymeris-Dosinia* assemblages within the K8 beds, and regarded the inhabitants to be subneritic to mesoneritic, respectively. According to Fujiwara (1992) and Saito & Fujiwara (1994), the middle to the upper part of the Aoso Formation lying several meters above the K7 tuff bed is correlated to Blow's N17b Zone. Therefore, the geologic age of the fossil bearing horizon is assignable to the latest Miocene. From another locality of the Aoso Formation, a small number of fingers referable to the families Callianassidae and Parthenopidae were collected by the same person who discovered the material described below.

Section Heterotremata Guinot, 1977
Superfamily Parthenopoidea MacLeay, 1838
Family Parthenopidae MacLeay, 1838
Subfamily Parthenopinae MacLeay, 1838
Genus *Daldorfia* Rathbun, 1904

Type species.—*Cancer horridus* Linnaeus, 1758, by monotypy (ICZN Opinion 1582); Recent, Indo-West Pacific.

Geologic range.—Late Miocene—Recent.

Daldorfia nagashimai, new species
Figs. 2–4

Material.—KMNH IvP 300,022, holotype (Kitakyushu Museum and Institute of Natural History, 6, Nishihonmachi 3-chome, Yahatahigashiku, Kitakyushu, 805 Japan), coll. H. Nagashima, 1994; MFM83058, 83059, 2 paratypes (Mizunami Fossil Museum, Yamanouchi, Akeyo, Mizunami, Gifu, 509-61 Japan), coll. S. Tomida, 1993.

Diagnosis.—Large parthenopid; dorsal carapace covered with irregular, large granulose tubercles; mesogastric lobe large, longitudinally hexagonal, without deep, eroded area behind it; major cheliped like *Daldorfia horrida,* large, long, with stout fingers.

Description.—A large *Daldorfia*; carapace appears to be broadly pentagonal in outline, width approximately 1.4 times length. Front broadly triangular, downturned, with shallow, ovate dorsal hollow. Orbits small, subovate, directed anterolaterally. Anterolateral margin strongly convex, bearing irregular, large tubercles; deep notch defined lateral termination of from cervical groove. Posterolateral margin strongly convex. Posterior margin obscured by poor preservation.

Dorsal surface with inflated, tuberculate regions separated by shallow, moderately well-defined grooves. Protogastric lobes strongly convex, with sharply pointed tubercles on highest parts, deep depressions between gastric and hepatic lobes. Mesogastric lobe with large, granulose tubercles, longitudinally hexagonal, gently convex; narrow anterior mesogastric process with tubercles longitudinally arranged; deep depression on either side of mesogastric lobe. Cardiac lobe broken. Highest part of strongly convex hepatic regions with sharply pointed tubercles. Branchial lobes uneven, with irregular, large, granulose tubercles and small setal pits. Intestinal region depressed, with irregular tubercles.

Dactylus and propodus of right major cheliped (paratype) preserved, but tips of both fingers, and proximal end and mesial

Fig. 2. *Daldorfia nagashimai*, new species, holotype, ×1.0; dorsal view; showing central and left side of carapace, parts of merus and carpus of left cheliped.

surface of propodus broken. Fingers with a wide gape. Dactylus stout, with irregular, granulose tubercles; occlusal surface missing. Imperfect fixed finger with a broad, flattened, molariform tooth on occlusal surface. Palm long, covered with longitudinal rows of irregular, conical, granulose tubercles decreasing in size proximally; greatest distal width about 1.5 times proximal width; tubercles large on dorsal and lateral surfaces, rather small on ventrolateral surface; ventral margin with conical, granulose tubercles; four longitudinal rows of spines present on ventromesial surface; two broken bases of large mesial spines present, others missing. Carpus and merus of left cheliped (holotype) with granulose tubercles, merus bearing acute spines on dorsal margin.

Pereiopods and ventral aspects unknown.

Derivation of name.—The species name honors H. Nagashima, who collected the holotype.

Remarks.—*Daldorfia* comprises nine Recent species from the Indo-Pacific and East Atlantic Oceans. Of these, *Daldorfia nagashimai* most closely resembles *D. horrida* (Linnaeus 1758) and *D. rathbuni* (de Man 1902), from the Indo-West Pacific Oceans, but the new species has a moderately uneven, not eroded dorsal surface with irregular, granulose tubercles. This new

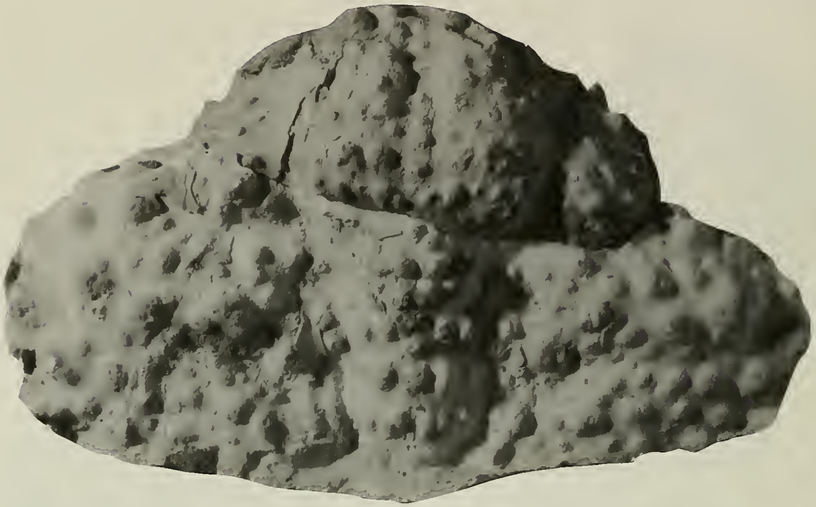

Fig. 3. *Daldorfia nagashimai,* new species, paratype, ×1.0. Dorsal view of carapace.

species has a large, longitudinally hexagonal mesogastric lobe with large, granulose tubercles, but *D. horrida* and *D. rathbuni* each have a small, rounded mesogastric lobe. Absence of a deep, eroded area behind the mesogastric lobe in the new species distinguishes it from *D. horrida* and *D. rathbuni.* There is, in the general features of the major cheliped, considerable similarity between *D. nagashimai,* and *D. horrida*: the latter bears two large, conical, distal tubercles, one on the lateral surface and the other on the dorsal surface of the propodus, but in *D. nagashimai,* the distal ends of the lateral and dorsal surfaces are covered with irregular, conical tubercles. Absence of spines on the mesial surface of the dactylus readily distinguishes *D. nagashimai* from *D. horrida.*

Recent *D. horrida* and *D. rathbuni* differ from most other parthenopine crabs, including the other species of *Daldorfia* (i.e., *D. investigatoris* (Alcock 1895), *D. spinosissima* (A. Milne Edwards 1862)), in having both fingers of the major cheliped with large blunt molariform denticles on the proximal occlusal surfaces.

Zipser & Vermeij (1978) observed that the Recent *Daldorfia horrida* uses the occlusal surfaces with molariform teeth of the major cheliped to crush gastropod shells (i.e., *Cerithium, Cypraea, Drupa, Cantharus, Vasum*) and to feed on hermit crabs. Ng & Rodríguez (1986) described detail the dentition on both chelipeds of *D. horrida.* There is, on the occlusal surface of the major chela, a great similarity between the fossil species and Recent *D. horrida.* Thus, *D. nagashimai* appears to have acquired the crushing behavior of feeding on gastropods and hermit crabs at least by the Late Miocene.

Daldorfia sp.
Fig. 5

Material.—SSME 13320 (Sendai Science Museum, 4-1, Forest Park, Dainohara, Aobaku, Sendai 981). 1 specimen, coll. Y. Takaizumi, 1991.

Description.—A large propodus of left minor cheliped, oval in cross section, covered on every surface except for fixed finger with large, conical tubercles. Tubercles vary in size, up to 1 cm in diameter. Lateral surface has flattened tubercles, dorsal border bears rather pointed ones. A hook-shaped projection with which carpus articulates on dorsal border situated near proximal articulation. Fixed finger short, about ⅕ of total length, slightly curved inward,

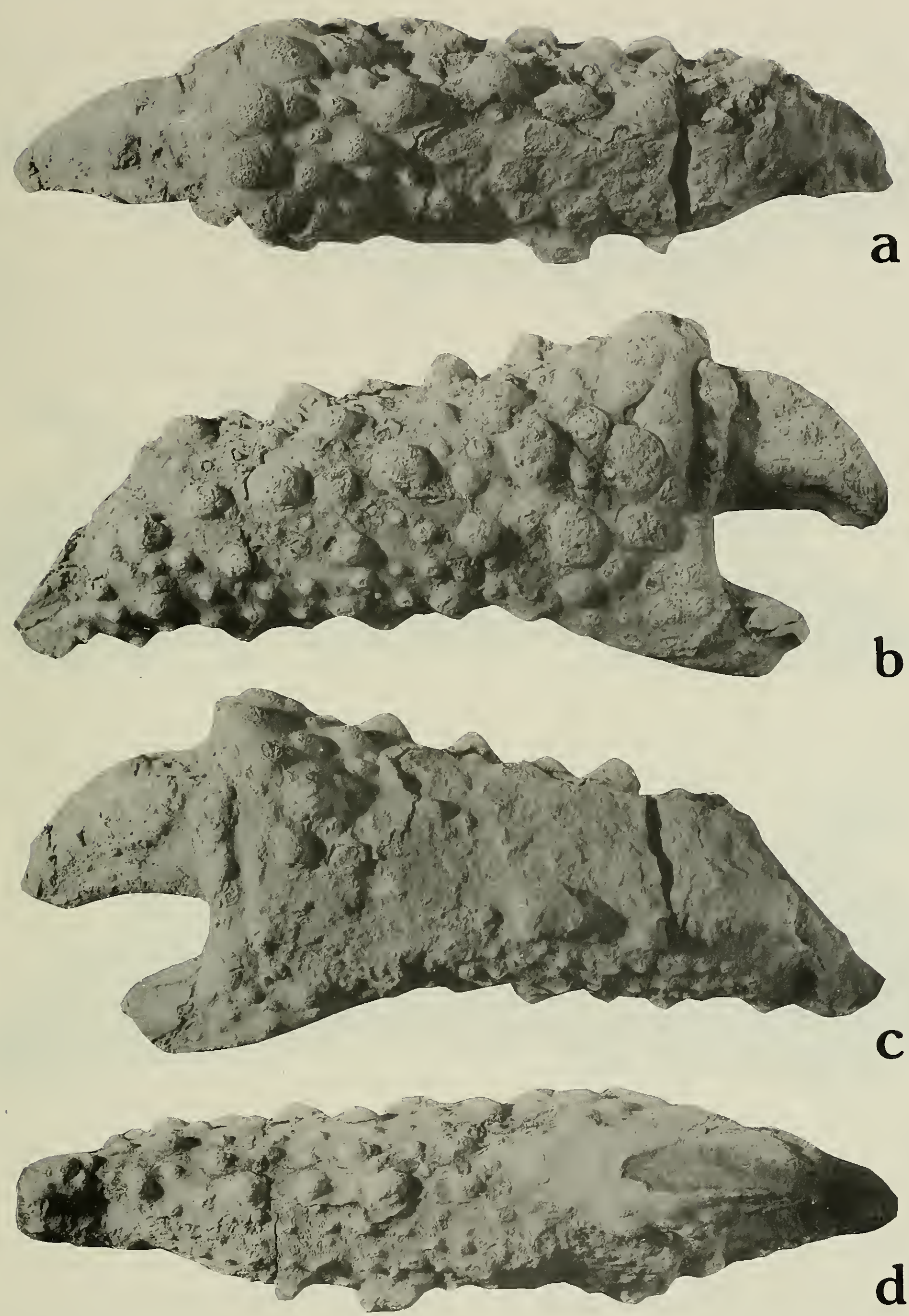

Fig. 4. *Daldorfia nagashimai,* new species, paratype, ×0.93. Right major cheliped: a, dorsal; b, lateral; c, mesial; d, ventral view.

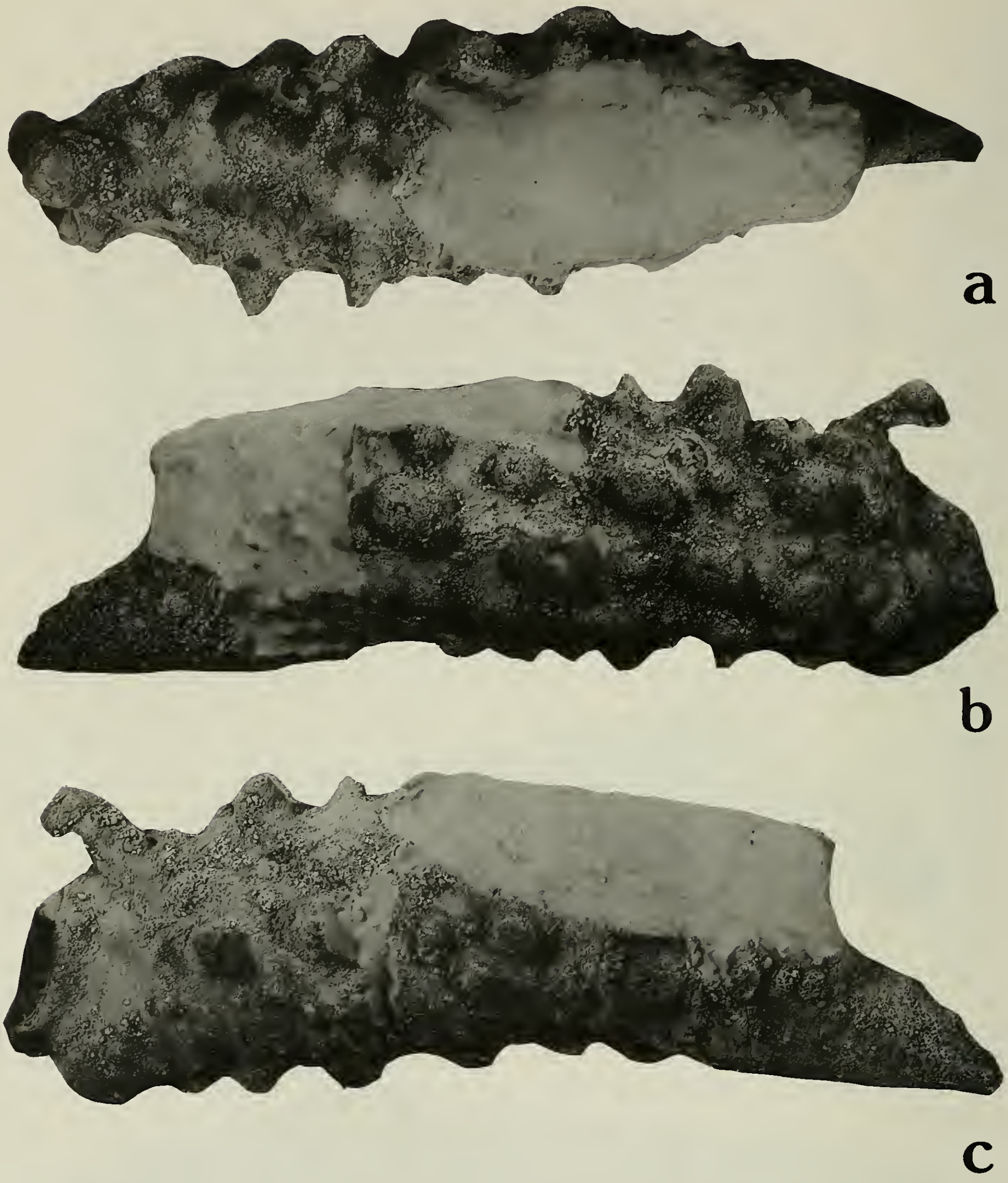

Fig. 5. *Daldorfia* sp., ×0.9. Propodus of left major cheliped: a, dorsal; b, lateral; c, mesial view.

stout with apex faintly curved downward. Occlusal surface with 3 blunt, subconical teeth. A shallow, short longitudinal furrow on apex below occlusal edge.

Remarks.—In general shape, the present chela most closely resembles the minor chela of *D. horrida,* but differs in lacking granulose tubercles on the lateral surface and spines on the ventral margin. The minor chela of *D. nagashimai* being as yet unknown, precludes comparison with *D.* sp.

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Systematics and distribution of the genus *Calocarides* (Crustacea: Decapoda: Axiidae)

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Abstract.—The nine currently recognized species of *Calocarides* are reviewed, and two new species are described: *C. capensis* from the south-east Atlantic Ocean off the Cape of Good Hope, and *C. macphersoni* from the Atlantic Ocean off Namibia. Species of the genus are particularly characterized by the possession of dentate median, submedian, and lateral carinae of the carapace, weakly pigmented or unpigmented eyes, and robust, quite heavily sclerotized, tuberculate and/or spinose first pereopods.

The approximately 100 described species of Axiidae show their greatest diversity in shallow tropical and subtropical seas, with several genera confined to the tropics, e.g., *Coralaxius* Kensley & Gore, 1982, *Paraxiopsis* De Man, 1905, *Paraxius* Bate, 1888, *Scytoleptus* Gerstaecker, 1856. A few genera, however, have colonized colder and deeper waters and show considerable diversity and broad geographic range, e.g., *Calocarides* Wollebaek, 1908, and *Eiconaxius* Bate, 1888, the latter an inquiline of hexactinellid sponges. *Calocarides* is geographically widespread in continental shelf-slope regions, and contains cold-water inhabiting, soft-bottom burrowing species, some of which may be associated with zones of upwelling. The genus is reviewed here, two new species are described, and a number of taxonomic and distributional problems noted, relating to species previously included in the genus.

Abbreviations: cl—carapace length; HUMZ—Laboratory of Marine Zoology, Hokkaido University; ICMB—Instituto de Ciencias del Mar, Barcelona; MNHN—Muséum National d'Histoire Naturelle, Paris; SAM—South African Museum, Cape Town; UBZM—Zoological Museum, University of Bergen; USNM—National Museum of Natural History, Smithsonian Institution.

Systematic Account

Family Axiidae

Genus *Calocarides* Wollebaek, 1908

Calocaris (Calocarides) Wollebaek, 1908: 3, 23.

Axiopsis (Calocarides).—De Man, 1925:1, 2, 6, 67, 71.—Balss, 1957:1579.

Calocarides.—Bouvier, 1940:97.—Sakai & de Saint Laurent, 1989:4, 78.—Poore, 1994:98.

Euconaxius [laps. cal. for *Eiconaxius* Bate, 1888] Trybom, 1904:384.

Type species.—By subsequent designation by Sakai & de Saint Laurent, 1989, *Euconaxius coronatus* Trybom, 1904. Type locality: Skagerrak, North Sea, 230–500 m. Gender: Masculine.

Diagnosis.—Gonochoristic. Carapace having small supraocular spine present, as part of lateral rostral series; post-cervical carina low, rounded, barely discernible in some species, lacking spines; rostrum at same level as anterior carapace, margins armed; median carina dentate; submedian carina dentate; lateral carina dentate.

Eye reaching to about midlength of rostrum, cornea weakly pigmented or unpig-

Table 1.—Branchial formula for *Calocarides coronatus*. r = reduced.

	Maxillipeds			Pereopods				
	1	2	3	1	2	3	4	5
Exopod	1	1	1	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	r	r	r	r	—	—
Arthrobranch	—	—	2	2	2	2	2	—
Pleurobranch	—	—	—	—	—	—	—	—
Setobranch	—	—	1	1	1	1	1	1

mented; eyestalk longer than eye. Antennal scaphocerite elongate. Maxilla 2, scaphognathite having spinulose flagellum. Maxillipeds 1–3 with exopods and epipods. Pereopod 1, chelipeds asymmetrical, somewhat sexually dimorphic. Propodi and dactyli of pereopods 3–5 slender, not expanded, dactyli simple. Pleopodal rami slender elongate; appendix interna present on pleopods 2–5. Pleopod 1 ♂ absent; pleopod 1 ♀ uniramous, of 2 articles. Pleopod 2 ♂ with appendix masculina of single lobe. Uropod with lateral ramus with suture. Telson longer than wide, or at least as long as wide, with dorsal spines.

Branchial formula: see Table 1.

Species:

Calocarides capensis, new species. Off Table Bay, South Africa, 1280 m.

Calocarides coronatus (Trybom, 1904). Swedish and Norwegian fjords, North Sea, 80–700 m.

Calocarides lev (Zarenkov, 1989). Gulf of California, 2000–2036 m.

Calocarides longispinis (McArdle, 1901). Bay of Bengal, 549 m.

Calocarides macphersoni, new species. Off Namibia, 300–480 m.

Calocarides quinqueseriatus (Rathbun, 1902). Off mouth of Columbia River, Oregon, to southern California, 292–2013 m.

Calocarides rostriserratus (Andrade & Baez, 1977). Off Chile, 320–400 m; off Peru, Gulf of Panama, 576–825 m.

Calocarides rudolfi (Zarenkov, 1989). Off Angola, 490–510 m.

Calocarides soyoi (Yokoya, 1933). Off northern Japan, 138–270 m.

Calocarides spinulicauda (Rathbun, 1902). Off Bodega Head, California, 113 m; Puget Sound, 70–256 m; British Columbia, 91–128 m.

Calocarides vigila Sakai, 1992. New Zealand, 74–146 m.

Taxonomic remarks.—The species *Calocaris lev* Zarenkov, 1989, described from a hydrothermal vent at 2000–2036 m in the Gulf of California, is almost certainly a species of *Calocarides.* The proportions and spination of the first chelipeds bear more resemblance to *C. rostriserratus* from Chile, Peru, and Panama, than to *C. quinqueseriatus* from southern California. Given that this species was taken from greater depth than either of the two abovementioned species, its relative isolation of the Gulf of California, and the lack of males, it seems prudent to await further material before deciding on the status of this species.

Calocaris rudolfi Zarenkov, 1989, from 490–510 m off Angola is likewise a species of *Calocarides,* and bears some resemblance to *C. macphersoni* (see Remarks under *C. macphersoni*).

Although Sakai & de Saint Laurent (1989) tentatively placed *Axiopsis tenuicornis* De Man, 1905, *Axius habereri* Balss, 1913, *Axius armatus* Smith, 1881, and *Axiopsis werribee* Poore & Griffin, 1979, within *Calocarides,* none of these possess a majority of the features that define the genus.

The specific identity of *Calastacus quinqueseriatus* and *Axius spinulicauda amurensis,* both recorded from Japan by Kobjakova (1937) will remain uncertain until the material can be located and examined.

Ecological and biological notes.—Little information exists for species of *Calocarides,* except for *C. coronatus* and *C. quinqueseriatus.* Both of these species are known to burrow into soft bottom sediments. In the case of *C. coronatus,* these sediments are usually mud with a high

(60%) silt content and a temperature of 6°–7.5°C. *Calocarides coronatus* overlaps in bottom distribution with the calocarid shrimp *Calocaris macandreae,* but dominates in deeper water (Brattegard 1966). For all the records of *C. quinqueseriatus,* the bottom sediments were recorded as either yellow or green mud, with temperatures ranging from 13°–16°C.

Even less is known of the prey organisms of species of *Calocarides. Calocarides macphersoni* from Namibia was taken from the gut-contents of two bottom feeders, viz. the scorpaenid fish *Helicolenus* sp., and the ray *Raja confundens,* again suggesting that the species burrows in soft sediments.

Regarding reproduction and fecundity, *C. coronatus* produces a about 65 eggs/female, with an egg diameter 15% of carapace length ($n = 2$). *Calocarides quinqueseriatus* produces about 180 eggs/female, with an egg diameter of about 7% of carapace length ($n = 4$). These egg sizes are in the high range for free-living axiids, suggesting that a fairly advanced larva hatches, having a relatively short planktonic larval lifespan. Species which produce thousands of eggs per female generally have much smaller eggs, e.g., *Oxyrhynchaxius caespitosa* with 16,000 eggs/female, egg diameter 1.3% of carapace length; *Axiopsis serratifrons* with 4000 eggs/female, egg diameter 2.7% of carapace length. The commensal species of *Eiconaxius* by contrast, produce far fewer large eggs, 8–30 eggs/female, with an egg diameter 16–38% of carapace length. Elofsson (1959) recorded a 10 mm stage II larva (Gurney 1942) of *C. coronatus* from 600 m.

Distribution.—From the depth ranges of the 11 species of *Calocarides* (see list of species), it is clear that they are continental shelf/slope dwellers, probably with a preference for soft-sediment bottoms into which they can burrow. In several cases, the shelf/slope habitat is also characterized by upwelling of deeper water, e.g., off the Cape of Good Hope and Namibia, off Pacific North America, off Chile, and in localized areas off Norway.

The widespread geographical distribution of the species of *Calocarides,* in the Atlantic, Indian, and Pacific oceans (Fig. 1), along with the most northerly (*C. coronatus*) and most southerly (*C. vigila*) records for the Axiidae, suggests a considerable age for the genus. If, as has been suggested, the axiid-like shrimps evolved from Tethyan ancestors (Kensley 1994), shallow-water precursors of *Calocarides* must have spread with tectonic plate movements and the opening of the present-day oceanic basins, at the same time penetrating to varying depths the waters of the continental shelves. The direction of this invasion from shallow to deeper shelf waters may be reflected in that some eye-pigment is retained in some species (e.g., *C. soyoi*) while other species completely lack eye-pigment (e.g., *C. capensis*).

Calocarides capensis, new species
Fig. 2

Calastacus longispinis.—Stebbing, 1910: 367, non McArdle, 1901.

Calocaris (*Calastacus*) *longispinis.*—De Man, 1925:8 (part), non McArdle, 1901.—Barnard, 1950:503, fig. 93 d-f.

Calocaris longispinis.—Kensley, 1981:30, non McArdle, 1901.

Calocarides coronatus.—Sakai & de Saint Laurent, 1989:79, non Trybom, 1904.

Material examined.—Holotype, SAM-A940, ovigerous ♀ cl 19.0 mm (carapace damaged), R/V *Pieter Faure* 40 miles N79°E of Table Mountain, Cape of Good Hope, South Africa, 1280 m.

Diagnosis.—Carapace surface minutely pitted, especially posteriorly; rostrum with 5–6 lateral teeth; median carina well marked, unarmed; submedian carina bearing 1 or 2 spines; lateral carina with 3 or 4 spines. Abdominal pleura ventrally rounded, pleuron 2 widest. Telson with 1 pair of small spines dorsally, 3–4 small mobile spines at posterolateral corner, posterior margin gently convex between posterolateral and median spines.

Fig. 1. Distribution of species of *Calocarides*.

Maxilliped 3, merus with 4 spines on posterior margin; carpus with single small distal spine. Pereopod 1, larger cheliped, ischium with single strong distal spine; merus with strong spine at midlength of posterior margin, few small tubercles in proximal half, anterior margin with 5 distal spines; carpus with few low tubercles on anterior margin and few small tubercles on lateral surface; propodal palm slightly longer than fingers, outer surface with tiny scattered acute tubercles and strong ridge near posterior margin reaching almost to tip of fixed finger, anterior margin with about 11 strong spines, cutting margin of finger finely toothed, with large proximal tubercle; dactylus with few tubercles on anterior margin, cutting edge finely toothed, with proximal tubercle. Smaller cheliped, ischium with strong distal spine; merus with strong spine at midlength of posterior margin, anterior margin with 3 distal spines; carpus with few tubercles on anterior margin and lateral surface; propodal palm longer than fingers, lateral surface with few scattered small tubercles and ridge near posterior margin, anterior margin with about 11 spines; fixed finger and dactylus as in larger cheliped. Pereopod 2, ischium with few small spines and strong distal spine on posterior margin; merus with 3 widely spaced spines on posterior margin. Pleopod 1 consisting of single slender elongate ramus. Pleopods 2–5 each with appendix interna on mesial margin of endopod. Lateral uropodal ramus with single small spine on outer margin; suture bearing 4–8 irregular spines; mesial ramus with 4 spines on middorsal ridge.

Remarks.—See 'Remarks' after *Calocarides macphersoni.*

Etymology.—The specific name derives from the type locality, the Cape of Good Hope.

Calocarides coronatus (Trybom, 1904)

Euconaxius coronatus Trybom, 1904:384–390, pl. 20, figs. 1–10, 13, 14, pl. 21, figs. 1–8.

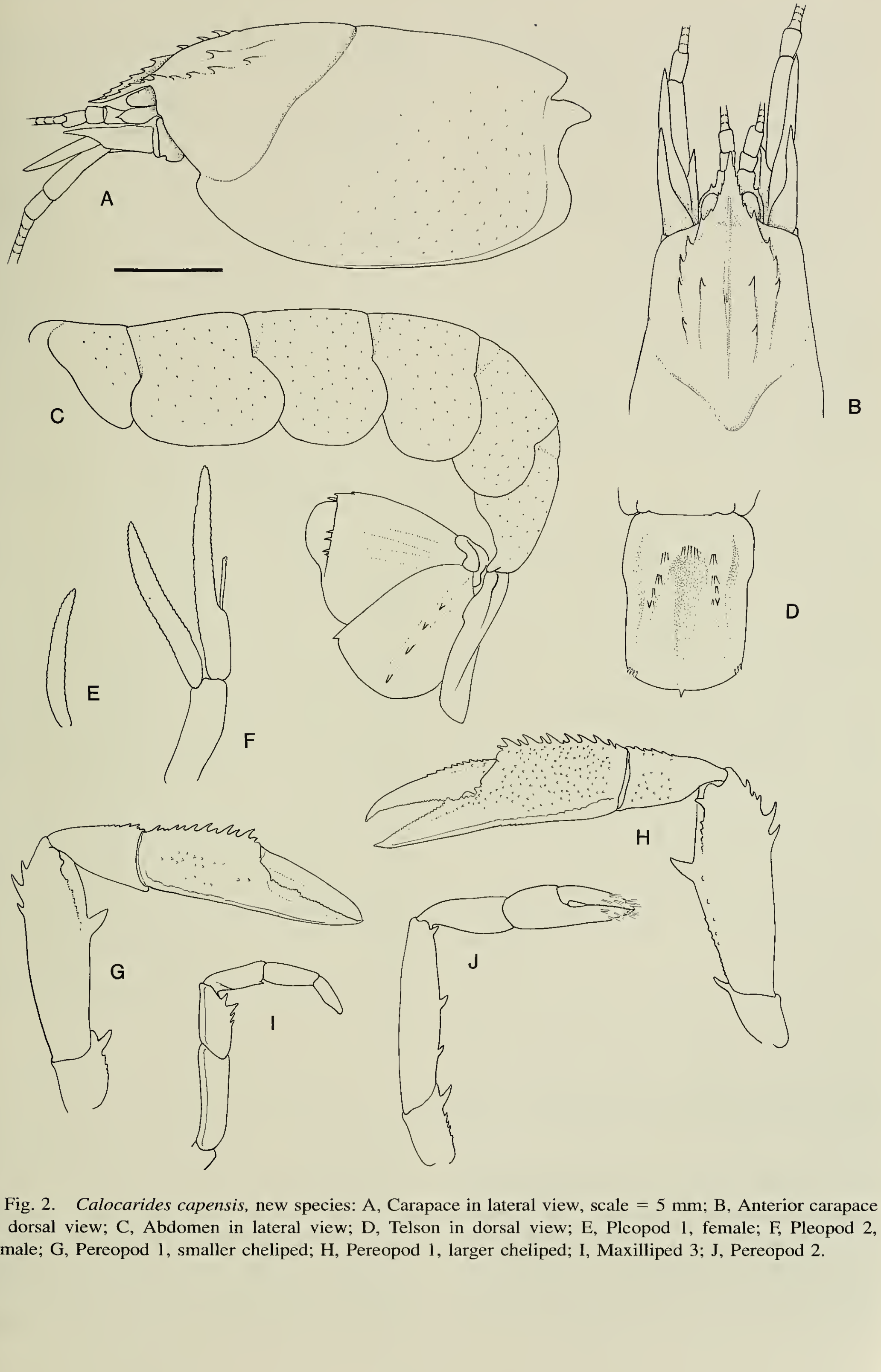

Fig. 2. *Calocarides capensis,* new species: A, Carapace in lateral view, scale = 5 mm; B, Anterior carapace in dorsal view; C, Abdomen in lateral view; D, Telson in dorsal view; E, Pleopod 1, female; F, Pleopod 2, female; G, Pereopod 1, smaller cheliped; H, Pereopod 1, larger cheliped; I, Maxilliped 3; J, Pereopod 2.

Calocaris (*Calocarides*) *coronatus.*—Wollebaek, 1908:3, 5, 13, 23.
Axiopsis (*Calocarides*) *coronatus.*—De Man, 1925:6, 67, 71.
Calocarides coronatus.—Bjorck, 1913:7.—Balss, 1925:209.—Poulsen, 1940:208, 216, fig. 4.—Bouvier, 1940:97.—Christiansen, 1955:1–4; 1972:40, fig. 45.—Elofsson, 1959:3–9, figs. 1–20.—Brattegard, 1966:45–52.—Sakai & de Saint Laurent, 1989:4, 80, 101, fig. 20.
Euconaxius crassipes Trybom, 1904:390–391, pl. 20, figs. 11, 12.
Calocaris (*Calocarides*) *crassipes.*—Wollebaek, 1908:3, 5–13, 17, 23, pl. 1–7.
Axiopsis (*Calocarides*) *crassipes.*—De Man, 1925:6, 67, 71.

Material examined.—UBZM 50400, ♂ cl 14.8 mm, Sorfjord, Norway, 60°11′N, 6°34′E, 589–600 m.—UBZM 49598, 4 ♂ cl 13.5, 13.9, 15.5, 15.5 mm, Kvinnheradfjord, Norway, 59°56′N, 5°45′E, 512 m.—UBZM 49595, ♀ cl 14.0 mm, Kvinnheradfjord, Norway, 59°59′N, 5°53′E, 660–670 m.—UBZM 50461, ovigerous ♀ cl 14.4 mm, Osafjord, Norway, 60°40′N, 6°55′E, 300.—UBZM 49589, Alfjord, Norway, 59°41′N, 5°34′E, 450–465 m.—UBZM, ovigerous ♀ cl 16.1 mm, Fusafjord, Norway, 60°12′N, 5°45′E, 240 m.—UBZM 49591, ♂ cl 15.1, ♀ cl 15.2 mm, Bomlafjord, Norway, 59°40′N, 5°22′E, 360 m.

Distribution.—From Malangenfjord, northern Norway, to southwestern Sweden, 80–700 m.

Diagnosis.—Carapace surface smooth. Rostrum with 4 pairs of lateral teeth, continuous with lateral carina bearing 3 teeth; median carina with 1 tooth anterior to tubercle; submedian carina bearing 2 teeth. Abdominal pleuron 1 ventrally narrowly rounded; pleuron 2 broadly rounded; pleura 3–5 rounded, with 1 or 2 small teeth on anterior margin. Telson with 5 or 6 lateral teeth, 2 mobile spines at posterolateral angle; posterior margin evenly convex, with median tooth; 1 or 2 small spines proximodorsally on rounded ridge.

Antennal scaphocerite reaching distal margin of peduncle article 4. Maxilliped 3, merus with 4 spines on posterior margin, 3 more distal spines large; carpus with small distal spine on posterior margin. Pereopod 1, larger cheliped: ischium with row of acute tubercles on posterior margin, distalmost a large spine; merus with posterior surface expanding distally, mesial and lateral margin defined by row of small acute tubercles, mesial margin with strong spine at about midlength, anterior margin bearing 1 strong spine and few blunt tubercles; carpus bearing small tubercles dorsodistally; fingers slightly more than half length of propodal palm, latter with lateral and most of mesial surface tuberculate, fixed finger with triangular tooth at about midlength of cutting edge; fingers widely gaping, dactylus downcurved, strongly tuberculate, with 1 or 2 stronger tubercles on cutting edge. Smaller cheliped: ischium, merus, and carpus as in larger cheliped; propodal palm with lateral and mesial surface tuberculate, tubercles along anterior margin forming spines, fingers about ⅔ length of palm, fixed finger with blunt proximal triangular tooth followed by regularly spaced small teeth; dactylus with row of spines along anterior margin, cutting edge with regularly spaced small teeth. Pereopod 2, ischium and basis each with single posterodistal spine; merus with 3 evenly spaced spines on posterior margin. Lateral uropodal ramus with about 18 spines along suture, 2 small distal spines on lateral margin; mesial ramus with single distolateral spine, dorsal ridge bearing 5 or 6 spines.

Calocarides macphersoni, new species
Fig. 3

Calastacus longispinis.—Macpherson, 1983:45, fig. 26; 1991:405, non McArdle, 1901.

Material examined.—Holotype, USNM 243561, ♂ cl 20.4 mm, R/V *Benguela II* sta 66, off Namibia, 20°55′S, 12°23′E, 475–480 m, 9 Sep 1980.—Paratypes, USNM

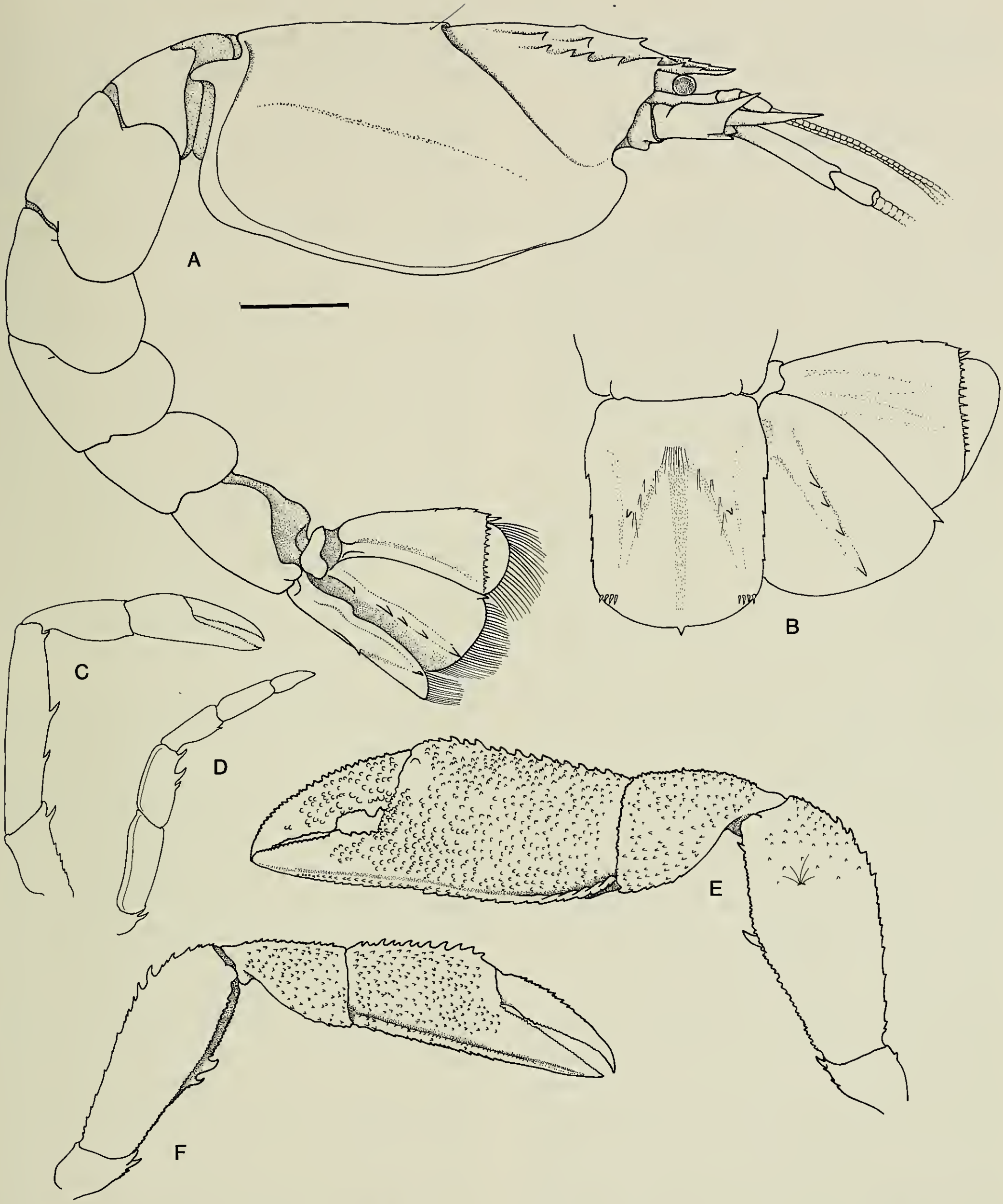

Fig. 3. *Calocarides macphersoni,* new species: A, Lateral view, scale = 5 mm; B, Telson and right uropod in dorsal view; C, Pereopod 2; D, Maxilliped 3; E, Pereopod 1, larger cheliped; F, Pereopod 1, smaller cheliped.

243562, ♂ cl 17.8 mm, R/V *Benguela II* sta 66, off Namibia, 20°55′S, 12°23′E, 475–480 m, 9 Sep 1980.—Paratype, ICMB, R/V *Benguela II* sta P-37, ♂ cl 21.5 mm, off Namibia, 21°33′S, 12°39′E, 380–390 m, from stomach of scorpaenid fish *Helicolenus* sp.—Paratypes, ICMB, R/V *Benguela II* sta P-66, 2 ♂ cl 20.3 mm, one damaged, off Namibia, 20°55′S, 12°23′E, 475–480 m.—Paratypes, ICMB, R/V *Benguela IV* sta P-95, 2 ♂ cl 21.0 mm, 21.2 mm, off Namibia, 20°42′S, 12°14′E, 410–417 m, one specimen from stomach of ray *Raja confundens,* one from stomach of scorpaenid fish *Helicolenus* sp.

Diagnosis.—Rostrum with 2–3 pairs of lateral teeth; median carina with single tooth anterior to tubercle, entire posterior to tubercle; submedian carina poorly defined, with 1 or 2 teeth; lateral carina with 3–5 teeth posterior to supraocular. Carapace surface smooth. First abdominal pleuron ventrally narrowly rounded, pleura 2–6 broadly rounded, small spine on anterior margin of pleura 3–6. Telson with 5 small fixed spines in posterior half of lateral margin, 3–4 small mobile spines mesial to posteriormost lateral spine; posterior margin gently convex between lateral spine and median spine; dorsal surface with one pair of small fixed spines.

Maxilliped 3, posterior margin of ischium unarmed; merus with 3–4 strong distal spines and 2–3 tiny more proximal spines on posterior margin; carpus with small posterodistal spine. Pereopod 1: larger chela, ischium with row of small denticles and single strong spine along posteromesial margin, small distal spine on anterior margin; merus with posteromesial surface tuberculate, having single strong tooth at about midlength, anterior margin with about 5 small spines and several small tubercles; outer and upper surface of carpus evenly tuberculate; propodal palm about ⅕ longer than fingers, entire surface evenly and fairly densely tuberculate, posterior margin with tuberculate carina extending onto fixed finger, anterior margin with row of somewhat larger tubercles; fingers proximally widely gaping, distally meeting, fixed finger with proximal half of cutting edge having few low rounded tubercles, distal half straight, bearing numerous small rounded teeth; surface of dactylus tuberculate, cutting edge as in fixed propodal finger. Smaller chela, ischium with few small spines and single strong spine on posterior margin, single distal spine on anterior margin; merus with row of small tubercles along posteromesial margin with 1 or 2 strong spines at about midlength, row of small tubercles along posterolateral margin, anterior margin with row of irregularly large and small spines and tubercles; outer and upper surface of carpus fairly densely tuberculate; propodal palm about ⅕ longer than fingers, posterolateral carina feebly tuberculate, extending almost to apex of fixed finger, outer and upper surfaces tuberculate, anterior margin with double row of large and small spines and tubercles; cutting margins of fixed propodal finger and dactylus only slightly excavate proximally, remainder of margin bearing row of small evenly-spaced teeth. Pereopod 2, posterior margin with row of small spines and single strong distal tooth; posterior margin of merus with 2–4 spines. Lateral uropodal ramus with 2 or 3 small distal spines on lateral margin, single mobile spine mesial to distalmost, transverse suture armed with row of 13–15 small spines; mesial ramus with single distal spine, dorsal ridge with irregular row of about 8 small spines.

Remarks.—From McArdle's (1901) description, and Alcock & McArdle's illustrations (1902, pl. 57, figs. 2, 2a), and De Man's (1925:118) key, the Bay of Bengal species *Calastacus longispinis* lacks spines on the anterior median carina, has five spines on the free lateral margins of the rostrum, and three spines on the submedian carina. The antennal scaphocerite reaches almost to the end of peduncle article 4. The single female lacked both chelipeds of pereopod 1. Given that the Namibian material has a strong spine anterior to the tubercle on the median carina, and that the antennal scaphocerite reaches only to the distal third of peduncle article 4, it seems unlikely that the Atlantic and Indian Ocean specimens are the same species, especially considering the considerable geographical separation.

The species described above as *Calocarides capensis,* differs from *C. macphersoni* in having more slender and less granular chelipeds of pereopod 1, with relatively more elongate spines on the anterior margin of the propodal palm; in having fewer but stronger distal spines on the anterior margin of the merus of pereopod 1; in having far fewer spines on the suture of the lateral ramus of the uropod; and in having a more elongate telson.

Major differences between *C. coronatus* and *C. macphersoni* are seen in the size (cl ovigerous ♀ 13.5–16.1 mm vs. cl ovigerous ♀ 17.8–25.0 mm resp.), and in the more spinose upper margin of the merus in *C. macphersoni.*

The species described as *Axius* (*Neaxius*) *laevis* by Bouvier (1915) from 698 m off Cape Bojador, Spanish Sahara, West Africa, (holotype, MNHN, ♀ cl 5.1 mm) was synonymized with *C. coronatus* by Sakai & de Saint Laurent (1989:81, fig. 21). The latter authors illustrated the single damaged specimen of *C. laevis,* the caption of their illustration erroneously referring to *Eiconaxius laevis.* Given the damaged condition of the specimen, and the fact that it lacks spines on the submedian carina, has an antennal scaphocerite shorter than in *C. coronatus,* has pereopod 1 lacking the fine tuberculation of the propodus and the anterior spination of the merus of *C. coronatus,* and a telson longer and narrower than in *C. coronatus,* it seems unlikely that the West African species is synonymous with *C. coronatus,* or indeed, that it is a species of *Calocarides.* From the figure of *Calocarides rudolfi* (Zarenkov, 1989, fig. 3) from Angola, several differences in spination suggests that it differs from *C. macphersoni.* In *C. rudolfi,* the merus of maxilliped 3 bears more elongate and numerous spines, and the merus of both chelae of pereopod 1 has larger and more numerous anterodistal and posterodistal spines than in the Namibian species; the carpus of pereopod 2 bears a posterodistal spine, and the telson bears two pairs of fixed dorsal spines, while *C. macphersoni* lacks a carpal spine on pereopod 2 and the telson bears a single pair of fixed spines. Posterolateral mobile spines on the telson were not illustrated for the Angolan species; *C. macphersoni* bears four such spines on each side.

Etymology.—The species is named for carcinologist Dr. Enrique Macpherson of Barcelona, Spain, who made the material from Namibia available for study.

Calocarides quinqueseriatus
(Rathbun, 1902)
Figs. 4, 5

Calastacus quinqueseriatus Rathbun, 1902: 887.—Schmitt, 1921:113, fig. 76.—Balss, 1925:209.

Calocaris (*Calastacus*) *quinqueseriata.*—De Man, 1925:8, 118.

Calocarides quinqueseriatus.—Sakai & de Saint Laurent, 1989:79, 103.

Material examined.—Syntypes, USNM 25240, 9 ♂ cl 15.5–22.7, 2 ovigerous ♀ cl 15.4, 18.2, 3 ♀ cl 17.5–19.4, 19.4, R/V *Albatross* sta 3196, San Luis Obispo Bay, California, green mud, 366 m.—USNM 28321, 5 ♂, cl 13.5–21.6, 1 ovigerous ♀ cl 16.9 mm, 9 ♀ cl 15.1–20.5, R/V *Albatross* sta 2909, Santa Barbara Channel, California, 375 m, green mud.—USNM 152525, 22 ♂ cl 18.9–26.0, 9 ovigerous ♀ 20.0–23.3, 11 ♀ cl 21.0–23.0, R/V *Albatross* sta 4436, San Miguel Island, California, 483–496 m, green mud.—USNM 28325, 16 ♂, cl 11.3–18.0, 1 ovigerous ♀ cl 24.0, 7 ♀ cl 10.2–19.2, R/V *Albatross* sta 3195, San Luis Obispo Bay, California, 461 m, green mud.—USNM 28236, 5 ♂ cl 14.8–24.0, 4 ♀ cl 13.0–22.5, R/V *Albatross* sta 3198, off Point Conception, California, 508 m, green mud.—USNM 28327, 7 ♂ cl 12.9–20.5, 3 ovigerous ♀ cl 19.0–20.0, 6 ♀ cl 10.3–19.5, R/V *Albatross* sta 3199, Santa Barbara Channel, California, 426 m, green mud.—USNM 28232, ♂ cl 18.0, 2 ♀ cl 21.0, 21.9 R/V *Albatross* sta 3187, off Point Sur, California, 545 m, brown and grey ooze.—USNM 28320, ♂ cl 20.3, ♀ cl 17.2, R/V *Albatross* sta 2892, off Point Conception, California, 520 m, yellow mud.—USNM 28528, 2 ♂, cl 18.1, 24.1, R/V *Albatross* sta 3200, Santa Barbara Channel, California, 485 m, green mud.—USNM 28319, 1 ♂ cl 19.0, 1 ♀ cl 12.1, R/V *Albatross* sta 2891, off Point Conception, California, 426

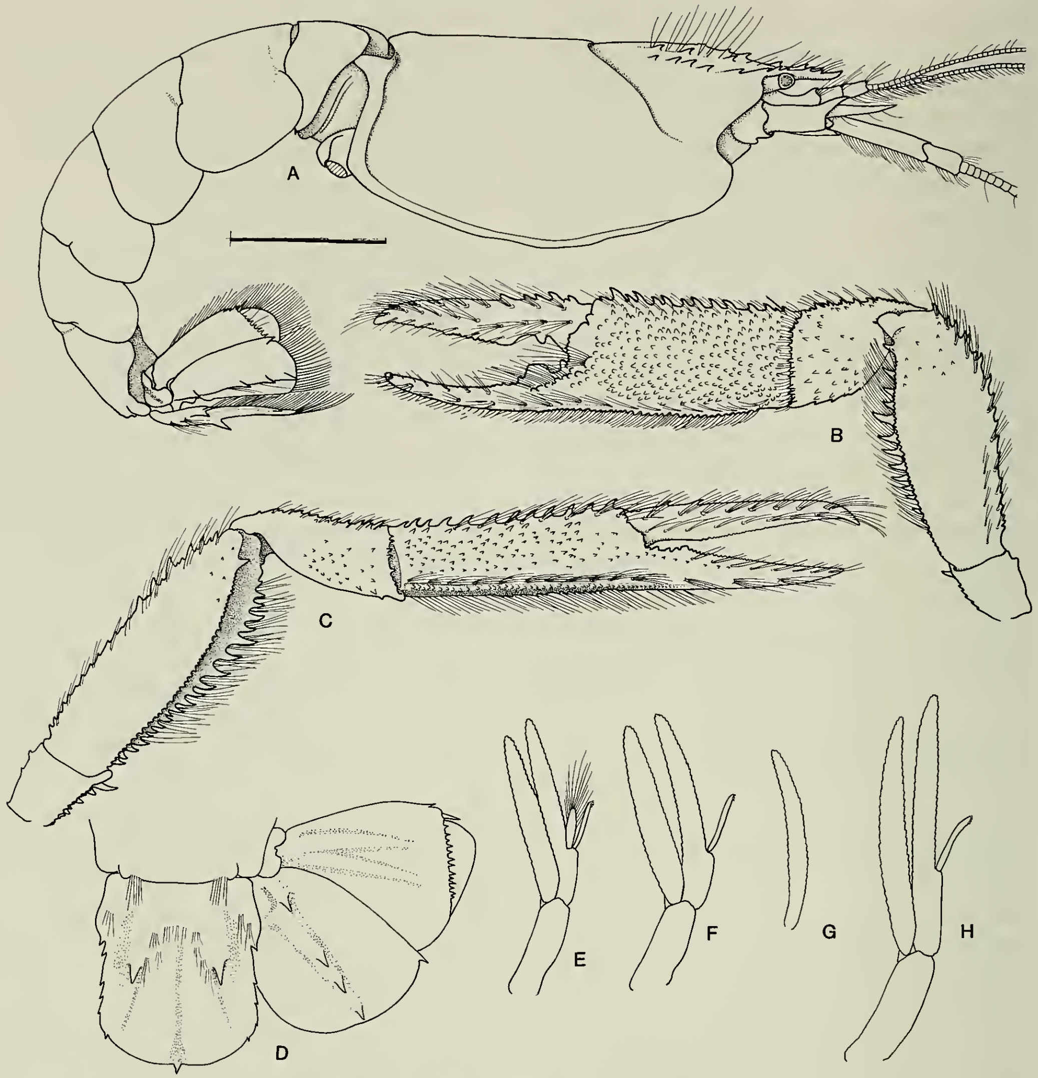

Fig. 4. *Calocarides quinqueseriatus*: A, Lateral view, scale = 10 mm; B, Pereopod 1, larger cheliped; C, Pereopod 1, smaller cheliped; D, Telson and right uropod in dorsal view; E, Pleopod 2, male; F, Pleopod 3, male; G, Pleopod 1, female; H, Pleopod 2, female.

m, brown ooze.—USNM 120119, ♀ cl 18.2, R/V *Commando* sta, mouth of Columbia River, Oregon, 732 m.—USNM 28324, ♂ cl 17.5, ♀ cl 15.0, R/V *Albatross* sta 3193, off San Simeon Bay, California, 293 m, green mud.—USNM 28329, ovigerous ♀ cl 19.5, R/V *Albatross* sta 3201, Santa Barbara Channel, California, 512 m.—USNM 28322, ♂ cl 17.4, R/V *Albatross* sta 2979, off Anacapa Island, California, 710 m, green mud.—USNM 53021, ♀ cl 16.2, R/V *Albatross* sta 4425, off San Nicolas Island, California, 2013 m, green mud, fine sand, globigerina ooze.—USNM 155735, ♂ cl 20.5, R/V *Albatross* sta 4387, off San Diego, California, 1830 m, green mud.—USNM 243350, ovigerous ♀ damaged, R/V *Commando* sta, SW mouth of Columbia River, Oregon, 1556 m.—USNM 243351, ♂ cl 18.4, R/V *Commando* sta, SW mouth

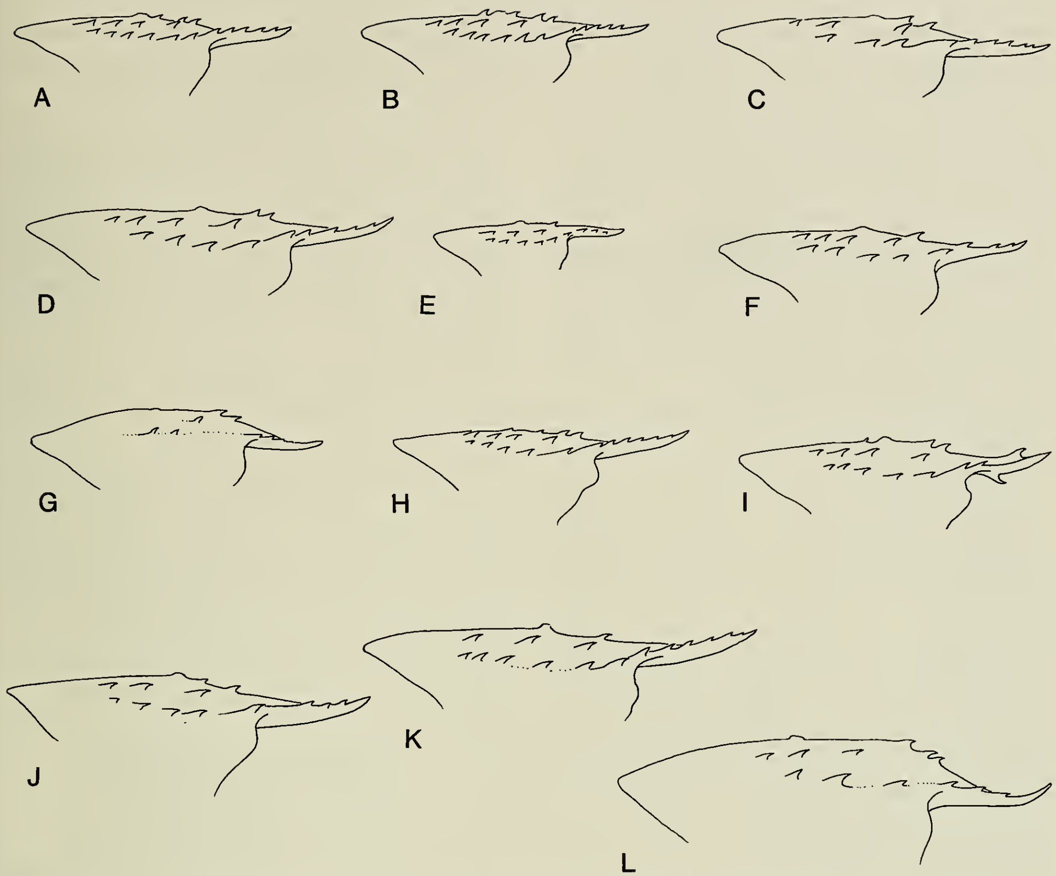

Fig. 5. *Calocarides quinqueseriatus,* variation in rostral and anterior carapace spination: A, Syntype, ovigerous female, San Luis Obispo Bay, California, cl 15.4 mm; B, Syntype, ovigerous female, San Luis Obispo Bay, California, cl 18.2 mm; C, Ovigerous female, San Miquel Is., California, cl 22.0 mm; D, Ovigerous female, San Miguel Is., California, cl 23.3; E, Female, Baja California, cl 12.0 mm; F, Female, Baja California, 20.7 mm; G, Male, Columbia River mouth, Oregon, 18.2 mm; H, Syntype, male, San Luis Obispo Bay, California, cl 19.1 mm; I, Syntype, male, San Luis Obispo Bay, California, cl 20.9 mm; J, Male, San Miguel Is., California, 24.2 mm; K, Male, San Miguel Is., California, cl 26.0 mm; L, Male, Columbia River, Oregon, cl 27.2 mm.

of Columbia River, Oregon, 1373 m.—USNM 243352, ♀ damaged, R/V *Commando* sta, SW mouth of Columbia River, Oregon, 1556 m.—USNM 243353, ♂ cl 17.3, 2 ♀ damaged, R/V *Commando* sta, SW mouth of Columbia River, Oregon, 1922 m.—USNM 243354, ♀ damaged, R/V *Commando* sta, SW mouth of Columbia River, Oregon, 1556 m.—USNM 155737, ♀ cl 20.0, R/V *Albatross* sta 5675, San Cristobal Bay, Baja California, 520 m.—USNM 155736, 2 ♂ cl 19.8–21.0, R/V *Albatross* sta 4433, off Santa Rosa Island, California, 445 m, green mud.—USNM 243355, 2 ♂ cl 16.5, 2 ♀ cl 13.8–15.0, R/V *Albatross* sta 4351, NE of Point Loma, California, 774 m, soft green mud.

Diagnosis.—Carapace smooth; 5–6 pairs rostral teeth including small supraocular; median carina with 1–4 spines anterior to tubercle, 1–2 posterior; 1–5 spines on submedian carina; 3–7 spines on lateral carina. Abdominal pleuron 1 with ventral spine usually present; pleuron 2 ventrally rounded; pleura 3–6 rounded with spine on anterior margin. Telson with lateral margin having 5–6 small spines; 1 pair spines on dorsal surface.

Maxilliped 3, ischium with about 10 small spines on posterior margin; merus with 5–6 small proximal spines, 3 large distal spines on posterior margin. Pereopod 1, larger (broader) cheliped: ischium with 1 strong distal and several small proximal spines on posterior margin; merus with inner and outer row of tiny tubercles flanking posterior row of about 17 strong spines, outer surface distally with few scattered tiny tubercles, upper (anterior) margin with irregular row of spines, distal spines largest; carpus with outer surface and distal margin bearing scattered acute tubercles; upper propodal palm subequal in length to fingers, posterior margin of palm and fixed finger a denticulate carina, upper (anterior) margin with about 14 strong spines, mesial and lateral surfaces of palm fairly densely granular/tuberculate, fixed finger with broad tubercle on proximal cutting edge, distally denticulate; dactylus cutting edge with proximal tubercle, distally denticulate, upper margin with several proximal spines. Pereopod 1, smaller (narrower) cheliped: ischium, merus, and carpus as in larger cheliped; upper propodal palm subequal in length to fingers, tuberculation as in larger cheliped, cutting edge of fixed finger with few small tubercles proximally, remainder of edge finely denticulate; dactylus, cutting edge finely denticulate, with about 2 spines on upper margin. Pereopod 2, ischium with 6 small spines on posterior margin; merus with 5 small proximal spines, single strong distal spine. Pleopod 1 in female a slender elongate ramus; pleopod 2 in male with rod-shaped appendix masculina bearing distal setae, slightly shorter than appendix interna; pleopods 2–5 in female, 3–5 in male with appendix interna at about proximal third of mesial margin of endopod. Uropod with lateral ramus having 2 small distal spines on lateral margin, single mobile submarginal spine; about 14 spines along suture; mesial ramus with single distolateral spine, 4 spines on dorsal surface.

Size ranges.—Male, maximum carapace length 26.0 mm; ovigerous females, carapace length 15.4–24.0 mm.

Remarks.—There is considerable variation in the spination of the anterior carapace (Fig. 5) and the chelipeds of pereopod 1 of this species, often made more marked either by injuries to the chelae that have healed, or by loss and regeneration of the chelipeds, resulting in a range of cheliped proportions and armature.

The majority of specimens have been taken from soft bottom sediments, especially from green mud.

The species recorded as *Calastacus quinqueseriatus* from 1150 m off Japan (Kobjakova 1937:142, pl. 2, fig. 8) appears to have the first pereopod chelae relatively shorter, more robust, and less granular than in true *C. quinqueseriatus*. It thus seems unlikely that the Japanese species is conspecific with the California/Oregon species.

Calocarides rostriserratus
Andrade & Baez, 1977
Fig. 6

Calastacus rostriserratus Andrade & Baez, 1977:65, fig. 1.

Calocarides quinqueseriatus.—Sakai & de Saint Laurent, 1989:78, 79, 103, non Rathbun, 1902.

Material examined.—USNM 173366, 4 ♂ cl 15.3 mm, 15.3 mm, 16.3 mm, 17.0 mm, 2 ♀ cl 14.5 mm, 15.9 mm, off Tumbes, Peru, 3°33.8′S, 81°01.4′E, 576 m, 28 Aug 1979.—USNM 243392, ♀ cl 16.1 mm, R/V *Gilliss* sta GS-22, Gulf of Panama, 7°28′N, 79°12′W, 825 m, 18 Jan 1972.

Diagnosis.—Carapace smooth; rostrum with 5–6 pairs of lateral teeth including small supraocular; 2 median carina teeth plus tubercle; 4–5 teeth on submedian carina; 4–6 teeth on lateral carina. Abdominal pleura 2–5 ventrally rounded. Telson with 2–3 pairs small lateral spines, 2 small distal mobile spines at posterolateral angle, 2 pairs spines on dorsal surface.

Maxilliped 3, ischium with 5 small prox-

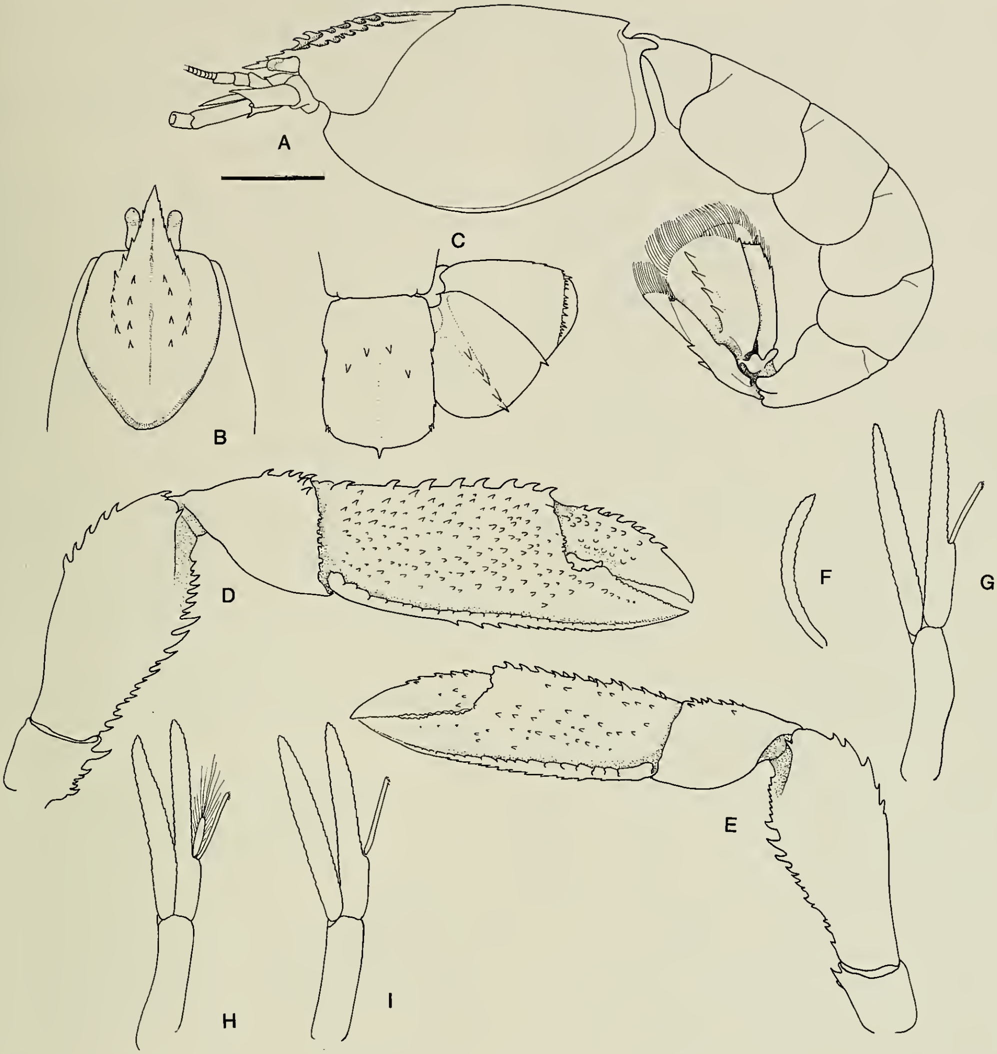

Fig. 6. *Calocarides rostriserratus*: A, Lateral view, scale = 5 mm; B, Anterior carapace in dorsal view; C, Telson and right uropod in dorsal view; D, Pereopod 1, larger cheliped; E, Pereopod 1, smaller cheliped; F, Pleopod 1, female; G, Pleopod 2, female; H, Pleopod 2, male; I, Pleopod 3, male.

imal teeth on posterior margin, distal margin entire; merus with 2 strong distal teeth on posterior margin. Pereopod 1, larger (broader) cheliped, ischium with about 5 small proximal and single strong distal spine on posterior margin; merus with 5 distal spines on upper (anterior) margin, posterior margin with single row of spines of varying length, those at about midlength longest; carpus with several (6–7) small spines on upper surface; upper propodal palm 1.2 times length of fingers, bearing row of 8 strong spines, lower border consisting of flattened distally narrowed ridge having dentate margins, medial and lateral surfaces bearing moderately dense scattered conical tubercles, cutting edge of fixed finger having rounded proximal cusp; dactylus with upper margin bearing about 8 strong spines, cutting edge having rounded proximal cusps, distally finely denticulate. Pereopod 1, smaller (narrower) cheliped, ischium with 2–3 small proximal and single strong distal spine on posterior margin; merus with 5–6 strong distal spines on anterior (upper) margin, single row of spines along posterior (lower) margin, those at about midlength longest; carpus with 8–10 spines on upper surface; upper propodal palm about 1.2 times length of fingers, bearing irregular row of about 12 spines, lower border formed by flattened ridge with dentate margins, inner and outer surfaces bearing scattered acute conical tubercles; dactylus with several small spines on upper surface, cutting edge more or less evenly denticulate. Pereopod 2, basis with single spine on posterior surface; ischium with proximal and one or 2 stronger distal spine on posterior margin; merus with 3 or 4 spines in midregion of posterior margin. Pleopod 1 in female a slender elongate ramus; pleopod 2 in male with rod-shaped appendix masculina bearing distal setae, noticeably shorter than appendix interna; pleopods 2–5 in female, 3–5 in male with appendix interna at about proximal third of mesial margin of endopod. Uropod with lateral ramus having 2–3 small lateral spines plus distal submarginal mobile spine; about 13 spines along suture; mesial ramus with single distal marginal spine, 4–5 spines on upper surface.

Remarks.—In spite of Sakai & de Saint Laurent's (1989:80) statement that *C. rostriserratus* is probably a synonym of *C. quinqueseriatus, Calocarides rostriserratus* differs from *C. quinqueseriatus,* its geographically nearest congener, in several easily seen features: in having two pairs of dorsal telsonic spines (one pair in *C. quinqueseriatus*), and two or three lateral telsonic spines (five or six in *C. quinqueseriatus*); and in having the chelae of pereopod 1 broader and less elongate, and with spines only in the distal half of the anterior margin of the merus (full anterior margin of merus bearing spines in *C. quinqueseriatus*).

Calocarides soyoi (Yokoya, 1933)

Axius soyoi Yokoya, 1933:49, fig. 25.—Horikoshi et al., 1982:30, 33, 38, 39, 120, 145, 168.

Axiopsis (*Axiopsis*) *soyoi.*—Sakai, 1987: 303.

Calocarides soyoi.—Sakai & de Saint Laurent, 1989:4, 83, 103.—Kensley & Komai, 1992:81, fig. 1.

Material examined.—USNM 243563, 2 ♀ cl 12.0 mm, 15.0 mm, ovigerous ♀ cl 17.9 mm, off Fukushima Prefecture, Japan, 37°04′N, 141°31.7′E, 270 m.—USNM 243564, ♂ cl 14.2 mm, ovigerous ♀ cl 18.8 mm, ♀ cl 11.8 mm, off Hachinohe, Aomori Prefecture, Japan.—HUMZ-C990, 3 ♀ cl 11.3 mm, 14.1 mm, 13.0 mm, off Hachinohe, Aomori Prefecture, Japan, 42°52.6′N, 145°22.2′E, 152 m.—HUMZ-C994, ♀ cl 16.9 mm, off Fukushima Prefecture, Japan, 37°17.3′N, 141°21.4′E, 141 m.—HUMZ-C998, 3 ♂ cl 12.4 mm, 15.0 mm, 15.3 mm, off Fukushima Prefecture, Japan, 37°04′N, 141°31.7′E, 270 m.

Remarks.—This species was recently redescribed and figured by Kensley & Komai (1992).

Calocarides spinulicauda
(Rathbun, 1902)
Fig. 7

Axius spinulicauda Rathbun, 1902:886; 1904:149, fig. 90.

Axiopsis spinulicauda.—Schmitt, 1921:111, fig. 74.—Butler, 1961:60, figs. 1, 2, pl. 1.

Axiopsis (*Axiopsis*) *spinulicauda.*—De Man, 1925:6, 67, 69.

Acanthaxius spinulicaudus.—Sakai & de Saint Laurent, 1989:4, 66, 103.

Material examined.—Holotype, USNM 25239, ♀ cl 15.5 mm, R/V *Albatross* sta 3172, off Bodega Head, California, 113 m.

Diagnosis.—Carapace surface smooth; rostrum with 5 (left) and 6 (right) lateral teeth, including supraocular; median carina barely reaching onto base of rostrum, with 3 spines anterior of tubercle, entire posterior to tubercle; postcervical median carina obsolete except close to posterior margin of carapace; submedian carina short, entire; lateral carina entire posterior to supraocular

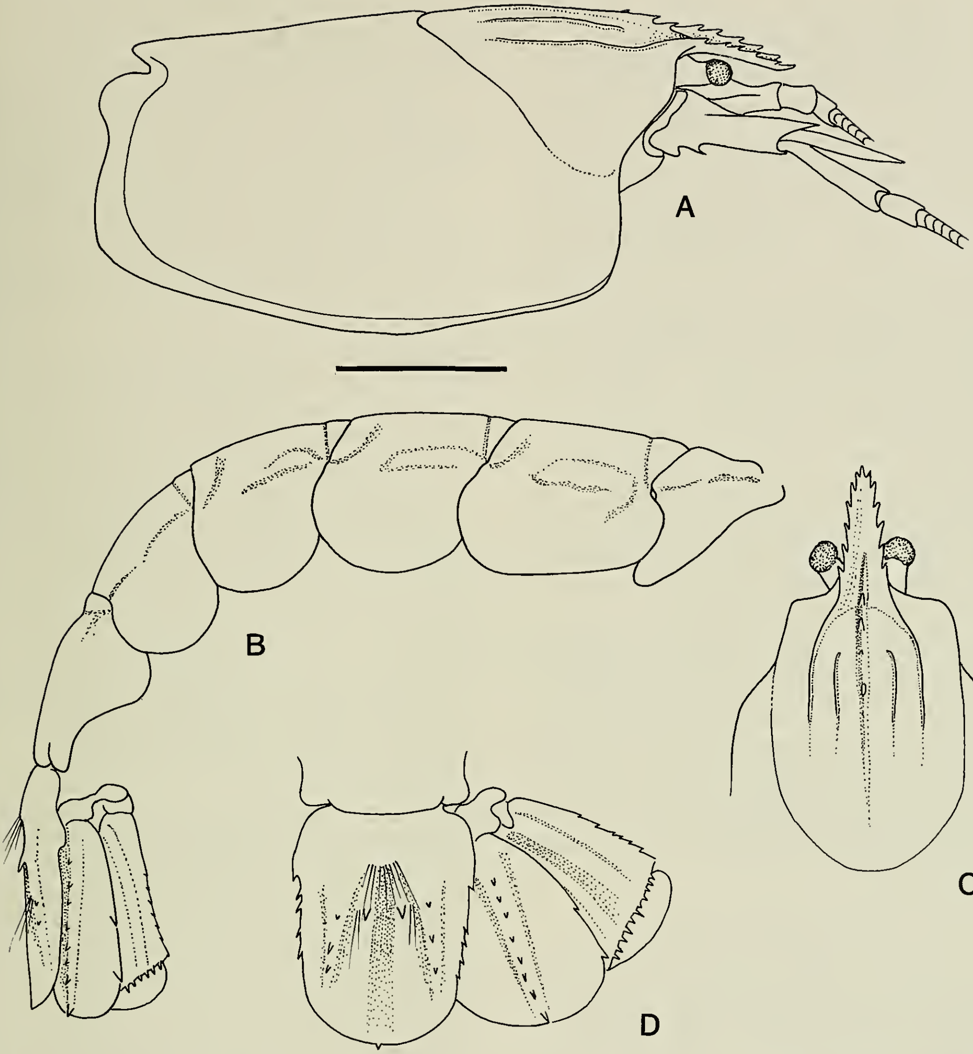

Fig. 7. *Calocarides spinulicauda*: A, Carapace in lateral view, scale = 5 mm; B, Abdomen in lateral view; C, Anterior carapace in dorsal view; D, Telson and right uropod in dorsal view.

spine of rostral series. First abdominal pleuron ventrally narrowed apically rounded with tiny denticle; pleura 2–6 broadly rounded. Telson with lateral margin bearing larger fixed anterior spine, 4–5 small more posterior fixed spines; posterior margin evenly convex; submedian longitudinal ridge bearing 3 fixed spines, pair of fixed anterior spines mesial to longitudinal ridge present.

Maxilliped 3, ischium with 1 or 2 tiny denticles on posterior margin; merus with 3 distal spines on posterior margin. Pereopod 1, both chelipeds missing. Pereopod 2, merus with 2 or 3 well separated spines on posterior margin. Lateral uropodal ramus with 7 small distal spines on lateral margin, transverse suture with row of 11–12 small spines; mesial ramus with 2 strong spines on lateral margin, dorsal ridge with 7 or 8 small fixed spines.

Remarks.—Rathbun (1902), in her description of *A. spinulicauda,* noted that the chelae of the first pereopod were missing.

Butler (1961) figured both chela of pereopod 1, from material from British Columbia. While the lateral and mesial faces of the propodal palm do not appear to be tuberculate, as is characteristic of *Calocarides,* the spination of the dactyli, propodi, carpi, and meri are characteristic of this genus. *Calocarides spinulicauda,* however, disagrees with *Calocarides* in lacking spination on the lateral and submedian carinae. Sakai & de Saint Laurent (1989) placed this species in their new genus *Acanthaxius,* which is characterized by a tendency to having a double cornea, and a lack of pleurobranchs, neither of which are seen in *C. spinulicauda.* With only the female holotype available for examination, the nature of the male pleopods and the first pereopods being uncertain, unambiguous generic placement is almost impossible.

Axius spinulicauda amurensis Kobjakova, 1937, (see also Derjugin & Kobjakova 1935:142), described from the Sea of Japan, while clearly not a subspecies of the Californian *Calocarides spinulicauda* Rathbun, 1902, is difficult to place generically, given the single small figure and the abbreviated description.

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I thank Dr. Enrique Macpherson of the Instituto Ciencias del Mar, Barcelona, Mrs. Michelle van der Merwe of the South African Museum, and Dr. A. Fosshagen of the Zoological Museum, Bergen, for the loan of material. The paper was considerably improved by the comments and suggestions of Dr. Rafael Lemaitre and anonymous reviewers, to whom I am very grateful.

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A new species of the axiid shrimp genus *Acanthaxius* from the Caribbean (Crustacea: Decapoda: Thalassinidea)

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Abstract.—*Acanthaxius kirkmilleri* is described from slope depths (420–440 m) in the Caribbean Sea off Anguilla, and is the first unambiguous record of the genus in the Atlantic. The species is characterized by a slender rostrum longer than the eyestalks, highly spinose and relatively slender chelipeds of pereopod 1, and seven spines on the suture of the lateral uropodal ramus.

A single female specimen of a distinctive axiid shrimp was collected by the R/V *John Elliott Pillsbury* in 1969, off Anguilla. The specimen is described here, as part of a series of papers documenting the diversity of the Axiidae in the western Atlantic, and is deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Family Axiidae
Genus *Acanthaxius*
Sakai & de Saint Laurent, 1989

Acanthaxius Sakai & de Saint Laurent, 1989:4, 12, 14, 66.—Poore, 1994:98 [key].—Sakai, 1994:192.

Type species.—By original designation, *Axiopsis* (*Axiopsis*) *pilocheira* Sakai, 1987. Type locality: off Honshu Island, Japan, 360 m. Gender: Masculine.

Diagnosis.—Gonochoristic. Rostrum at same level as anterior carapace, narrow, lateral margins dentate; carapace glabrous to faintly rugose; with median, submedian and lateral carinae dentate; post-cervical carina absent. Eye with cornea pigmented; eyestalk relatively elongate. Antennal scaphocerite (acicle) just reaching distal margin of peduncle article 4, slightly arcuate. Maxilliped 3, exopod not clearly bent; ischial crest well developed. Pereopod 1, chelipeds asymmetrical, with spines on anterior (upper) margin of propodal palm and dactylus. See Table 1 for branchial formula. Pleopodal rami slender; pleopod 1 in female uniramous; pleopods 2–5 with appendix interna. Lateral uropodal ramus with transverse suture. Telson longer than wide, with dorsal submedian fixed spines (Table 1).

Remarks.—The definition of this genus contains some uncertainties, as the type species, *A. pilocheira* Sakai, 1987, is known only from the holotypic female. Important characters of pleopods 1 and 2 of the male are is thus unknown, although the absence of pleopod 1 was deduced from other species placed in the genus. Three of the species assigned to this genus by Sakai & de Saint Laurent (1989) and Sakai (1994), *A. caespitosa* (Squires, 1979), *A. hirsutimana* (Boesch & Smalley, 1972), and *A. spinosissimus* (Rathbun, 1906), do not fit the generic definition, in that all three have pleopod 1 of the male present, and the carapace is covered with granules, both features more characteristic of *Oxyrhynchaxius* Parisi, 1917. The species *A. spinulicauda* (Rathbun, 1902), also included in *Acanthaxius* Sakai & de Saint Laurent, 1989, is clearly a species of *Calocarides* Wollebaek, 1908. The use of the post-cervical carina, present in some species, absent in others, also needs reassessment as a diagnostic character.

The advanced characters of the genus

Table 1.—Branchial formula for *Acanthaxius pilocheira*. r = reduced.

	Maxillipeds			Pereopods				
	1	2	3	1	2	3	4	5
Exopod	1	1	1	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	r	r	r	r	r	—	—
Arthrobranch	—	—	2	2	2	2	2	—
Pleurobranch	—	—	—	—	—	—	—	—
Setobranch	—	—	1	1	1	1	1	1

would appear to be the relatively slender and dentate rostrum, with its basal pair of spines in a supraorbital position; the form of the chelipeds of pereopod 1, and especially that of the smaller chela with the slender dentate fingers being 1.5–2.0 times longer than the propodal palm; the presence of spines on the upper margins of the dactylus and propodus of pereopod 1 chelae; the absence of pleurobranchs; and the presence of epipods on pereopods 1–4.

Species:

Acanthaxius amakusana (Miyake & Sakai, 1967). Amakusa Island, Kyushu, Japan, 20–40 m.

Acanthaxius kirkmilleri, new species. Off Anguilla, 421–439 m.

Acanthaxius miyazakiensis (Yokoya, 1933). Southern Miyazaki-ken, Japan, 137 m; Philippines, 136–210 m.

Acanthaxius pilocheira (Sakai, 1987). Off Honshu Island, Japan, 360 m.

Acanthaxius polyacantha (Miyake & Sakai, 1967). East China Sea, 118 m.

Acanthaxius polychaetes Sakai, 1994. Off Great Barrier Reef, Australia, 260 m.

Acanthaxius kirkmilleri, new species

Figs. 1, 2

Material examined.—Holotype, USNM 243492, ♀ carapace length 12.0 mm, R/V, *John Elliott Pillsbury* sta P-984, off Anguilla, 18°26.4′N, 63°12.6′W, 421–439 m, brown mud bottom, 22 Jul 1969.

Diagnosis.—Female: Carapace glabrous; rostrum slender, with 2 pairs of strong dorsal teeth (apex missing); median carina starting at rostral base, with 2 teeth anterior to tubercle, 1 posterior; submedian carina with 4 teeth; lateral carina with single strong tooth posterior to basal rostral tooth; postcervical carina poorly defined, most marked anteriorly. Abdominal pleuron 1 ventrally narrowed; pleuron 2 broad, ventrally truncate; pleura 3–5 with tiny denticle on anterior margin, anteroventrally rounded, posteroventrally slightly angled. Telson with lateral margin having single anterior tooth, 2 mobile posterolateral spines, posterior margin convex, with median tooth; dorsal surface with 2 pairs of teeth (posteriormost tooth on right side doubled).

Antennal scaphocerite (acicle) slender, acute, reaching to distal margin of peduncle article 4. Maxilliped 3, ischium with 3 teeth on posterior margin; merus with 5 teeth increasing in length distally on posterior margin. Pereopod 1, larger chela, ischium with 4 teeth on posterior margin; merus with 7 teeth and several smaller denticles on posterior margin, 5 strong distal teeth on anterior margin; carpus with 3 strong teeth on anterior margin, several smaller denticles on lateral surface, including strong submarginal tooth; fingers subequal in length to propodal palm, propodus strongly setose on upper and lower surfaces, with 4 strong teeth on anterior margin, row of 12 submarginal teeth on ventrolateral surface, lateral surface of palm with many small acute denticles; fixed finger with cutting edge bearing numerous small rounded teeth; dactylus bearing 5 strong teeth on upper margin, cutting edge bearing numerous small rounded teeth. Smaller chela, ischium, merus, and carpus as in larger chela; fingers about ⅓ longer than propodal palm, latter setose, with 4 strong teeth on upper margin, row of about 10 submarginal teeth ventrally, lateral surface with several small acute denticles, fixed finger with cutting edge straight, bearing numerous small serrations; dactyl bearing 4 strong teeth on upper margin, cutting edge straight, bearing numerous

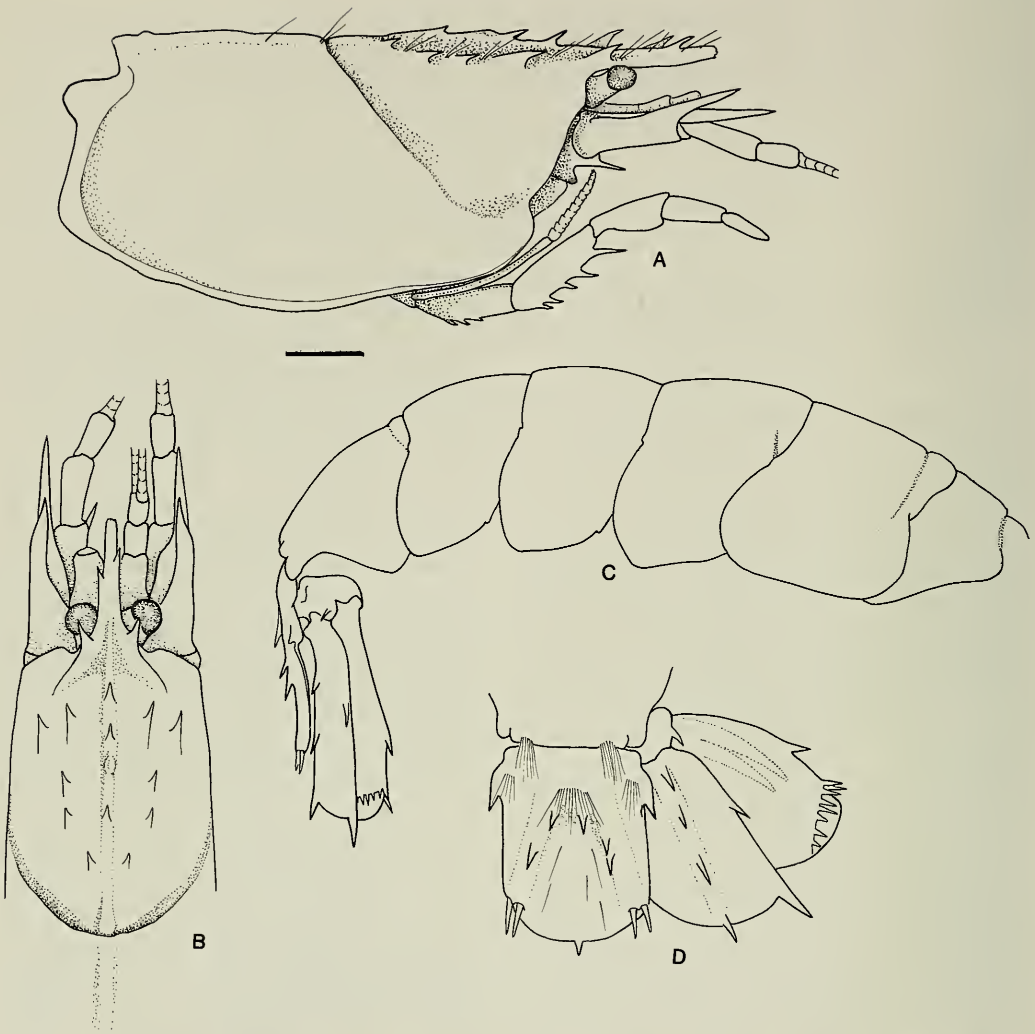

Fig. 1. *Acanthaxius kirkmilleri,* new species, holotype (USNM 243492). A, Carapace in lateral view; B, Anterior carapace in dorsal view; C, abdomen in lateral view; D, telson and right uropod in dorsal view. Scale = 2 mm.

small serrations. Pereopod 2, anterior and posterior margins of all articles setose; ischium with single strong posterodistal tooth; merus with 3 strong teeth on posterior margin; carpus with single strong tooth at midlength of anterior margin. Pereopod 3, merus with 3 teeth on posterior margin; propodus with 5 small clumps of short spines on posterior margin. Pereopod 4, merus with single small posterodistal tooth; dactylus setose; propodus with 4 small clumps of tiny spines on posterior margin. Pereopod 5, propodus with distolateral cluster of setae; dactylus setose. Pleopod 1 a single slender ramus, distally flagelliform. Pleopods 2–5 with slender appendix interna articulating at about proximal third of endopod. Uropod with lateral ramus having 2 teeth on lateral margin, mobile spine at angle of suture, 6 spines along suture; mesial ramus with 2 teeth on lateral margin, 4 teeth on dorsal ridge including distal marginal tooth.

Remarks.—The major differences be-

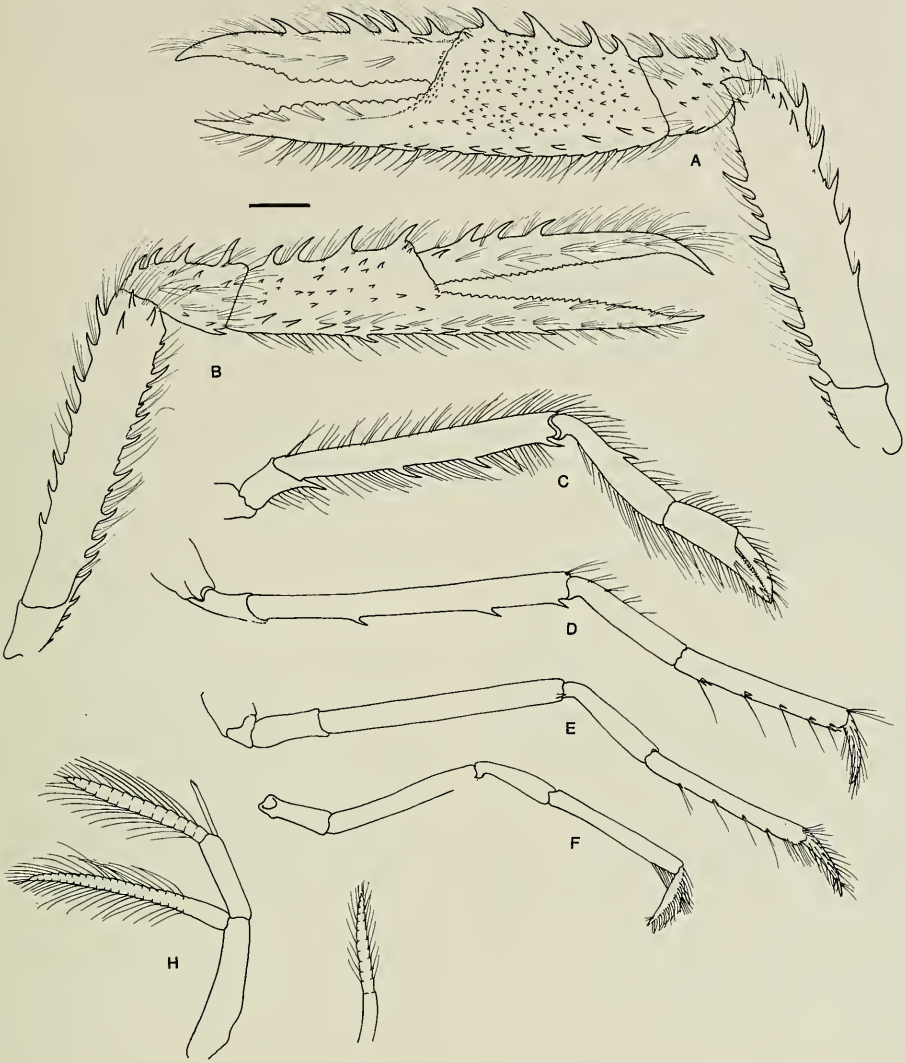

Fig. 2. *Acanthaxius kirkmilleri,* new species, holotype (USNM 243492). A, Pereopod 1, larger cheliped; B, Pereopod 1, smaller cheliped; C, Pereopod 2; D, Pereopod 3; E, Pereopod 4; F, Pereopod 5; G, Pleopod 1; H, Pleopod 2. Scale (A–F) = 2 mm.

tween this western Atlantic species and the holotype of *A. pilocheira* (USNM 231418) lie in the lateral ramus of the uropod (lateral margin more spinose than *A. kirkmilleri*), the generally more spinose and slightly more robust chelipeds of pereopod 1 in *A. pilocheira,* and the more elongate telson (1.5 times longer than basal width) in *A. kirkmilleri* (1.25 times longer than basal width in *A. pilocheira*).

The differences between the present species and the other Japanese congeners are easily discerned: *A. miyazakiensis* is a far more setose species, especially on the chelipeds and carapace; *A. polyacantha* possesses a markedly tuberculate carapace, and relatively more robust chelipeds; *A. amakusana* has a rostrum shorter than the eyestalks, and a relatively broader telson. The Australian species *A. polychaetes* is more setose, especially on the carapace and abdomen, and possesses squatter and more setose chelipeds of pereopod 1

Etymology.—The species is named for Dr. Kirk D. Miller, longtime friend and companion.

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A new genus for *Anapagrides* sensu De Saint Laurent-Dechancé, 1966 (Decapoda: Anomura: Paguridae) and descriptions of four new species

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Abstract.—*Anapagrides* De Saint Laurent-Dechancé, 1966, as originally diagnosed by its author, has recently been found not to agree with several essential characters of its type species, *Eupagurus (Spiropagurus) facetus* Melin, 1939. Since *Anapagrides* necessarily is restricted to the taxon exemplified by its type species, the new genus, *Laurentia,* is proposed for the four undescribed species previously referred to the former genus. These species are now fully described and the systematic relationship of *Anapagrides* sensu stricto to the new genus is discussed.

In a study of the hermit crabs of Maluku, Indonesia, collected during the *Alpha Helix* Expedition of 1975, to northern Australian and eastern Indonesian waters, Haig & Ball (1988) recognized and illustrated a species, referable to the genus *Anapagrides* as defined by De Saint Laurent-Dechancé (1966). Haig & Ball (1988) declined to describe or name their taxon as a new species in deference to Michèle de Saint Laurent, who had indicated, at the time of her original generic diagnosis (De Saint Laurent-Dechancé 1966) and subsequently (De Saint Laurent 1968), that three new IndoPacific species of *Anapagrides* remained to be described. Although De Saint Laurent-Dechancé (1966) based her diagnosis of *Anapagrides* on these undescribed taxa, she designated the nominal species *Eupagurus (Spiropagurus) facetus* Melin, 1939, as the type of the genus.

McLaughlin & Sandberg (1995) recently completed a review of three of Melin's (1939) species, including *Anapagrides facetus.* These authors found that Melin's species differed from De Saint Laurent-Dechancé's (1966) generic diagnosis to such a significant extent, that a major emendation of *Anapagrides* was required. *Anapagrides* sp. of Haig & Ball (1988), while agreeing with *Anapagrides* sensu De Saint Laurent, can no longer be assigned to *Anapagrides* as emended. In addition to Haig & Ball's (1988) Maluku specimen, we have now been able to examine De Saint Laurent's undescribed species. These are described herein as new species in *Laurentia,* new genus.

Specimens for this review are from the Dutch *Siboga,* U.S. Philippine *Albatross,* U.S., and Australian/Indonesian *Alpha Helix* expeditions. The holotype of Haig & Ball's species has been deposited in the Indonesian National Institute of Oceanography, Jakarta (NIOJ). Specimens from the *Albatross* Expedition have been returned to the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and the *Siboga* material to the Zöologisch Museum, Amsterdam (ZMA). One measurement, shield length (SL), measured from the tip of the rostrum to the midpoint of the posterior margin of the shield, provides an indication of animal size.

Laurentia, new genus

Anapagrides De Saint Laurent-Dechancé, 1966:262 (in part).—Miyake, 1978:142 (in part), see remarks.

Anapagrides: De Saint Laurent, 1968: 1115.—Haig & Ball, 1988:177; not *Anapagrides* De Saint Laurent-Dechancé, 1966.

Type species.—*Laurentia albatrossae,* new species. Gender: feminine.

Diagnosis.—Eleven pairs of trichobranchiate gills. Rostrum narrowly triangular, produced beyond bases of ocular acicles. Ocular acicles slender. Antennular peduncles with elongate ultimate segment often provided with 1 or more long setae at distal margin. Antennal peduncle with supernumerary segmentation. Maxillule with external lobe of endopod somewhat produced, not recurved. Crista dentata of third maxilliped without accessory tooth. Sternite of third maxillipeds unarmed, but with shallow median depression. Chelipeds unequal or subequal, right appreciably stouter. Ambulatory legs with elongate dactyls; carpi with dorsodistal spine. Fourth pereopods with single row of scales in propodal rasp. Sternite of fifth pereopods developed as single small subovate or subquadrate lobe. Coxa of left fifth pereopod in males with moderately long or long, sometimes coiled, sexual tube (Fig. 1E, F) provided with terminal tuft of stiff setae; right fifth coxa with gonopore; 3 uniramous or unequally biramous unpaired left pleopods. Females with paired gonopores; no paired pleopods, unpaired left pleopods on somites 2–5. Uropods markedly asymmetrical. Telson with transverse suture only weakly indicated; posterior lobes usually asymmetrical, terminal margins oblique; posterolateral margins delineated at least on left.

Etymology.—This genus is named in honor of the noted French carcinologist, Michèle de Saint Laurent.

Remarks.—Miyake (1978) included *Anapagrides* sensu lato among the hermit crab genera reported from Japan. Although he cited the gill structure as being phyllobranchiate, the remainder of his generic diagnosis was based on that of De Saint Laurent-Dechancé (1966); *A. facetus* was listed as the only species. Miyake (1978) gave no indication that he had any personal knowledge of the taxon.

Laurentia albatrossae, new species

Figs. 1, 2, 3A, B

Holotype.—♂ (SL = 3.2 mm), Philippine Islands, Sulu Archipelago, 5.5 mi NW of Jolo Light, 06°09′N, 120°58′E, *Albatross* station 5141, 153 m; 15 Feb 1908; USNM 275922.

Paratype.—Ovigerous ♀ (SL = 1.97 mm), ? Banda, 9–36 m; ZMA Crust.: De.201763.

Description.—Shield (Fig. 1A) slightly longer than broad; anterior margin between rostrum and lateral projections concave; anterolateral margins sloping; posterior margin truncate; dorsal surface glabrous. Rostrum triangular, well developed, reaching nearly half length of ocular acicles, terminating subacutely. Lateral projections well developed, triangular, with submarginal spine. Ocular peduncles (including corneae) approximately ⅘ shield length; corneae slightly dilated. Ocular acicles subtriangular, with submarginal spine.

Antennular peduncles, when fully extended, overreaching ocular peduncles by ¾ to nearly entire length of ultimate segment; ultimate segment with 1 or 2 long setae on dorsodistal margin; penultimate segment with 1 or 2 short setae; basal segment with statocyst region expanded laterally and dorsoventrally flattened, with distal hook-like process; dorsolateral margin with small distal spine.

Antennal peduncles overreaching ocular peduncles by approximately ½ length of ultimate segment. Fifth and fourth segments with few long setae. Third segment unarmed or with small ventrodistal spinule. Second segment with dorsolateral distal angle produced, terminating in acute spine and with small secondary spine on mesial

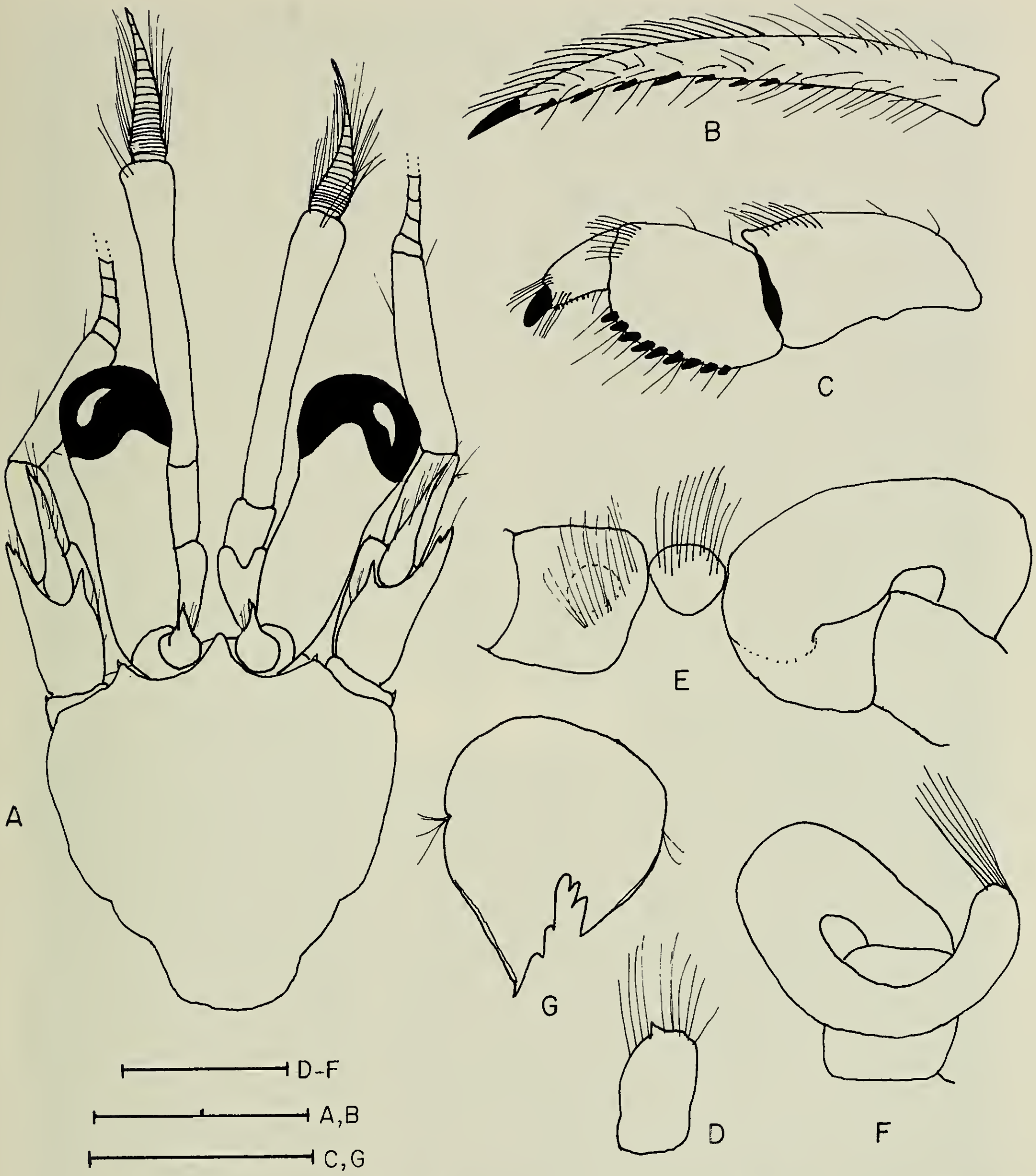

Fig. 1. *Laurentia albatrossae,* new species. Holotype, USNM 275922: A, shield and cephalic appendages; B, dactyl of second right pereopod (mesial view); C, dactyl, propodus and carpus of left fourth pereopod (lateral view); D, anterior lobe of sternite of third pereopods; E, coxae and sternite of fifth pereopods (ventral view); F, coxa of left fifth pereopod and sexual tube (dorsal view); G, telson. Scales equal 2.0 mm (A, B), 1.0 mm (C, E–G), and 0.5 mm (D).

margin distally; dorsomesial distal angle with prominent acute spine. First segment sometimes with spinule at dorsolateral distal angle; small spine on ventrolateral margin distally. Antennal acicle reaching to base of cornea or slightly beyond; terminating in acute spine and with long setae on mesial margin. Antennal flagellum with 2 or 3 long and sometimes 1 or 2 shorter setae every 1 to 3 articles.

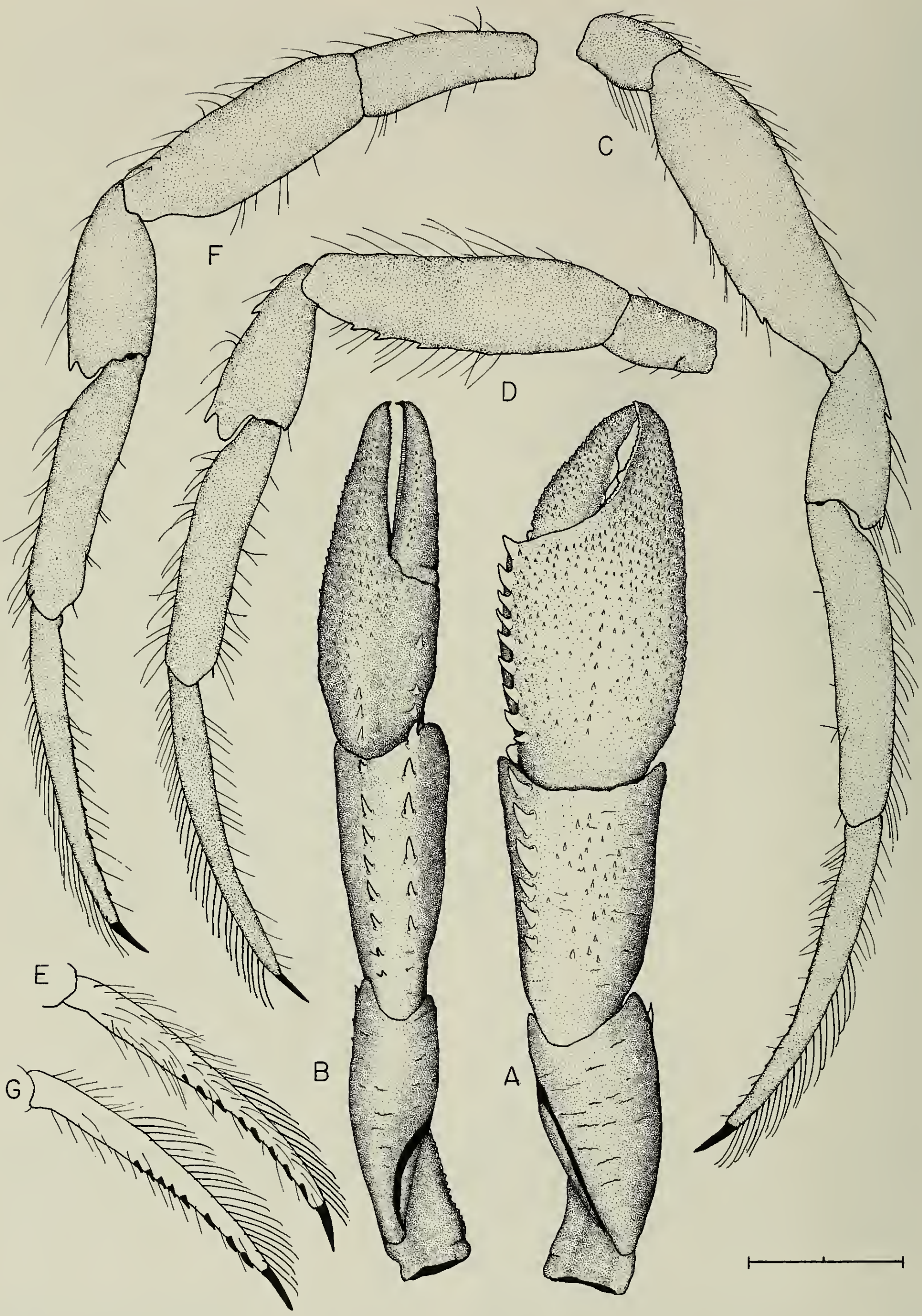

Fig. 2. *Laurentia albatrossae,* new species. Holotype, USNM 275922: A, right cheliped (setae omitted); B, left cheliped (setae omitted); C, right second pereopod (lateral view); D, left second pereopod (lateral view); E, dactyl of left second pereopod (mesial view); F, left third pereopod (lateral view); G, dactyl of left third pereopod (mesial view). Scale equals 2.0 mm.

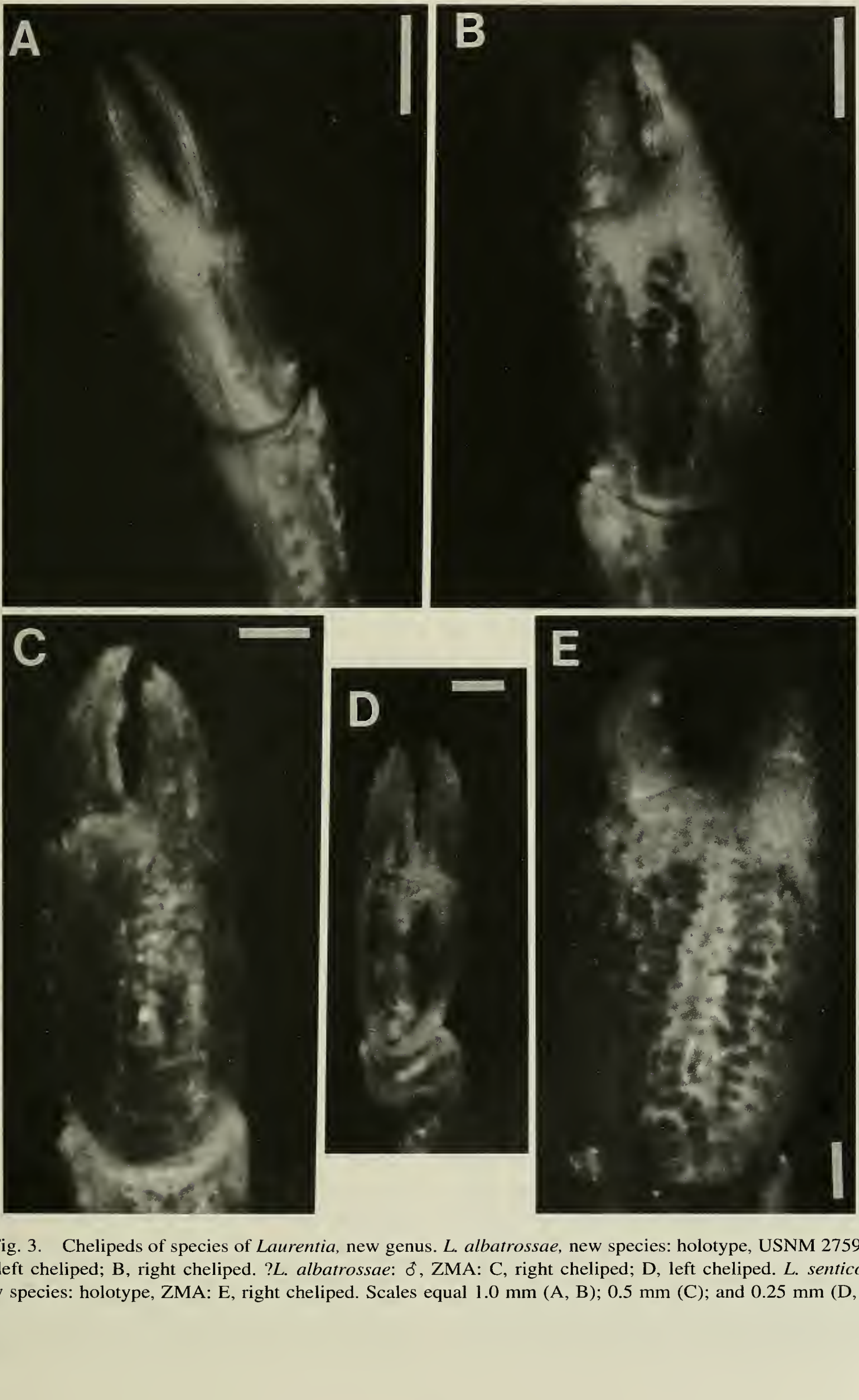

Fig. 3. Chelipeds of species of *Laurentia,* new genus. *L. albatrossae,* new species: holotype, USNM 275922: A, left cheliped; B, right cheliped. ?*L. albatrossae*: ♂, ZMA: C, right cheliped; D, left cheliped. *L. senticosa,* new species: holotype, ZMA: E, right cheliped. Scales equal 1.0 mm (A, B); 0.5 mm (C); and 0.25 mm (D, E).

Crista dentata with 10 to 15 regularly-spaced, small teeth.

Right cheliped [Figs. 2A (setae omitted), 3B] moderately elongate, rather slender. Dactyl approximately ⅘ length of palm; cutting edge with 1 small calcareous tooth proximally and 1 prominent calcareous tooth near mid-margin, row of very small calcareous teeth distally; terminating in very small corneous claw; dorsomesial margin not clearly delimited; dorsal surface convex, armed with numerous, scattered small spines or very fine spinules extending onto mesial face dorsally, and partially obscured by long setae; ventral surface with scattered long setae. Palm only slightly shorter than carpus; dorsomesial margin with row of slender, sometimes irregular, acute spines and long setae, dorsal surface convex, armed with scattered small spines and fine spinules practically obscured by long setae, dorsolateral margin with long setae proximally, but with small spines or fine spinules distally and on fixed finger; dorsal surface of fixed finger with scattered fine spinules also obscured by long setae, cutting edge with 1 calcareous tooth in proximal half, very small calcareous teeth distally, terminating in small weakly calcified claw. Carpus slightly longer than merus; dorsomesial margin with short, transverse rows of long setae proximally and more distal row of moderately slender, acute spines, dorsal surface with 3 very irregular rows of small spinules, decreasing in size laterally, dorsolateral margin not delimited; mesial face with transverse rows of long setae, lateral and ventral surfaces also with transverse rows of long setae, but fewer in number. Merus with transverse rows of setae on dorsal surface, extending onto lateral face dorsally; ventrolateral margin with 1 prominent and 1 smaller spine distally, ventromesial margin with 1 prominent spine at distal angle, 1 spine at midlength, and 1 transverse setal row and smaller spine proximally. Ischium with row of transverse setal tufts adjacent to mesial margin ventrally. Coxa with prominent spine on ventrolateral distal angle and second, smaller spine on ventromesial margin in distal half.

Left cheliped [Figs. 2B (setae omitted), 3A] (missing in paratype) slender, not much shorter than right. Dactyl approximately ¼ longer than palm; cutting edge with row of very small corneous teeth, terminating in corneous claw; dorsal surface with irregular, nearly double row of very small spinules in midline, partially obscured by long setae, dorsomesial margin rounded and armed with scattered tiny spinules. Palm about ⅔ length of carpus, dorsomesial margin with 3 acute spines, 2 proximally separated by broad space from medianly placed third spine, dorsal surface with numerous tiny spinules generally obscured by long setae and 3 slightly stronger spines proximally on weakly delimited dorsolateral margin; fixed finger with dorsal surface similarly armed with tiny spinules and long dense setae, cutting edge with row of very small calcareous teeth interspersed with corneous teeth, terminating in tiny corneous claw; ventral surfaces all with weakly defined transverse rows of long setae. Carpus approximately as long as merus; dorsomesial margin with row of slender, acute spines, dorsolateral margin with slightly smaller row of spines, both partially obscured by long setae; lateral and mesial faces with transverse rows of long setae, ventrolateral margin with small spine distally. Merus with long setae on dorsal, lateral and mesial surfaces; ventrolateral margin with 3 prominent acute spines and transverse rows of long setae; ventromesial margin with 1 spine near distal angle and 2 rather widely-spaced spines in proximal half. Ischium with long setae on ventral margin.

Second and third pereopods (Figs. 1B, 2C–G) (right third missing in holotype, both second pereopods missing in paratype) generally similar from left to right. Dactyls slightly longer than propodi, slender, in dorsal view slightly twisted, terminating in long, slender corneous claws; in lateral view curved ventrally; dorsal margins each with a row of stiff setae, mesial faces with long setae, ventral margins also with long setae and with 5 to 8 corneous spines in distal half to ⅔. Propodi with 1 or 2 corneous spines on ventrodistal margin, long setae dorsally and ventrally. Carpi each with 1 spine on dorsal surface adjacent to dorsodistal angle (third) and 1 additional spine on dorsal surface proximally (second). Meri each with 1 spine on ventral margin in distal third (second) or unarmed (third), dorsal margins with tufts of long setae. Ischia unarmed. Fourth pereopod (Fig. 1C) without preungual process; carpus with small spine at dorsodistal margin. Sternite of third pereopod (Fig. 1D) with small, subovate or subquadrate anterior lobe armed distally with 1 small spine. Sternite of fifth pereopods (Fig. 1E) semisubovate, with long distal setae.

Male pleopods unequally biramous; exopod well developed, endopod reduced. Telson (Fig. 1G) with posterior lobes strongly asymmetrical, each with prominent spine at outer angle (largest on left) and 1 or 2 additional spines on oblique terminal margin.

Affinities.—Laurentia albatrossae most closely resembles *L. senticosa,* new species in having the dorsal surfaces of the chelae armed with numerous tiny spines; however, the right chela of *L. albatrossae* is more elongate and slender than that of *L. senticosa.* The dorsomesial margin of the palm of the right cheliped of *L. albatrossae* carries a row of moderate to strong spines that are lacking in *L. senticosa.* Other distinguishing characters are pointed out under *L. senticosa.*

Etymology.—Named for the U.S. Fish Commission Steamer *Albatross.*

Distribution.—Philippines, Sulu Archipelago and Banda, Indonesia; 5 to 53 m.

Remarks.—In her original report on *Anapagrides* sensu lato, De Saint Laurent-Dechancé (1966:262) commented that a species collected in the Indo-Pacific by the *Albatross* and *Siboga* was very near Melin's (1939) species [*Eupagurus* (*Spiropagurus*) *facetus*] and that her genus *Anapagrides* was proposed for the former and two other new species from the same region. Of the specimens from the three *Albatross* stations initially considered by De Saint Laurent, only one, from station 5141, actually represents *Laurentia.* One specimen, from *Siboga* station 99 [Sulu Archipelago, 6°7.5′N, 120°26′E], appears to be one of the specimens specifically referred to by De Saint Laurent-Dechancé (1966). It is a male (SL = 1.79 mm; ZMA Crust.: De.201764) that closely resembles *L. albatrossae,* but is now almost entirely lacking calcification, and morphological details are difficult to interpret. Therefore, we tentatively assign this specimen (Fig. 3C, D) to *L. albatrossae,* but do not consider it a paratype. The female paratype presumably from the *Siboga* Expedition carries only the label "? Banda, 5–20 fms" in what appears to be De Saint Laurent's hand writing.

Laurentia sibogae, new species
Fig. 4

Holotype.—♀, ovigerous (SL = 1.5 mm), Sailus Ketjil, Paternoster Island, "Siboga" station 37, dredged to 18 m, 30, 31 Mar 1899, ZMA Crust.: De.201762.

Description.—Shield (Fig. 4A) slightly longer than broad; anterior margin between rostrum and lateral projections distinctly concave; anterolateral margins terraced; posterior margin roundly truncate; dorsal surface glabrous. Rostrum well developed, appreciably overreaching lateral projections, triangular, terminating rather bluntly. Lateral projections prominently developed, obtusely triangular, with strong marginal or submarginal spine.

Ocular peduncles (including corneae) approximately ¾ length of shield, moderately stout, corneae only slightly dilated. Ocular acicles narrowly triangular, terminating acutely and with small submarginal spine.

Antennular peduncles elongate, when fully extended, overreaching distal margin of cornea by approximately ⅔ length of ultimate segment. Ultimate segment with few

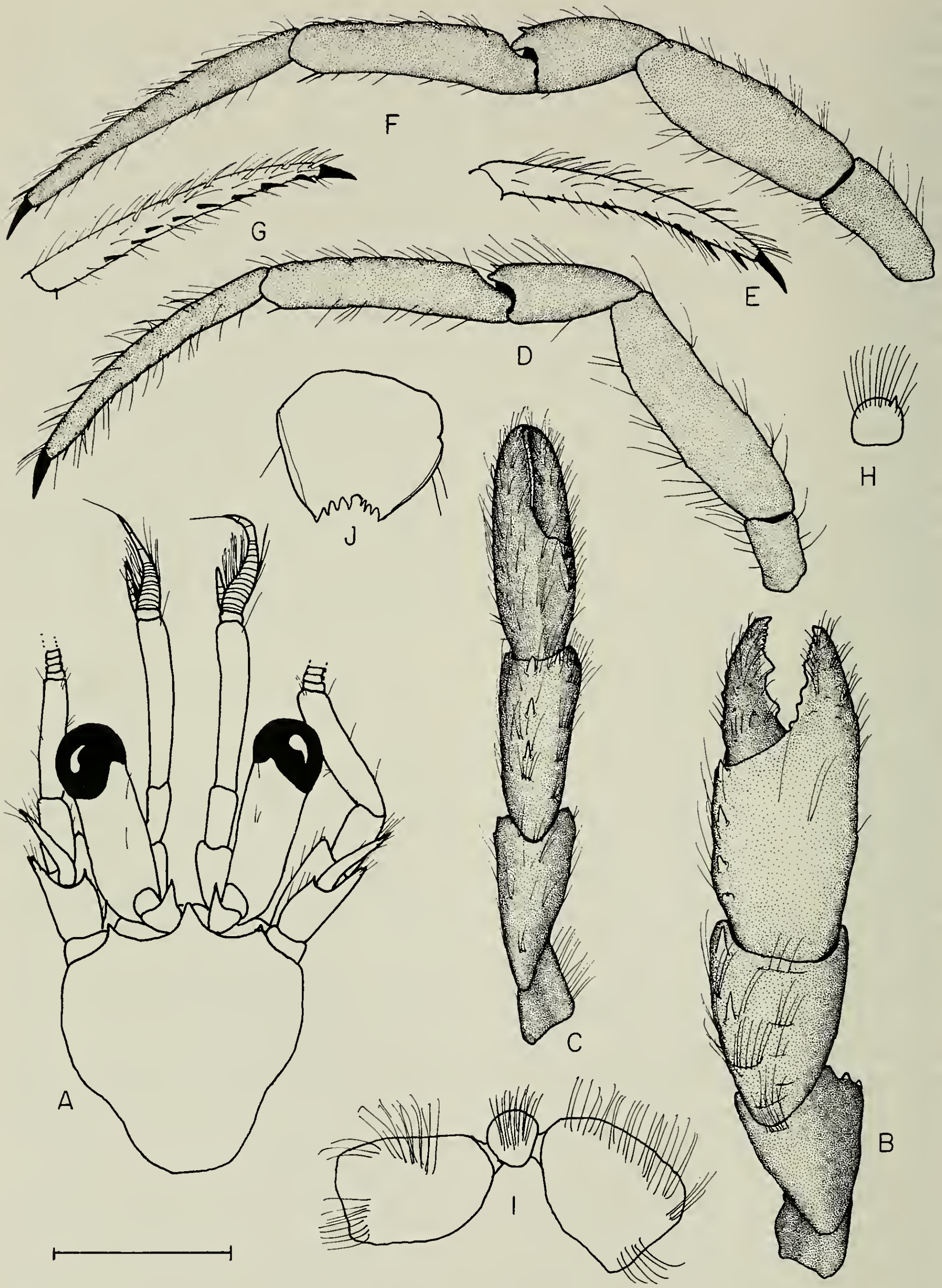

Fig. 4. *Laurentia sibogae,* new species. Holotype, ZMA Crust.: De.201762: A, shield and cephalic appendages; B, right cheliped; C, left cheliped; D, right second pereopod (lateral view); E, dactyl of right second pereopod (mesial view); F, left third pereopod (lateral view); G, dactyl of left third pereopod (mesial view); H, anterior lobe of sternite of third pereopods; I, coxae and sternite of fifth pereopods; J, telson. Scales equal 1.0 mm (A–G) and 0.5 mm (H–J).

short setae on ventral surface. Penultimate segment glabrous. Basal segment with 1 small acute spine- on dorsolateral margin distally.

Antennal peduncles overreaching ocular peduncles by ⅓ to ½ length of ultimate segment. Fifth and fourth segments with scattered, moderately long setae. Third segment with very small spinule on ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in simple or bifid spine; dorsomesial distal angle with moderately strong spine. First segment with 1 acute spine ventrolateral margin distally. Antennal acicle moderately short, not reaching beyond proximal margin of ultimate peduncular segment. Antennal flagellum with 1 or 2 quite long and 1–4 shorter setae practically every article.

Third maxilliped with 7 or 8 small teeth on crista dentata; proximal 3 or 4 more prominent.

Right cheliped (Fig. 4B) with chela moderately slender. Dactyl only slightly longer than palm; dorsomesial margin with 3 low spinulose protuberances, dorsal surface with few scattered very small spinules and sparse tufts of long setae; cutting edge with 2 widely spaced large calcareous teeth in proximal ⅔ and few small calcareous teeth interspersed with corneous teeth distally. Palm with 4 widely-spaced spines or spinulose tubercles on dorsomesial margin, dorsal surface convex, apparently completely unarmed, but with scattered long setae, dorsolateral margin not delimited on palm, but marked by tufts of long, stiff setae on fixed finger, dorsal surface of fixed finger also with numerous low protuberances and tufts of long, stiff setae; cutting edge with 2 large and several smaller calcareous teeth; ventral surfaces of dactyl, palm, and fixed finger all with tufts of long setae. Carpus approximately as long as palm; dorsomesial margin with 2 widely spaced, strong spines and proximal transverse row of long stiff setae, dorsal surface with few transverse rows of long, stiff setae, dorsolateral margin not delimited, lateral and ventral surfaces with scattered long setae, 1 acute spinule at ventrolateral distal angle. Merus approximately as long as carpus; dorsodistal margin with long setae, and few scattered long setae on dorsal surface; ventrolateral margin with 2 spines in distal half, ventromesial margin with small spine at distal angle. Ischium unarmed, but with few long setae.

Left cheliped (Fig. 4C) with moderately long slender chela; dactyl and fixed finger lacking distinct hiatus, and not noticeably curved ventrally. Dactyl slightly longer than palm; dorsal and ventral surfaces unarmed, but with numerous tufts of long setae. Palm somewhat elevated in midline, perhaps minutely serrate and with long setae, dorsomesial and dorsolateral faces sloping, unarmed but with scattered long setae. Carpus approximately ⅓ longer than palm, covered dorsally, mesially and to lesser extent laterally and ventrally with long setae; dorsomesial distal angle with acute spine, dorsolateral margin with row of 3 acute, rather widely-spaced spines and long setae; ventrolateral distal angle with acute spine. Merus approximately equaling length of carpus; dorsal and ventral surfaces with scattered long setae; ventrolateral margin with 2 acute spines distally, ventromesial margin with 1 acute spine at distal angle. Ischium with long setae on ventral margin.

Ambulatory legs (Fig. 4D–G) generally similar from left to right; dactyls slender, ¼ to ⅓ longer than propodi; terminating in long slender corneous claws; dorsal margins each with row of long, corneous, spine-like bristles in distal ⅔ and long setae, ventral margins each with row of corneous spines (6 to 8) in distal ¾ or slightly more and additional long setae; mesial and lateral faces with scattered setae. Propodi with 1 corneous spinule at least on left second and third; dorsal and ventral surfaces all with tufts of long setae. Carpi each with small almost transparent spine at dorsodistal margin, few long setae on dorsal and ventral margins. Meri with long setae dorsally and ventrally. Ischia also with long setae on ventral margins. Fourth pereopod without preungual process at base of claw; carpus without dorsodistal spine. Sternite of third pereopods (Fig. 4H) with anterior lobe roundly subquadrate, anterior margin with long setae and 1 spine. Sternite of fifth pereopods (Fig. 4I) subovate, with median tuft of long setae.

Telson (Fig. 4J) with transverse suture indicated in part by tuft of setae (left side); terminal margins oblique, each with 4 spines, stronger on left and/or at outer angles.

Affinities.—Of the four species of *Laurentia* currently recognized, *L. sibogae* appears most closely related to *L. balli* new species. In both species the dorsomesial margin of the right chela is similarly armed with a row of spines; however, the dactyl of the right chela has only a few low protuberances in *L. sibogae,* whereas in *L. balli* this margin is provided with a row of spines; the dorsal surfaces of the palm and fixed finger have a few small spines. Additionally, the dorsodistal margin of the carpus of the right cheliped is unarmed in *L. sibogae,* but carries a prominent median spine in *L. balli.*

Etymology.—Named for the Dutch research vessel "Siboga."

Distribution.—At present, known only from the type locality; 18 m.

Laurentia balli, new species
Fig. 5

Anapagrides sp.: Haig & Ball, 1988:177, Fig. 8.

Holotype.—♂ (SL = 2.0 mm), off Pulau, Saparua, Indonesia, 3°37.9′S, 128°38.6–39′E, *Alpha Helix* Saparua station 3, 29 Mar 1975, coll. E. Ball, NIOJ.

Description.—Shield (Fig. 5A) approximately as long as broad; anterior margin between rostrum and lateral projections concave; anterolateral margins sloping; posterior margin roundly truncate. Rostrum triangular, produced beyond bases of ocular acicles, terminating subacutely. Lateral projections well developed, triangular, terminating acutely and with marginal or submarginal spinule.

Ocular peduncles approximately equaling length of shield, cylindrical, with corneae slightly dilated. Ocular acicles narrowly triangular, with small marginal or submarginal spine.

Antennular peduncles (when extended) overreaching corneae by ½ to ⅔ length of ultimate segment. Ultimate segment with 1 or 2 long setae on dorsodistal margin. Penultimate segment with few scattered setae. Basal segment with statocyst area broad and dorsoventrally flattened, with acute, curved spine on lateral margin.

Antennal peduncles equaling or slightly overreaching distal margins of corneae. Fifth and fourth segments with few scattered setae. Third segment with acute spine on ventral margin. Second segment with dorsolateral distal angle produced, terminating in acute spine, lateral margin with few setae; dorsomesial distal angle with moderately strong spine, mesial and lateral surfaces with few long setae. First segment with spinule on dorsolateral distal angle and 1 acute spine ventrolaterally. Antennal acicle reaching beyond base of fifth peduncular segment, slightly arcuate, terminating in small spine and 1 to 3 long setae. Antennal flagellum moderately short, with 1 or 2 long and 0 to 4 short setae every article.

Crista dentata of third maxilliped with 10 to 13 small teeth, most proximal 3 largest.

Right cheliped with dactyl slightly shorter than palm; dorsomesial margin with row of very small, moderately widely-spaced spinules, surfaces all with numerous long setae; cutting edge with 2 prominent calcareous teeth in proximal half, row of small calcareous teeth distally; terminating in small corneous claw. Palm (Fig. 5B) slightly shorter than carpus; dorsomesial margin with row of 4 slender spines, dorsolateral margin not delimited, dorsal surface with scattered setae and few spinules laterally, more numerous on fixed finger; lateral face with short transverse rows of long setae; cutting edge of fixed finger with 2 promi-

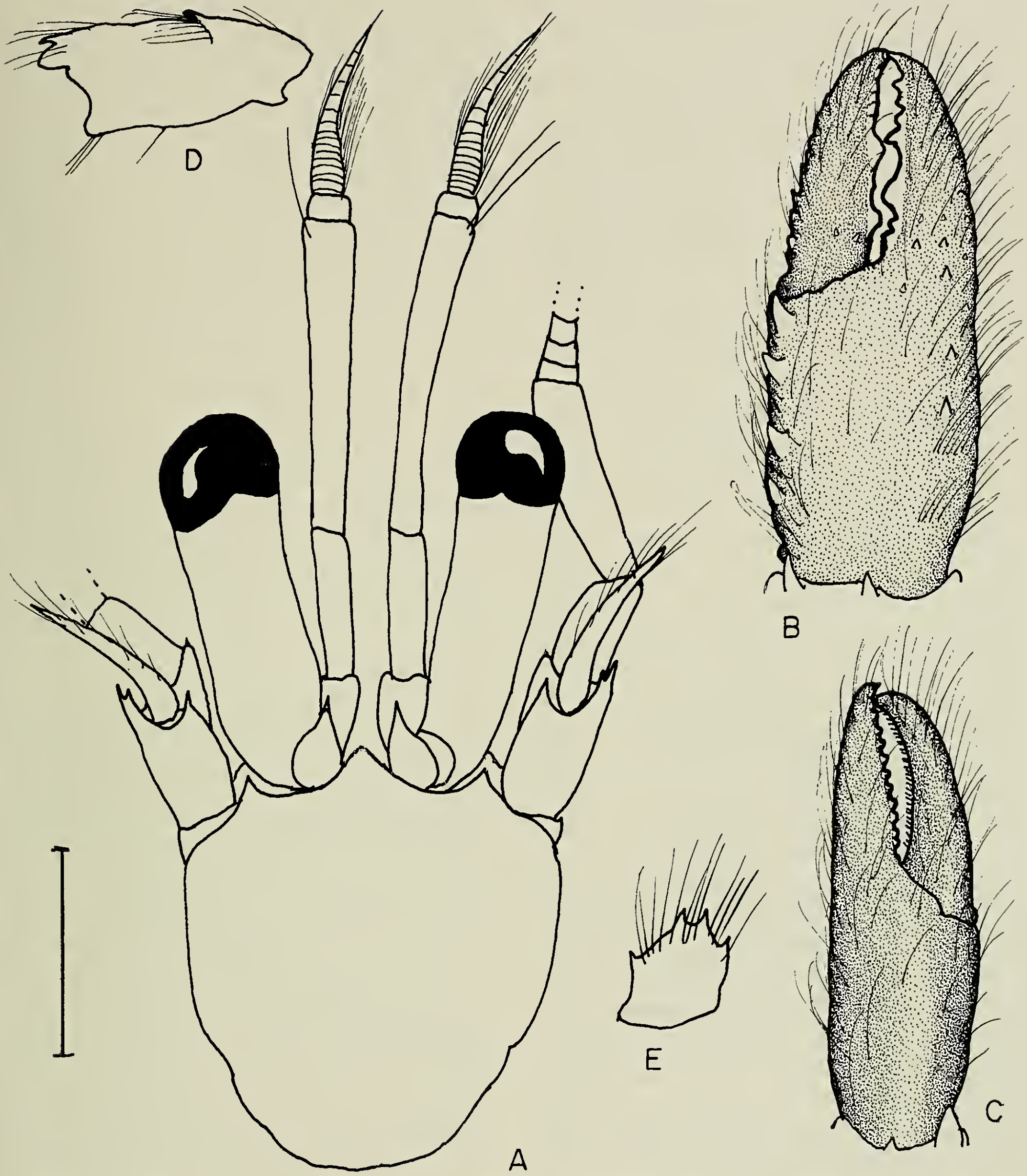

Fig. 5. *Laurentia balli,* new species. Holotype, NIOJ: A, shield and cephalic appendages; B, chela of right cheliped; C, chela of left cheliped; D, carpus of second right pereopod (mesial view); E, anterior lobe of sternite of third pereopods. Scale equals 1.0 mm (A–D) and 0.5 mm (E).

nent and 2 smaller calcareous teeth proximally, row of small calcareous teeth distally. Carpus slightly longer than merus; dorsomesial margin with 2 widely-spaced acute spines distally and 2 spinulose protuberances proximally, 1 additional spine on distal margin medially; ventrolateral margin with acute spine distally; all surfaces with scattered tufts of long setae. Merus subtriangular; dorsal margin with tufts of moderately long setae; ventrolateral distal angle with acute spine and tuft of long setae. Ischium with scattered long setae dorsally and ventrally.

Left chela (Fig. 5C) with distinct hiatus between dactyl and fixed finger. Dactyl slightly longer than palm; unarmed but with long setae on mesial face; cutting edge with row of small corneous teeth, terminating in small corneous claw. Palm with dorsal surface slightly elevated in midline, with few scattered moderately short setae mesially and laterally, dorsolateral margin with long setae, more numerous on fixed finger; cutting edge of fixed finger with row of small calcareous teeth. Carpus slightly longer than palm, approximately equaling length of merus; dorsolateral margin with row of 3 widely-spaced spines, dorsomesial margin with 1 strong spine distally and 3 short, transverse ridges and long setae in proximal ⅔, extending onto mesial face dorsally; lateral face with scattered somewhat shorter setae. Merus subtriangular; dorsal margin with row of moderately long setae; ventromesial margin with long setae and 1 acute spine at distal angle; ventrolateral margin row of long setae and 2 prominent spines in distal half. Ischium damaged in holotype.

Ambulatory legs with dactyls at least 1½ times longer than propodi; in lateral view, straight (second left missing in holotype) or curved (third); dorsal surfaces each with row of long, moderately stiff setae; mesial and lateral faces each with few scattered setae; ventral margins each with 6 corneous spines in distal ⅔. Propodi with scattered setae dorsally and ventrally; ventrodistal margins each with corneous spine. Carpi each with small spine on dorsal surface near distal angle, second (Fig. 5D) with additional small spine in proximal half, long setae dorsally and to lesser extent ventrally. Meri and ischia with long setae dorsally and ventrally. Fourth pereopod with unarmed carpus. Sternite of third pereopods with anterior lobe (Fig. 5E) roundly subquadrate, with 4 small marginal spines. Sternite of fifth pereopods subquadrate, with long marginal setae.

Telson (now missing from holotype) with transverse suture not distinct; posterior lobes markedly asymmetrical, with terminal margins oblique, each with 3 or 4 spines, strongest at outer angle, lateral margin of left with narrow corneous plate.

Affinities.—As previously mentioned, *L. balli* appears most closely allied to *L. sibogae.* In addition to the characters already cited that separate the two species, there are differences in the armature of the anterior lobe of the sternite of the third pereopods and the asymmetry of the telsonal lobes. In *L. balli,* the anterior lobe of the sternite carries 4 marginal spines; only 1 is present in *L. sibogae.* The posterior lobes of the telson are strongly asymmetrical in *L. balli,* but very weakly so in *L. sibogae.*

Etymology.—It gives us great pleasure to name this species for Eldon E. Ball, in recognition of his work on Pacific hermit crabs.

Distribution.—Saparua and possibly Banda, Indonesia.

Remarks.—The figures of "*Anapagrides* sp." (Haig & Ball 1988) are generally diagrammatic, and some do not accurately depict certain characters. Specifically, the dorsolateral distal angle of the second antennal peduncular segment is illustrated as a simple spine; however, there actually is a second spine on the mesiodistal margin; the first peduncular segment has a small spinule at the dorsolateral distal angle. The dactyl, fixed finger, and dorsolateral surface of the palm of the right cheliped appear unarmed in Haig & Ball's Fig. 8B. As may be seen in our figure (Fig. 5B), the dactyl has a few small spines on the dorsomesial margin and there are a few small spines laterally on the palm; on the fixed finger, a few spinules are present on the dorsal surface proximally and on the dorsolateral margin. The right second pereopod appears to have only a dorsodistal spine on the carpus in Haig & Ball's fig. 8E. In lateral view, the typical second spine on the proximal half of the dorsal surface is not readily observable; however, in mesial view (Fig. 5D) it is quite obvious.

One ♂ (SL = 2.32 mm, ZMA Crust.: De.201765) lacking chelipeds and ambulatory legs, from "Siboga" station "Banda," is tentatively assigned to *L. balli.* It shares with the holotype the strongly asymmetrical telsonal lobes, and similarly armed anterior lobe of the sternite of the third pereopods. However, as variation among species of *Laurentia* is not known, we are not considering this Banda specimen a paratype.

Laurentia senticosa, new species
Figs. 3E, 6

Holotype.—♂ (SL = 1.79 mm), Seram Ceram, Indonesia, 02°28.5′S, 131°3.3′E, *Siboga* station 166, 118 m, 22 Aug. 1899, ZMA Crust.: De.201760a.

Paratypes.—1 ♂, 1 ♀ (SL = 1.28, 1.40 mm), Seram Ceram, Indonesia, 02°28.5′S, 131°3.3′E, *Siboga* station 166, 118 m, 22 Aug 1899, ZMA Crust.: De.201760b.

Description.—Shield (Fig. 6A) slightly to considerably longer than broad; anterior margin between rostrum and lateral projections concave; anterolateral margins sloping or terraced; posterior margin truncate. Rostrum triangular, well developed, reaching approximately half length of ocular acicles, terminating bluntly or subacutely. Lateral projections well developed, triangular, with marginal or submarginal spine.

Ocular peduncles subcylindrical, approximately ⅔ shield length; corneae dilated. Ocular acicles subtriangular, with small submarginal spine.

Antennular peduncles overreaching ocular peduncles by about ⅘ length of ultimate segment; ultimate segment with 1 or 2 long, simple or plumose setae on dorsodistal margin; penultimate segment glabrous; basal segment with statocyst region expanded laterally and dorsoventrally flattened, dorsolateral margin with long slender spine distally.

Antennal peduncles overreaching ocular peduncles by ⅔–¾ length of ultimate segment. Fifth and fourth segments with few long setae. Third segment unarmed or with small ventrodistal spinule. Second segment with dorsolateral distal angle produced, terminating in acute spine and sometimes with prominent slender spine. First segment with small spine on ventrolateral margin distally. Antennal acicle reaching to base of cornea or slightly beyond, terminating in acute spine and with long setae on mesial margin. Antennal flagellum missing.

Crista dentata with 5–10 large or irregularly-sized teeth, largest 3 or 4 often proximal.

Right cheliped (Figs. 3E, 6B) moderately long and stout; with hiatus between dactyl and fixed finger. Dactyl approximately ⅔ length of palm; cutting edge with 2 widely-spaced calcareous teeth in proximal ⅔, row of very small calcareous teeth distally; terminating in very small corneous claw; dorsomesial margin with row of very small spines; dorsal surface convex, with scattered long setae, midline with irregular rows of very small spinules; ventral and mesial surfaces also with scattered long setae. Palm as long or slightly longer than carpus; dorsomesial margin not delimited, dorsal surface convex, armed with scattered, very fine spinules extending onto mesial face and few scattered long setae, dorsolateral margin with few long setae but otherwise not delimited proximally, with fine spinules distally and on fixed finger; dorsal surface of fixed finger with scattered fine spinules and long setae; cutting edge with 3 broad calcareous teeth, terminating in small corneous claw. Carpus approximately equal to length of merus; dorsomesial margin with row of moderately slender, acute spines, dorsal surface with 2 to 4 irregular longitudinal rows of small spinules, dorsolateral margin not delimited; mesial face with transverse rows of long setae, lateral and ventral surfaces also with scattered long setae. Merus with transverse rows of setae on dorsal margin, extending onto lateral face dorsally; ventrolateral margin with 2 prominent spines distally, ventromesial margin with 1 prominent spine at distal angle, 1 additional spine originating from se-

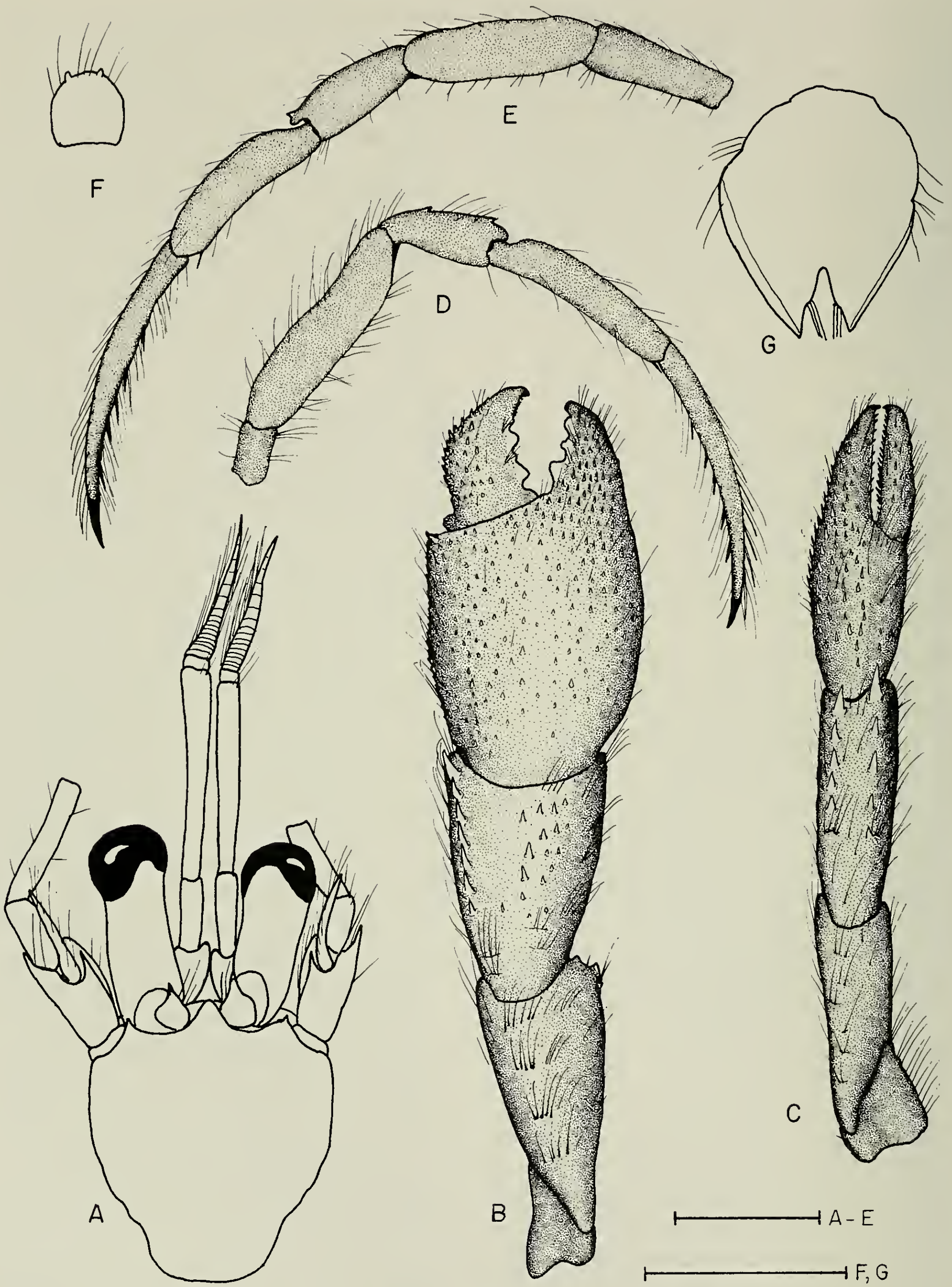

Fig. 6. *Laurentia senticosa,* new species. Holotype, ZMA Crust.: De.201760a: A, shield and cephalic appendages; B, right cheliped; C, left cheliped; D, right second pereopod (lateral view); E, left third pereopod (lateral view); F, anterior lobe of sternite of third pereopods; G, telson. Scale equals 1.0 mm (A–E) and 0.5 mm (F, G).

tal protuberance at midlength, and 1 transverse setal row and smaller spine proximally. Ischium with setae mesially and ventrally. Coxa sometimes with prominent spine on ventrolateral distal angle.

Left cheliped (Fig. 6C) slender; not appreciably shorter than right but much less robust. Dactyl approximately equal to or slightly longer than palm; cutting edge with row of very small corneous teeth, terminating in corneous claw; dorsal surface convex, with 4 or 5 spinules and tufts of long setae in midline, low protuberances and long setae on dorsomesial margin. Palm about ⅔ length of carpus; dorsal surface convex, armed with irregular longitudinal rows of tiny spinules, fewer on dorsomesial side and on fixed finger, dorsolateral margin with row of slender acute spines; palm and fixed finger both with scattered long setae; cutting edge of fixed finger with row of widely-spaced corneous teeth, terminating in small corneous claw; ventral surfaces all with weakly defined short transverse rows of long setae. Carpus approximately as long as merus; dorsolateral margin with row of slender, acute spines, dorsomesial margin also with row of spines strongest distally, both rows partially obscured by long setae; mesial and ventral faces with transverse rows of long setae; lateral face with scattered long setae, ventrolateral margin with acute spine distally. Merus with long setae on dorsal, lateral and ventral surfaces; ventrolateral margin with 2 prominent acute spines distally, continued as row of smaller spinules on lateral face ventrally; ventromesial margin with 1 spine near distal angle. Ischium with long setae on ventral margin. Coxa with prominent spine at ventrolateral distal angle.

Second and third pereopods (Fig. 6D, E) (holotype with only third left remaining) generally similar from left to right. Dactyls slightly to considerably longer than propodi, slender; in dorsal view, slightly twisted; in lateral view, curved ventrally; terminating in long, slender corneous claws; dorsal margins each with a row of stiff setae, mesial faces with long setae, ventral margins also with long setae and 5–8 long corneous spines in middle half to ⅔. Propodi with 1 or 2 corneous spines on ventrodistal margin, long setae dorsally and ventrally. Carpi each with 1 spine on dorsal surface adjacent to dorsodistal angle (third) and 1 additional spine on dorsal surface proximally (second). Meri each with 1 spine on ventral margin in distal third (second) or unarmed (third), dorsal margins with tufts of long setae. Ischia unarmed. Fourth pereopod with small preungual process at base of claw; carpus unarmed. Sternite of third pereopods with small, subovate or subtriangular anterior lobe (Fig. 6F) usually with 1 or 2 marginal spines.

Telson (Fig. 6G) with posterior lobes only slightly asymmetrical, each outer angle acutely developed and 1 or 2 slight protuberances and tufts of setae on oblique terminal margins.

Affinities.—In having the dorsal surfaces of the palms of both chelipeds armed with spinules, *L. senticosa* closely resembles *L. albatrossae.* However, the two species are immediately distinguished by the presence in the latter species of a row of distinct spines on the dorsomesial margin of the palm of the right chela and the more numerous, smaller and more regular teeth of the crista dentata. The telsons of the two species are also distinctly different.

Etymology.—From the Latin *senticosus* meaning full of thorns, and referring to the spinulose dorsal surfaces of the chelae of this species.

Distribution.—Currently known only from the type locality, Seram Ceram, Indonesia.

Discussion

As previously indicated, Melin's (1939) *Eupagurus (Spiropagurus) facetus* [also cited by Melin as *Eupagurus (Catapagurus) facetus*], not only was originally designated as the type species of *Anapagrides,* but, as the only nominal species assigned to the genus, must be considered the type species whether or not it agrees with the generic diagnosis given by De Saint Laurent-Dechancé (1966) (L. B. Holthuis, pers. comm.). As emended by McLaughlin & Sandberg (1995), *Anapagrides* sensu stricto is characterized as follows: 1) phyllobranchiate gills; 2) males with short sexual tube on right fifth coxa; 3) prominent accessory tooth on the crista dentata; 4) females with single gonopore on coxa of left third pereopod; 5) coxa of the male third left pereopod frequently with female-type gonopore. In contrast, *Laurentia* has: 1) trichobranchiate gills; 2) males with long sexual tube arising from the coxa of left fifth pereopod and provided with a terminal tuft of stiff setae; 3) no accessory tooth on the crista dentata; 4) females with paired gonopores; 5) males without female-type genital pore on coxa of left third pereopod.

All of the species presently recognized in *Laurentia* are morphologically quite similar. Among the materials reviewed initially by M. de Saint Laurent, is an additional lot from the *Siboga* Expedition, which is assignable, at least in part to *Laurentia*; however, none of the specimens are in sufficiently good condition now to permit us to assign them with confidence to any of the described taxa. *Siboga* station 260 contains the bodies of at least five specimens of *Laurentia,* but also representatives of at least two other genera. Of the remaining appendages, some most probably belong to the *Laurentia* specimens, but none can be matched with certitude to any of the bodies.

Acknowledgements

We are deeply indebted to Michèle de Saint Laurent for having made the *Albatross* and *Siboga* specimens available for study. The photographs are the work of E. J. McGeorge. This is a scientific contribution from the Shannon Point Marine Center.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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Rediscovery of *Cymodocella algoense* from South Africa (Crustacea: Isopoda: Sphaeromatidae)

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Abstract.—The tiny sphaeromatid isopod *Cymodocella algoense,* which is characterized by a bulbous tubular posterior pleotelson, is rediscovered 120 years after having been described from a single specimen from Algoa Bay. The new material was collected from the delta of the Nahoon River on the east coast of South Africa.

Stebbing (1875) described a single tiny sphaeromatid isopod taken from the sand and fragments in a collection of sponges and gorgonians sent to him from Algoa Bay, South Africa. The species has not been recorded since. In 1910, Stebbing cast some doubt on the accuracy of the original locality data. Barnard (1940), in his list of *Cymodocella* species from South Africa, mentions *C. algoensis* with the annotation "species dubia, juv." thereby casting uncertainty on its identity.

In the course of an ecological survey of the benthos of the flood-tidal delta of the Nahoon River estuary, East London, on the east coast of South Africa, seven intertidal and seven subtidal sites were sampled by portable hydraulic suction sampler. Seven tiny adult female sphaeromatids were collected at two of the sites. On examination they proved to be the long forgotten *Cymodocella algoense,* which is here redescribed. The Nahoon River estuary is about 200 km north-east of the type locality, Algoa Bay. Three specimens have been deposited in the National Museum of Natural History, Smithsonian Institution (USNM 253240), two in the South African Museum, Cape Town, and two in the East London Museum, South Africa.

Family Sphaeromatidae
Subfamily Dynameninae
Cymodocella algoense (Stebbing, 1875)
Figs. 1–3

Sphaeroma algoense Stebbing, 1875:187, pl. 15, fig. 3.
Cymodocella algoensis.—Stebbing, 1905: 30; 1910:430.—Barnard, 1940:492 (species dubia).—Bruce, 1995:14.

Material.—5 non-ovigerous ♀, total length 2.9–4.0 mm, dissected ♀ 3.3 mm; Nahoon River estuary flood-tidal delta, East London, South Africa, 1.6 m at bottom of channel at mouth, low spring tide, coarse sand, coll. M. Bursey, 22 Feb 1993.—2 non-ovigerous ♀, total length 3.0–4.0 mm; Nahoon River estuary flood-tidal delta, East London, South Africa, 2 m on steep sloping bank 500 m from mouth, low spring tide, sand, coll. M. Bursey, 8 Feb 1993.

Description.—Female: Body dorsally strongly arched; surface of cephalon, pereon, and pleon smooth. Epistome roughly triangular, distally rounded, lateral margins slightly convex, leading to short, rounded, diverging 'legs'. Pleotelson reaching well beyond uropodal rami, consisting of broad, inflated basal half having 2 obscure, submedian protuberances, posterior half tubu-

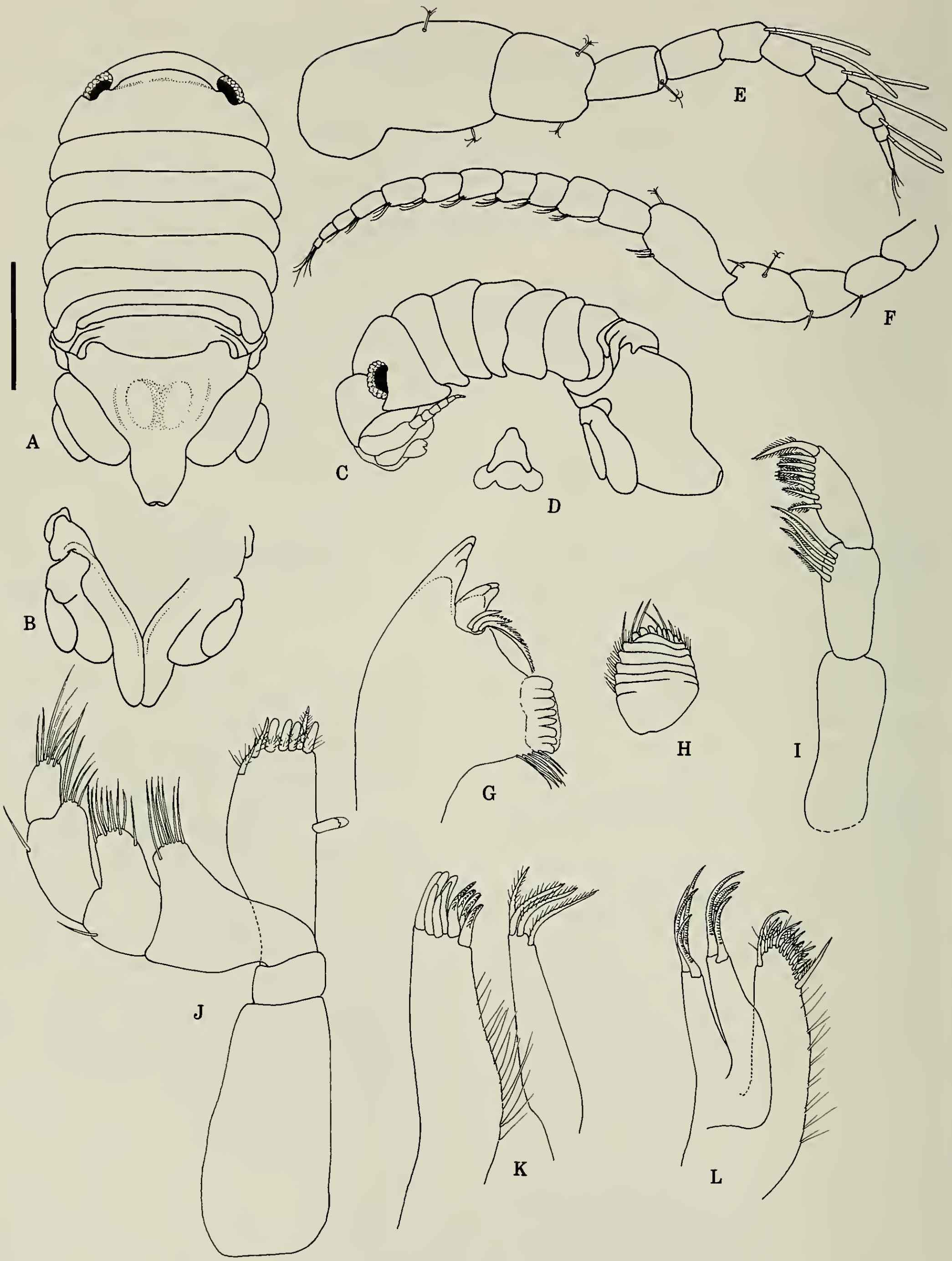

Fig. 1. *Cymodocella algoense*: A, Female in dorsal view, scale = 1 mm; B, Posterior pleon in ventral view; C, Female in lateral view; D, Epistome; E, Antennule; F, Antenna; G, Mandible; H, Grinding surface of mandibular molar; I, Mandibular palp; J, Maxilliped; K, Maxilla 1; L, Maxilla 2.

Fig. 2. *Cymodocella algoense*: A–G, Pereopods 1–7 respectively.

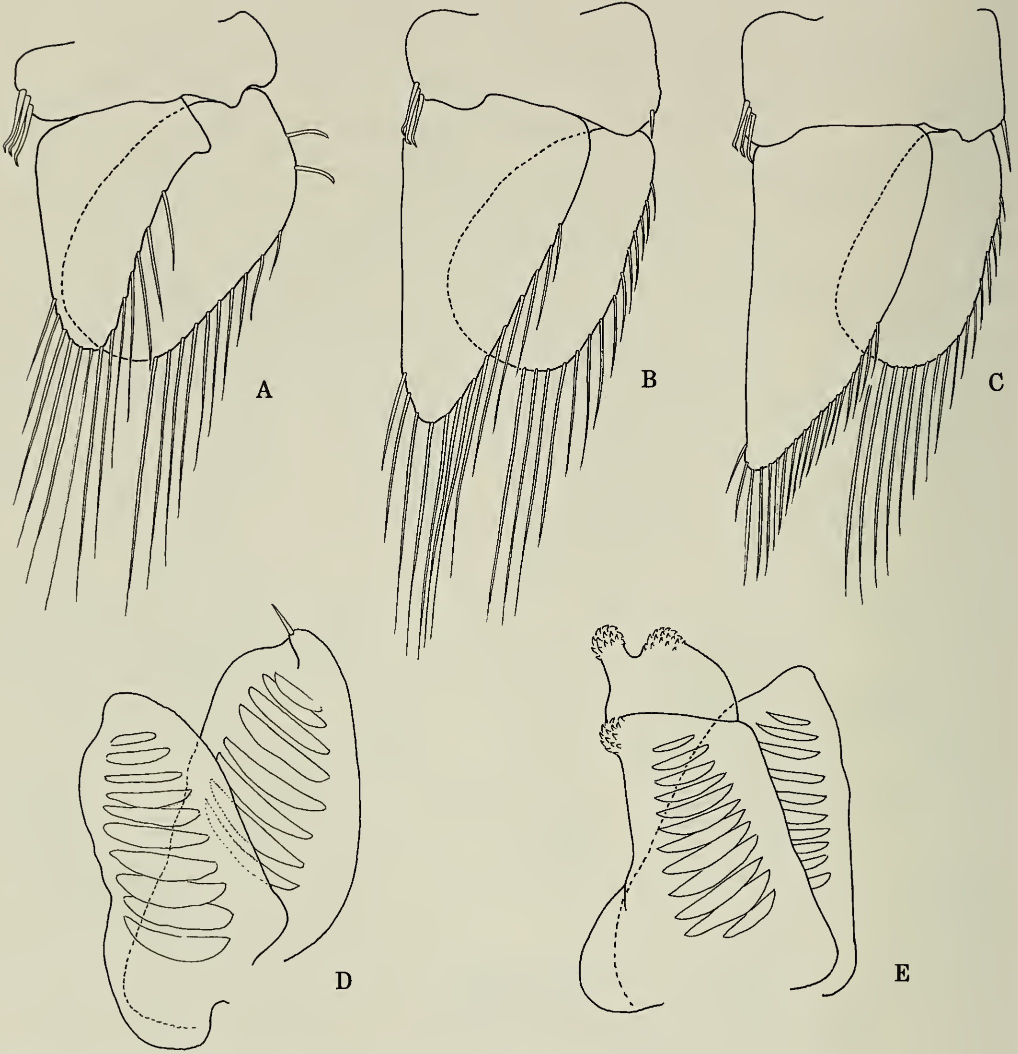

Fig. 3. *Cymodocella algoense*: A–E, Pleopods 1–5 respectively.

lar, apically slightly narrowed with circular foramen.

Antennular peduncle with robust basal article twice length of article 2, flanking and reaching anteriorly beyond epistome; article 3 slightly shorter and about half width of article 2; flagellum of 9 articles, single aesthetasc present on articles 3–8. Antennal peduncle of 5 articles, articles 1 and 2 short, subequal; articles 3–5 increasing in length distally; flagellum of 11 articles. Mandible with sclerotized incisor having 3 cusps; lacinia mobilis with 2 cusps; 2 short plus 2 more elongate fringed spines in spine-row; molar truncate, grinding surface subcircular, ridged, with marginal setae; palp with 4 fringed setae distally on article 2, 8 stout fringed setae on article 3. Maxilla 1, outer ramus with 5 broad simple and 4 denticulate distal spines; inner ramus with 4 circumplumose setae. Maxilla 2, inner ramus with about 12 mesiodistal circumplumose setae; outer ramus with 4 elongate denticulate spines distally on each lobe. Maxilliped, endite distally having 7 stout, basally circumplumose and distally rounded setae, with single coupling hook on mesial margin; articles 2–5 of palp distomesially setose, articles 2 and 3 mesiodistally somewhat lobed. Pereopod 1 more robust but shorter than following pereopods; basis having pile of short stiff setules on dorsal surface; ischium with several simple setae on dorsal surface; merus with single stout anterodistal and posterodistal fringed seta; carpus triangular, with very short free anterior margin, with stout posterodistal fringed seta; propodus with 3 stout fringed setae on posterior surface; dactylus having bilobed accessory spine at base of unguis. Pereopod 2 more slender than following legs; basis with pile of short stiff spinules on anterior surface; ischium with 3 elongate simple setae on anterior surface; merus with 2 simple anterodistal setae; carpus rectangular, ⅔ length of propodus. Pereopods 3–7 essentially similar, pereopod 7 slightly more slender than preceding legs; basis and ischium with pile of short spinules on anterior surface; ischium with 4–6 elongate simple setae on anterior surface; merus much shorter than ischium, with 2–4 simple setae on rounded anterodistal lobe; carpus with single bifringed seta distally, except in pereopod 7 which has 6 bifringed setae; anterior surfaces of merus, carpus, and propodus having numerous short scales/spinules; dactylus with bifid accessory spine at base of unguis. Pleopods 1–3 each with elliptical exopod bearing plumose marginal setae; endopod triangular, subequal in length to exopod in pleopod 1, reaching well beyond exopod in pleopods 2 and 3, bearing plumose marginal setae. Pleopod 4, both rami pleated, exopod with single short distal seta. Pleopod 5, both rami pleated, exopod with transverse suture in distal half, armed with 3 spinulose lobes. Uropod with exopod freely articulating under endopod, elliptical, considerably shorter than endopod, latter distally rounded.

Male: unknown.

Remarks.—Bruce (1995), in a revision of the tube-tailed sphaeromatids, demonstrated that the genus *Cymodocella* was polyphyletic, defined a second genus, *Diclidocella,* to accommodate some of the species, moved two southern African species to *Ischyromene,* and removed *C. hawaiiensis* Bruce, 1994, from the group altogether.

The genus *Cymodocella* Pfeffer, 1887, currently contains four species (see Bruce 1995:5). The type species, *C. tubicauda* Pfeffer, 1887, was redescribed by Brandt & Wägele (1989). *Cymodocella algoensis* can now be included in this group, agreeing well with the revised diagnosis provided by Bruce (1995). Although Stebbing's description of *C. algoense* is limited, the figure of the whole animal in dorsal view shows the distinctively shaped convex-sided pleotelsonic tube. The remaining four South African species are of uncertain generic status, and require redescription, given the lack of detail in existing descriptions.

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The first author thanks Leon Engelbrecht, Robson Ntsabo, and Deon Smit for helping to operate the hydraulic pump during sampling. Dr. Niel Bruce of the Zoological Museum, Copenhagen, commented on the manuscript, and generously shared his unpublished work on the tube-tailed sphaeromatids, which greatly improved this short contribution. We are also grateful to Ms. Marilyn Schotte for reading a draft of the paper.

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Spelaeomysis villalobosi, a new species of mysidacean from northeastern México (Crustacea: Mysidacea)

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Abstract.—*Spelaeomysis villalobosi,* a new species of mysid is described from subterranean habitats in Nuevo León, México. This is the third known species of *Spelaeomysis* from México. *Spelaeomysis villalobosi* is similar to *Spelaeomysis quinterensis* (Villalobos-Figueroa, 1951) previously described from caves in Tamaulipas and San Luis Potosí, but differs in the rounded shape of the anterolateral lobe of the eyestalk, in the 4 cusped incisor of the mandible, the presence of three spines on the dactylus of the maxilliped, and three claws on the dactylus of pereopod 1; the exopod of pleopod 4 is 2-segmented; the margin of the telson is convex. A key to the known species of *Spelaeomysis* is given.

Resumen.—*Spelaeomysis villalobosi,* es una nueva especie de misidáceo hipogeo encontrada en el Estado de Nuevo León, México. Esta especie es la tercera conocida de *Spelaeomysis* en México. *Spelaeomysis villalobosi* presenta parecido morfológico con *Spelaeomysis quinterensis* Villalobos-Figueroa, 1951 ubicada en cuevas de Tamaulipas y San Luis Potosí, pero existen diferencias notorias entre ambas especies, principalmente con respecto a la forma de los pedunculos oculares, la dentición del proceso incisivo de la mandíbula, la presencia de espinas en el dactilo del maxilipedio, el número de uñas en el dactilo del pereíopodo 1, pleópodo 4 con su exopodo con 2 segmentos en vez de 4, y la forma y ornamentación del telsón y el urópodo. Se incluye una clave para las especies de *Spelaeomysis* conocidas.

The freshwater mysids of México are poorly known. *Antromysis cenotensis, A. reddelli, Spelaeomysis olivae* and *S. quinterensis* have been found in hypogean habitats (Bowman 1982). *Taphromysis louisianae* is the first freshwater epigean mysidacean recorded from México (García-Garza et al. 1992). *Spelaeomysis quinterensis* was recorded from caves in Tamaulipas and San Luis Potosí (Villalobos-Figueroa 1951; Reddell 1981), and *S. olivae* is known from caves in Oaxaca (Bowman, 1973), both species have disjunct distributions.

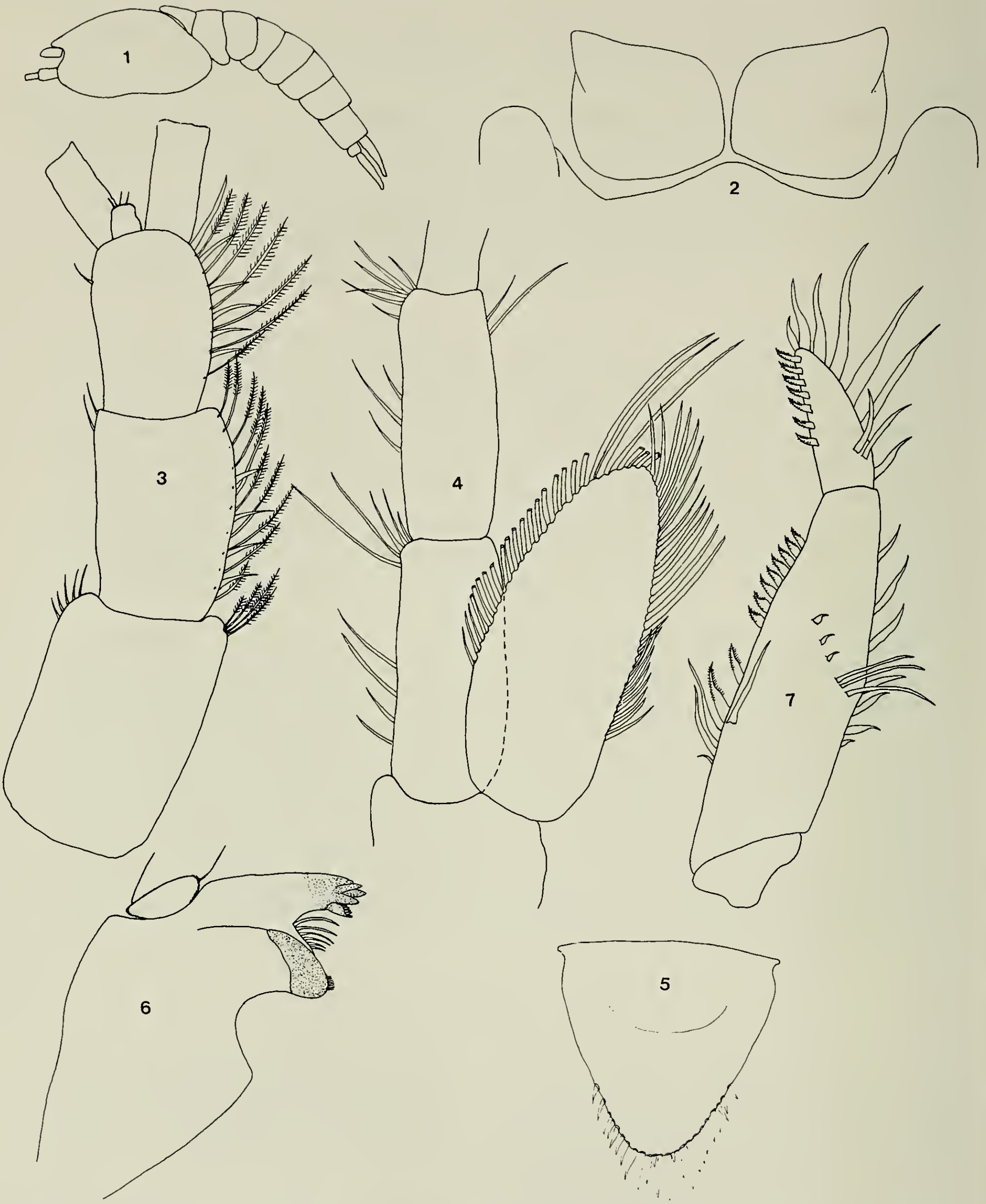
Family Lepidomysidae Clarke, 1961

Genus *Spelaeomysis* Caroli, 1924

Spelaeomysis villalobosi, new species

Figs. 1–18

Material examined.—Holotype male, UANL (Universidad Autónoma de Nuevo León) CCRMY001, 1 female paratype (UANL CCRMY002) from a draw-well, Rancho Monte Carmelo, Cerralvo, Nuevo León, 100 Km Northeast of Monterrey, Nuevo León, about 26°04′N, 99°37′W, 21 Oct 1989, leg. María Elena García-Garza, 1 male paratype (UANL CCRMY003) from



Figs. 1–7. *Spelaeomysis villallalobosi* n. sp., Male holotype: 1, Male, lateral; 2, Eyestalks; 3, Antenna 1; 4, Antenna 2; 5, Telson; 6, Mandible; 7, Mandible palp.

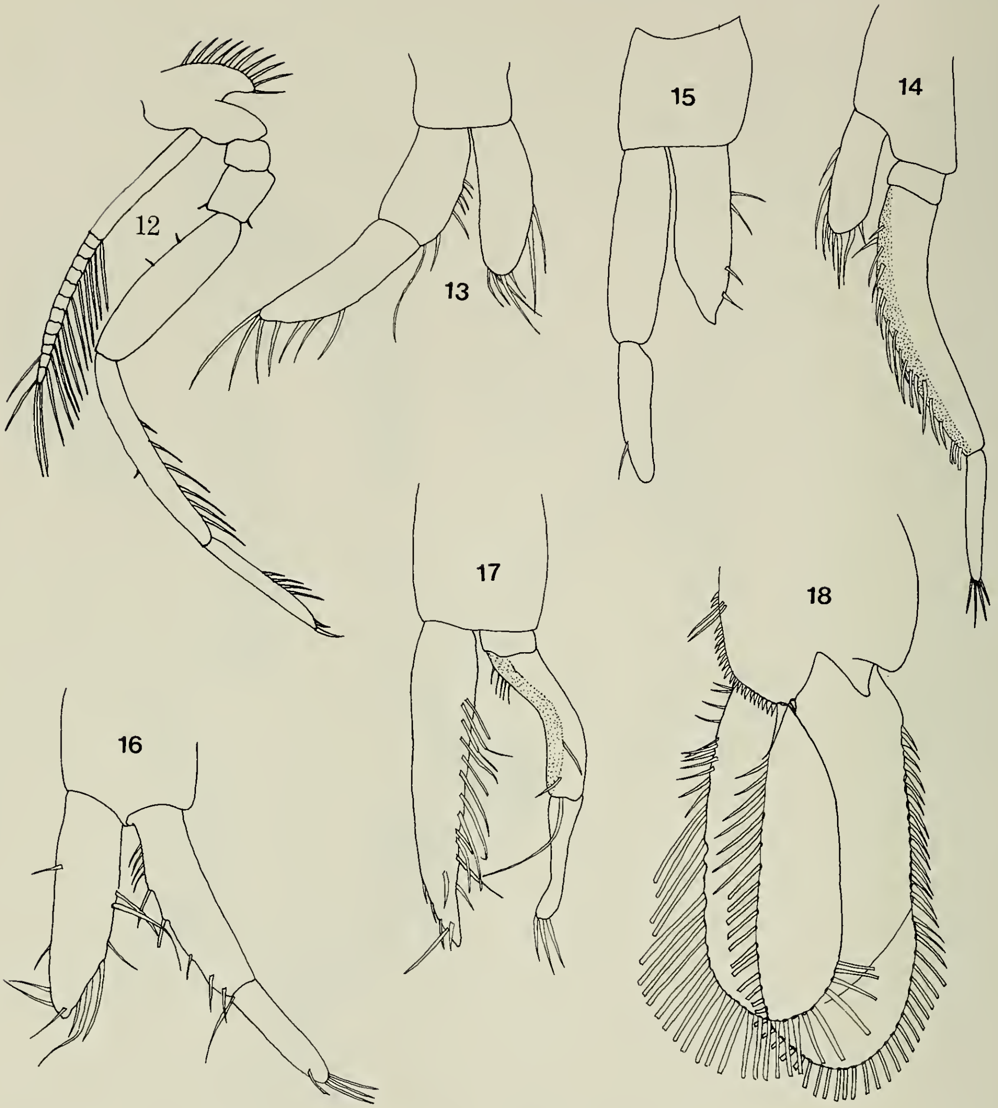
a small spring near the Pilon River, Montemorelos, Nuevo Leon, about 25°11′N, 99°48′W, 17 May 1990, leg. M. Valdez-Marroquín. 3 male paratypes (UANL CCRMY004) from Chorrera Cave, Highway Linares-Galeana, Linares, Nuevo León, 24°46′N, 99°37′W, 4 Apr 1994, leg. Carlos Cavazos-Camacho.

Description.—Length of holotype 7 mm. Caparace with triangular rostrum (Fig. 2)

Figs. 8–11. *Spelaeomysis villalobosi* n. sp. Male holotype: 8, Maxilla 1; 9, Maxilla 2; 10, Maxilliped; 11, Pereopod 1.

not covering eyestalks; anterolateral lobe of caparace reaching to midlength of eyestalks. Eyestalk without ommatidia slightly wider than long, produced anterolaterally into pointed lobe.

Pleuron of pereonite 7 produced poste-



Figs. 12–18. *Spelaeomysis villalobosi* n. sp. Male holotype: 12, Pereopod 7; 13, Pleopod 1; 14, Pleopod 2; 15, Pleopod 3; 16, Pleopod 4; 17, Pleopod 5; 18, Uropod.

riorly into lobe. Telson linguiform (Fig. 5), as long as wide at base; posterior 0.4 armed, with 24 marginal spines; apex with 2 long spines flanked by 2 short spines.

Antenna 1 peduncle (Fig. 3), segment 1 widest, about 1.1 times longer than segment 2; segment 3, shortest 0.95× as long as segment 2; segment 1, with 4 plumose setae at distomedial corner and 5 naked setae at distolateral corner; segment 2, with row of plumose and naked setae on medial margin and 2 small setae on distolateral corner; segment 3 with naked and plumose setae on medial margin and small seta on distal part of lateral the margin; distal lobe as wide as long; bearing 3 small apical setae. Flagellum with 45 segments. Antenna 2 (Fig. 4), scale 2.5× longer than wide, reaching to first third of last segment of peduncle, flagellum broken.

Table 1.—Differences between *Spelaeomysis quinterensis* and *S. villalobosi.*

	S. quinterensis	*S. villalobosi*
Eyestalk anterolateral lobe	Rounded	Pointed
Telson length/width	1.3×	1.0×
Telson shape	Narrows at anterior	Margins evenly convex
Mandibular incisor	3 strong teeth	4 strong teeth
Mandibular palp	With slightly concave margins	
Mandibular palp segment 2/segment 3	1.8×	2.6×
Maxilla 2 endopod	Segment 1 longer than segment 2, not produced distomedially	Segment 1 shorter than segment 2, produced distomedially
Maxilliped, merus of endopod	4 setae	7 setae
Pereopod 1 merus	2 setae	6 setae
Pereopod 1 dactyl	1 terminal claw	3 terminal claws
Pleopod 4 exopod	4 segments	2 segments
Uropod: exopod/endopod	1.25×	1.30×

Left Mandible (Fig. 6), incisor with 4 conspicuous cusps; lacinia mobilis bearing 5 denticles; spine row with 6 naked setae; molar process armed with minute setae; palp (Fig. 7), segment 22.6× longer than segment 3, both segments with stout barbed setae on distal part of outer margin.

Maxilla 1 (Fig. 8), inner lobe with 4 pectinate terminal setae and 3 naked subterminal setae; 3 small setae on outer margin and one long setae on proximal inner margin. Outer lobe with 14 long apical setae of different types; inner margin with row of fine hairs extending onto surface.

Maxilla 2 (Fig. 9), segment 1 shorter than segment 2, produced medially to midlength of segment 2; segment 2 with 7 setae on distomedial margin; exopod 3× longer than wide, with about 15 long plumose marginal setae.

Maxilliped (Fig. 10), merus of the endopod with 7 plumose setae, carpus with 7 plumose setae. Propodus, distal outer margin with 2 long plumose setae and 3 smaller naked setae; dactylus with 3 spines and 4 naked setae in distal part.

Pereopod 1 (Fig. 11), endopod is robust; merus with 6 naked setae; outer margin propodus with a long setae and 3 smaller setae; dactylus ending in 3 claws. Pereopds 2–7 as in Fig. 12.

Pleopod 1 (Fig. 13), endopod with 2 long naked setae on medial margin and 5 long naked distal setae; exopod proximal segment with 4 short and 3 longer naked medial setae; distal segment with 7 long naked setae. Pleopod 2 (Fig. 14), endopod elongate, 2.8 times longer than width; segment 3 of exopod about half length of segment 2, setae on segment 2 short.

Pleopod 3 (Fig. 15), endopod not reaching distal part of exopod segment 1, with 4 small setae on inner margin; segment 2 of exopod with a subterminal seta. Pleopod 4 (Fig. 16), exopod with 2 segments. Pleopod 5 (Fig. 17), exopod subequal in length to endopod; segment 2 about 1.25× longer than segment 3, bent laterally at midlength, with 5 small proximolateral setae, 2 longer subterminal setae, and a terminal seta as long as 3rd segment.

Uropod protopod (Fig. 18), medial lobe with numerous curved spines and a long tooth; proximal part with 2 slender setae. Endopod reaching oblique suture of exopod. Exopod, proximal segment with 15 spines of almost equal size.

Etymology.—Named in memory of Dr. Alejandro Villalobos-Figueroa, distinguished Mexican carcinologist.

Remarks.—*Spelaeomysis villalobosi* is the third species of the genus known for México. *Spelaeomysis quinterensis* (Villalobos-Figueroa, 1951) and *S. villalobosi,* new species, have similar distribution in northeastern México; and *S. olivae* (Bowman, 1973) is known only from Oaxaca state in southern México. *Spelaeomysis villalobosi* is similar to *S. quinterensis*; the principal differences are listed in Table 1. The seven known species of *Spelaeomysis* may be distinguished by the following key.

Key to the Species of *Spelaeomysis*

1\. Eyes with small anteriolateral area of ommatidia 2
– Eyes without visual elements 3
2\. Apical spine of telson about 2× length of 2 flanking spines . . . . *S. serratus* (Fage, 1924)
– Apical spine of telson more than 6× length of 2 flanking spine . . . *S. cardisomae* Bowman 1973
3\. Eyestalks fused medially, forming single plate . . . . *S. longipes* (Pillai & Mariamma, 1963)
– Eyestalks separate 4
4\. Eyestalks produced anterolaterally into subtriangular lobe. 5
– Eyestalks subquadrilangular, not produced anterolaterally 6
5\. Pleopod 4 with L/W 4 segmented exopod; telson about 1.2; lateral margins slightly concave near midlength . . . . . .*S. quinterensis* (Villalobos-Figueroa, 1951)
– Pleopod 4 with L/W 2 segmented exopod; telson about 1.0; lateral margins evenly convex . . . .*S. villalobosi* n. sp.
6\. Telson L/W 1.5, with about 20 marginal spinal . . . .*S. nuniezi* Bacescu & Orghidan, 1971
– Telson L/W 1.1–1.2, with about 40 marginal spines . . . . . *S. olivae* Bowman, 1973

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A new copepod species from California, U.S.A.: *Hesperodiaptomus californiensis* (Crustacea: Copepoda: Calanoida: Diaptomidae)

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Abstract.—*Hesperodiaptomus californiensis,* new species (Copepoda: Calanoida: Diaptomidae) was collected from vernal pools in Lassen County, northern California, U.S.A. It differs from its three most morphologically similar congeners, *Hesperodiaptomus schefferi, Hesperodiaptomus victoriaensis* and *Hesperodiaptomus kiseri* in having both leg 5 endopods of the male relatively long, the left lateral protrusion on the genital double somite of the female directed dorsally, and in other details. Co-occurring diaptomids were *Hesperodiaptomus novemdecimus* and *Leptodiaptomus tyrrelli.*

A new species of diaptomid copepod was collected in Lassen County, California, as part of a study of vernal pools (described by King et al. 1996). The new copepod occurred in three pools and at the time of collection was abundant in every pool.

Wilson (1959) listed 16 species of *Hesperodiaptomus* in North America; since then no new species has been recognized from this continent. However, the taxon *Hesperodiaptomus arcticus* (Marsh, 1920) s.l. may be composed of several cryptic species. Boileau & Hebert (1988) and Boileau (1991) found genetic differences between different North American populations of *H. arcticus,* which were accompanied by subtle morphological differences. On the other hand, Stepanova (in Borutskii et al. 1991) rejected efforts by Streletskaya (1983, 1986) to split Siberian *H. arcticus* into three taxa: *H. koolensis* Streletskaya, 1983, *H. judayi* Streletskaya, 1986 and *H. kurenkovi* Streletskaya, 1986, because of the supposedly minor degree of morphological differences.

Some other members of *Hesperodiaptomus* are so similar morphologically that the females cannot be reliably assigned to a particular species with present knowledge. These possible species complexes are *H. breweri* (Wilson, 1958a), *H. eiseni* (Lilljeborg in Guerne & Richard, 1889), and *H. arcticus*; as well as *H. kiseri* (Kincaid, 1953) and *H. victoriaensis* (Reed, 1958). The high degree of morphological similarity between *H. kiseri* and *H. victoriaensis* creates some difficulty in establishing the species from California as a new taxon, because it shares several characters with both these species.

Hesperodiaptomus species and other diaptomid copepods are characterized classically by the features of the fifth legs of the males and females, the right antennule of the male and setation of the left antennule of the male and both antennules of the female, and features of the somites, particularly the shape of the thoracic "wings" (expansions of the sixth thoracic somite). Pending eventual revision of the genus *Hesperodiaptomus* and the possible discovery of additional morphological and genetic characteristics, we describe the new species using these traditional discriminators.

The copepod specimens were originally fixed in buffered formalin and transferred to 70% ethanol for long term storage. Field sampling methods were described by King et al. (1996). Descriptions were made from whole specimens in glycerin and/or lactic acid; dissected specimens were mounted either in CMC-10 or in commercial polyvinyl lactophenol with a little Chlorazol Black E added. All measurements were made from specimens in glycerin. Specimens were deposited in the collections of the United States National Museum of Natural History, Smithsonian Institution (USNM) and the Natural History Museum of Los Angeles County, California (LACM).

Family Diaptomidae G. O. Sars
Genus *Hesperodiaptomus* Light, 1938
Hesperodiaptomus californiensis, new species
Figs. 1–3

Type material.—Holotype ♂, USNM 264057; allotype ♀, USNM 264058; paratypes: 3 ♂♂ 3 ♀♀, each dissected on slide in PVL or in CMC-10, and 464 ♂♂ ♀♀ + copepodids, USNM 264059; 463 ♂♂ ♀♀ + copepodids, LACM 95-50.1; all from California, Lassen County, pool #41, 40°37′N, 121°03′W, immediately adjacent to west side of Route 44, 1.4 km north of Bogart Safety Rest Area/Ranger Station, 2 m tow of wet meadow edge with plankton net, sample 215.

Additional, non-type material.—372 ♂♂ ♀♀ + copepodids, California, Lassen County, pool #42, 40°32′N, 121°0′W, 30 m west of Route 44, just south of railroad track crossing, 2 m tow of wet meadow lake edge with plankton net, sample 218, USNM 264060. 894 ♂♂ ♀♀, pool #42 bottom, sample 217, LACM 95-50.3. 41 ♂♂ ♀♀, pool #41, sample 214, USNM 264061. 400+ ♂♂ ♀♀, pool #42 surface, sample 216, LACM 95-50.4. 28 ♂♂ ♀♀, California, Lassen County, pool #43 (Long Lake), 40°31′N, 120°59′W, 100 m west of Route 44, about 0.36 km south of pool #41 (about 1.5 km south of intersection with Route A21), 2 m tow of wet meadow lake bottom with plankton net, sample 220, USNM 264062. 10 ♂♂ ♀♀, pool #43 (Long Lake), sample 219, LACM 95-50.2. All collected 23 April 1992 by J. L. King, D. Gluesenkamp and J. Tritt. Undissected specimens preserved in 70% ethanol.

Co-occurring species (determined by JWR).—Pool #41: *Hesperodiaptomus novemdecimus* (Wilson, 1953), *Leptodiaptomus tyrrelli* (Poppe, 1888), *Acanthocyclops carolinianus* (Yeatman, 1944), *Diacyclops crassicaudis* var. *brachycercus* (Kiefer, 1927), *Microcyclops rubellus* (Lilljeborg, 1901), *Bryocamptus washingtonensis* Wilson, 1958b; pool #42: *H. novemdecimus, L. tyrrelli, A. carolinianus, Acanthocyclops vernalis* (Fischer, 1853) s.l., *Diacyclops navus* (Herrick, 1882); pool #43 (Long Lake): *H. novemdecimus, L. tyrrelli, A. carolinianus, B. washingtonensis.*

Male.—Length (mm) of holotype 2.21; of ten paratypes, mean = 2.14, median = 2.18, range = 1.93–2.32. Pediger 5 (sixth thoracic somite) (Fig. 1a), lateral "wings" symmetrical, each with two sensilla. Urosome (Fig. 1a) symmetrical except urosomites 1 and 4 slightly produced laterally and posteriorly. Urosomites 2–4 and caudal rami with pore-canals, middle dorsal pore-canal of urosomite 4 displaced slightly to left of dorsal midline. Inner sides of caudal rami with long hairs, rest of ramal surfaces with short sparse hairs. Rostral points (Fig. 1b) short, acute.

Antennules (Fig. 1a, c, d) reaching middle of urosomite 2. Right antennule with two setae on segment 6; segment 8 with one seta and one spine; segment 10 with one seta and one stout spine reaching middle of segment 12; segment 11 with one seta and one stout spine, reaching distal end of segment 13; segment 13 with one stout spine reaching past middle of segment 14; segment 14 without spine; segment 15 with small acute process pointing distally; segment 16 with two setae. Segment 23 (Fig. 1d), process at distal end straight, reaching

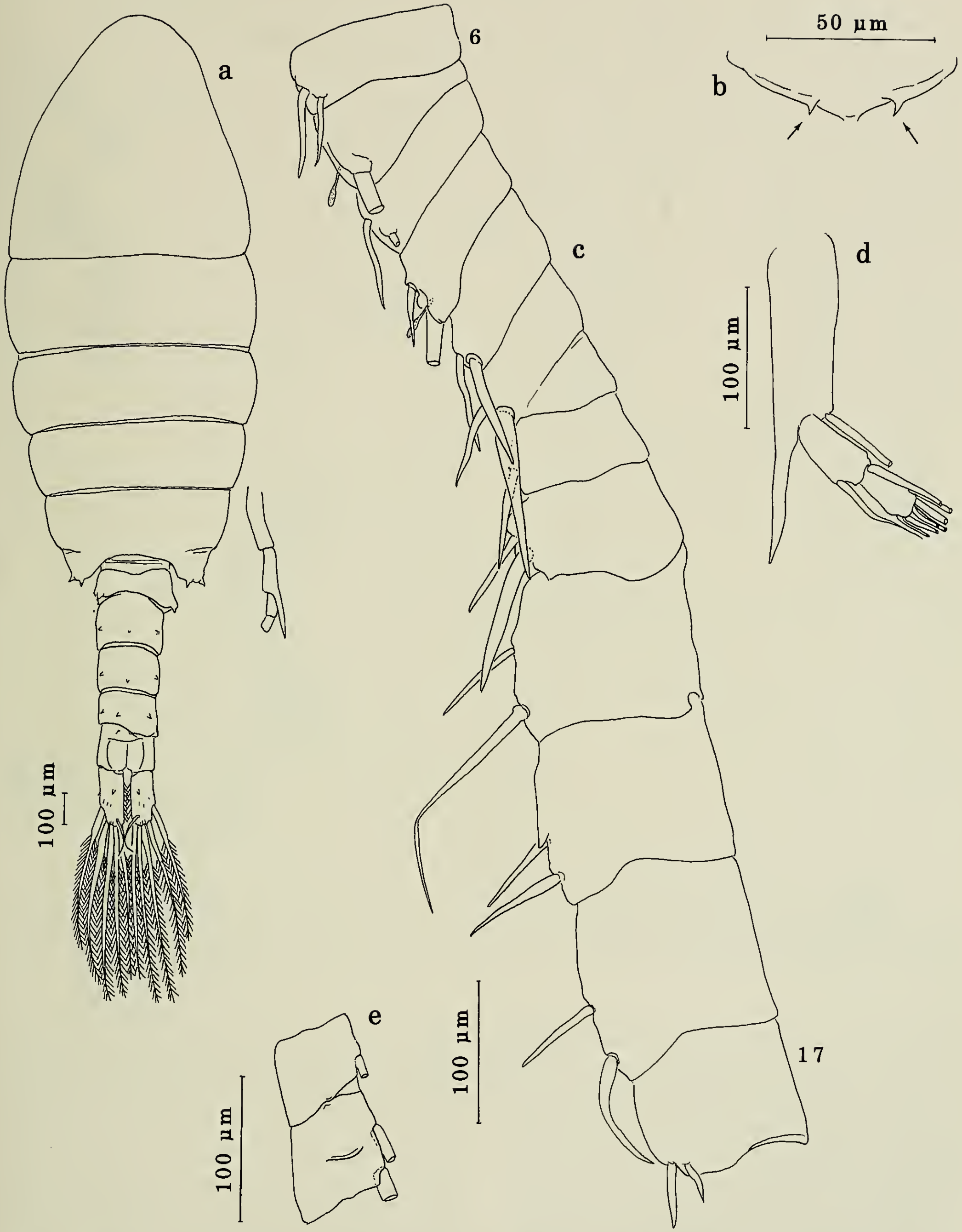

Fig. 1. *Hesperodiaptomus californiensis,* new species, male: a, Habitus, dorsal; b, Rostral points (indicated by arrows); c, Right antennule, segments 6–17; d, Right antennule, segments 23–25; e, Leg 2 endopod, segments 1 and 2, posterior.

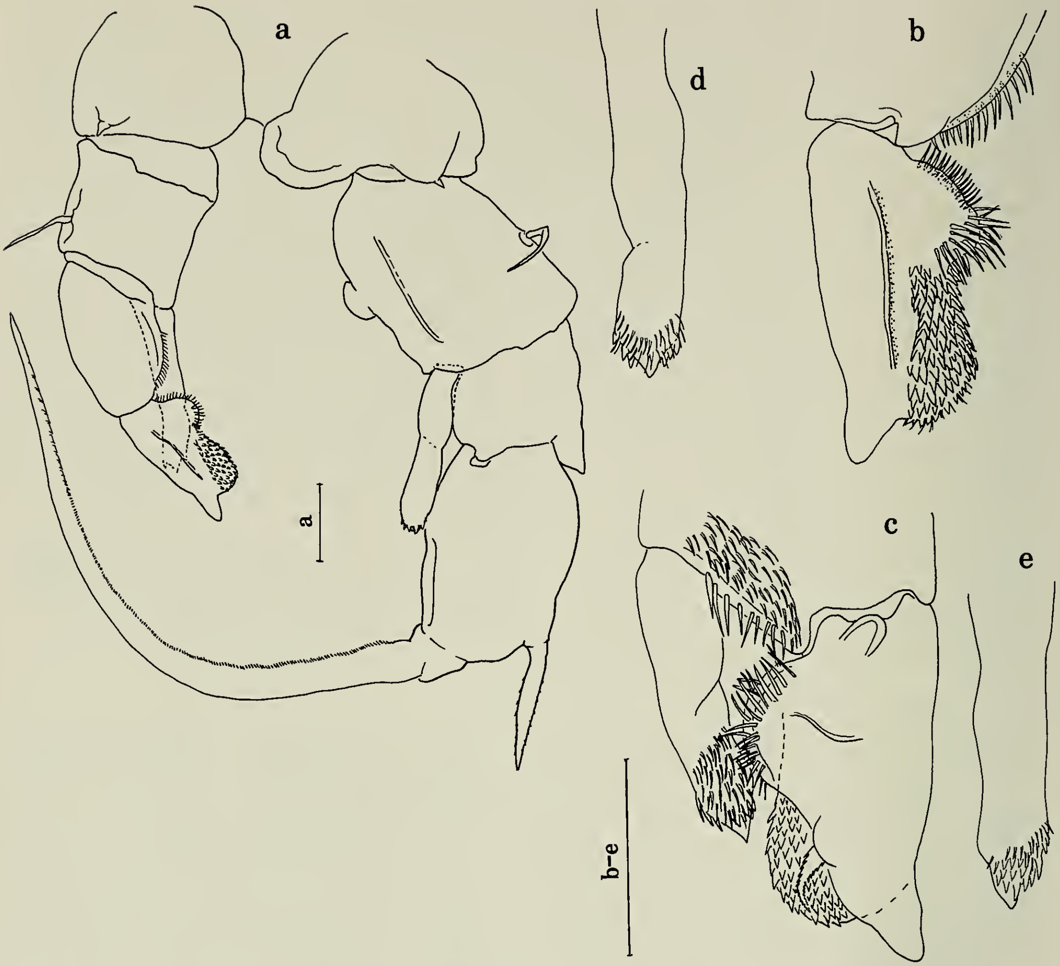

Fig. 2. *Hesperodiaptomus californiensis,* new species, male: a, Leg 5, posterior; b, Left leg 5 exopod, posterior; c, Left leg 5 exopod and endopod, anterior; d, Left leg 5 endopod, posterior; e, Right leg 5 endopod, anterior. Both scales = 50 μm.

end of last segment of antennule. Setation of left antennule as in female.

Leg 2 endopod segment 2 (Fig. 1e) without defined Schmeil's organ, but with small transverse ridge, more or less developed on different specimens.

Left leg 5 (Fig. 2a–d): Coxa, small process tipped with sensillum near outer posterodistal margin. Basis with lateral seta. Exopod segment 1 longer than segment 2, with haired pad on inner margin, hairs thick and as long as about half width of endopod. Exopod 2, tip forming stout, blunt, smooth lateral process; also with serrate digital process. Inner margin of exopod 2 with two pads, proximal pad haired, proximal hairs of this pad thinner and shorter than distal hairs; distal pad covered with rows of teeth and few tiny hairs near tip of exopod. Posterior surface of exopod 2 with longitudinal groove. Endopod reaching midlength of exopod 2, of one segment, narrowing at distal ⅓. Tip of endopod narrowing in acute process; also with five small subterminal spines and group of subterminal hairs.

Right leg (Fig. 2a, e): Coxa with small posterodistal process ending in sensillum. Basis with lateral seta, shallow longitudinal

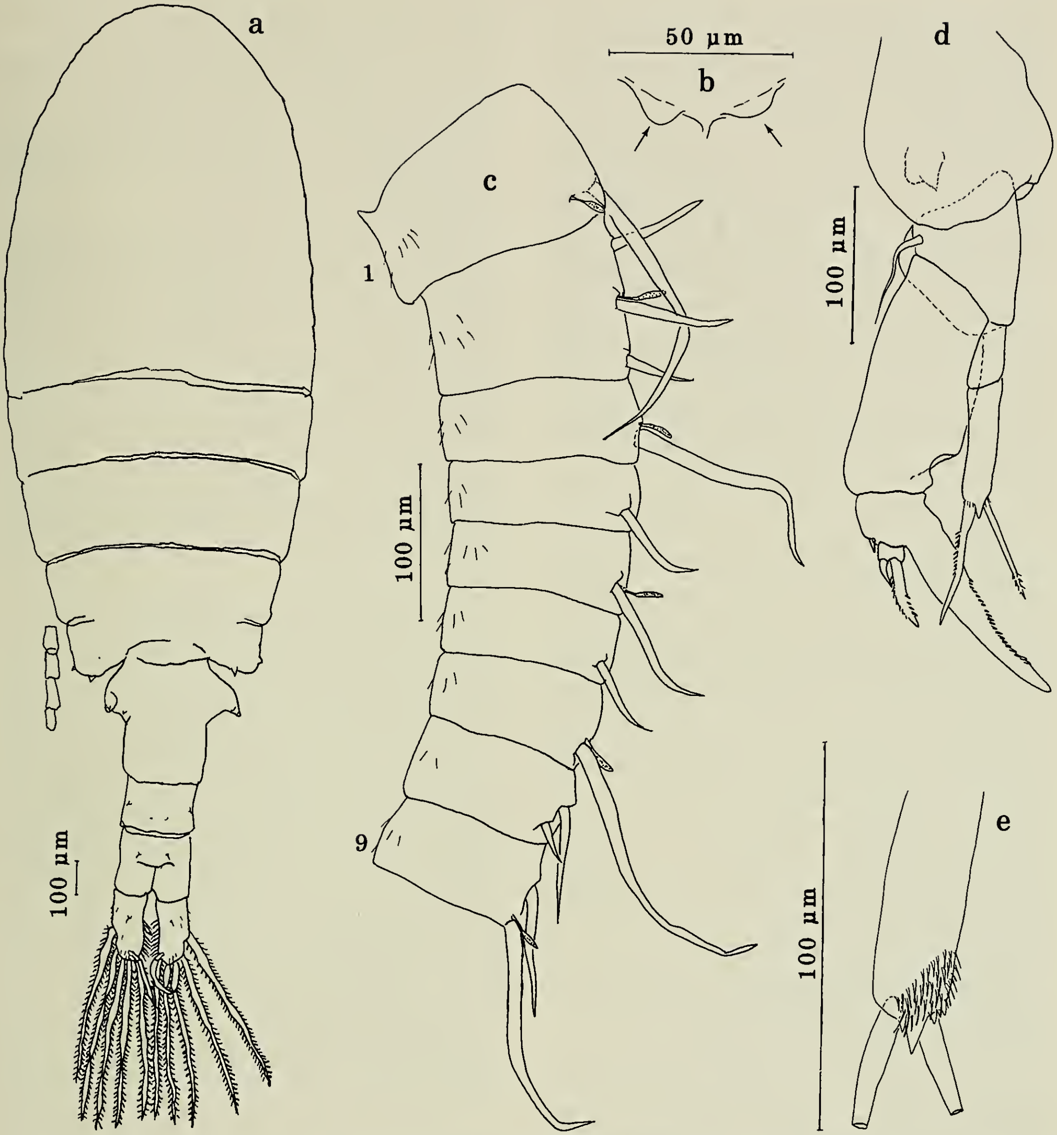

Fig. 3. *Hesperodiaptomus californiensis,* new species, female: a, Habitus, dorsal; b, Rostral points (indicated by arrows); c, Antennule, segments 1–9; d, Leg 5, anterior; e, Tip of leg 5 endopod, posterior.

groove on posterior surface, and rounded, unornamented protrusion on middle of inner margin; length of protrusion equal to width of endopod, its width equal to ½ width of endopod. Outer margin of exopod 1 with large, distally directed conical process on distolateral corner. Exopod 2 almost twice length of exopod 1, with shallow longitudinal groove along distal ½ of inner margin; lateral spine at distal ¾ of exopod 2, ½ thickness of endopod and ½ length of exopod 2, straight, finely denticulate. Terminal claw tapering gradually from enlarged base, twice length of exopods 1 and 2 combined, with row of teeth extending from tip of claw almost to base. Right endopod without suture on posterior surface, suture visible on anterior surface where endopod narrows slightly at midlength; endopod tapering to blunt point; with 3–5 spines near outer distal margin, and subterminal group of small hairs.

Female.—Length (mm) of allotype 2.39; of ten paratypes, mean = 2.20, median = 2.22, range = 1.95–2.33. Prosome (Fig. 3a) symmetrical, thoracic wings symmetrical, each with two sensilla located on lateral and posterior margins. Genital double somite extended laterally in asymmetrical conical projections each tipped with sensillum, left projection directed dorsally, right projection laterally. Caudal rami haired in pattern similar to that of male. Rostral points (Fig. 3b) low, rounded.

Antennule (Fig. 3a, c) reaching midlength of genital double somite. Segments 1–8 or 9 each with few tiny hairs irregularly scattered on posterior surface. Seta on segment 1 long, reaching midlength of segment 4. Appendages per segment as follows (Roman numerals = segment, Arabic numerals = number of setae, a = aesthetasc, sp = spine): I(1+a), II(3+a), III(1+a), IV(1), V(1+a), VI(1), VII(1+a), VIII(1+sp), IX(2+a), X(1), XI(2), XII(1+sp+a), XIII(1), XIV(1+a), XV(1), XVI(1+a), XVII(1), XVIII(1), XIX(1+a), XX(1), XXI(1), XXII(2), XXIII(2), XXIV(5+a).

Leg 2 (not figured) of all females examined without trace of Schmeil's organ or transverse ridge on endopod 2.

Leg 5 (Fig. 3d, e): Coxa with posterior lateral protrusion ending in sensillum. Basis with lateral seta reaching ⅓ of length of exopod 1. Endopod two-segmented, distal segment twice length of proximal segment. Endopod 2 with two setae at tip, tip protruding in acute point between these setae, and 3–5 subterminal teeth surrounding tip of endopod. Exopod 2 a little longer than exopod 1, claw with inner margin toothed. Exopod 2 with small articulated spine lateral to outer margin of exopod 3, reaching from slightly beyond middle to end of exopod 3. Exopod 3 distinct from exopod 2. Inner spiniform seta of exopod 3 serrate on one or both margins, longer and stouter than outer, naked spiniform seta.

Type locality.—Pool #41, 40°37′N, 121°03′W, Lassen County, California.

Etymology.—The species name is given after the State of California, in which the type locality is located.

Habitat description.—The three pools (41, 42 and 43—Long Lake) are relatively large for vernal pools (400 × 400 m, 300 × 300 m and 800 × 200 m respectively at time of sampling), shallow (maximum depths 0.15–0.6 m), clear, and covered 70–90% with aquatic grasses. The electrical conductivity was low (30, 60 and 10 μMHO), water temperature 16, 16 and 23 C, pH 7.7, 7.7 and 8.2, alkalinity 20, 28 and 8 ppm, and total dissolved solids 10, 30 and 0 ppm respectively.

Discussion and comparisons.—*Hesperodiaptomus californiensis* differs from *H. schefferi* (Wilson, 1953) in the male leg 5: the conical process on the coxa of the right leg is larger; the inner protrusion on the basis of the right leg of *H. californiensis* is rounded, not quadrate as in *H. schefferi*; and the endopods of both left and right legs are longer in *H. californiensis.* In leg 5 of the female, *H. californiensis* has the endopod extended in a terminal point. The genital double somite in *H. schefferi* has very slight lateral projections.

Hesperodiaptomus victoriaensis is morphologically closest to *H. californiensis.* The male of *H. californiensis* differs from *H. victoriaensis* in having the right leg 5 with longer endopod, and in having the inner process on the basis larger and placed at about midlength rather than at the inner proximal corner. In the female of *H. victoriaensis,* the lateral projections of the genital double somite are slightly asymmetrical, the left projection being directed posterolaterally rather than dorsally.

Both *H. schefferi* and *H. victoriaensis* possess an acute process on the distal margin of segment 16 of the right antennule of the male. Such a process is lacking in *H. californiensis.*

The differences between *H. kiseri* and *H. californiensis* are primarily in leg 5 of the male: in *H. californiensis* there is no proximal protrusion on the inner margin of the right basis, and only one protrusion on the middle of the inner margin. There is no distally placed spiniform projection on the inner margin of the right exopod 1. The small protrusion on the posterior surface of the right exopod 2, present in *H. kiseri,* is lacking in *H. californiensis.* The claw is smoothly tapered in *H. californiensis,* without angles as in *H. kiseri.* The lateral projections of the genital double somite of the female are asymmetrical in *H. californiensis,* symmetrical in *H. kiseri.* The thoracic wings are not expanded laterally in *H. californiensis.*

In *H. californiensis,* the left lateral projection on the female double somite is dorsally directed. The second (middle) urosomite is relatively long. On leg 5 of the male, the endopodites are relatively longer than in other similar species.

In the most recent diagnosis of the genus *Hesperodiaptomus,* Borutskii et al. (1992) stated that the left antennule of the male is like that of the female. However, *H. hirsutus* (Wilson, 1953) always, and *H. schefferi* sometimes, display sexual dimorphism in setation on some segments (Wilson 1953). The observed setation pattern of *H. californiensis* was constant, similar in both sexes, and the most common pattern found in the genus (cf. Wilson 1953).

Species of the genus *Hesperodiaptomus* are supposed to lack Schmeil's organ (Wilson 1953). Schmeil's organ (Schmeil 1896) is a small protuberance of unknown function, which in diaptomids if present is located on the posterior surface of leg 2 endopod 2. If the small transverse ridge in this position which was noted in some of the males of *H. californiensis* examined, does correspond to Schmeil's organ, this is the first reported occurrence of this structure in the genus.

Most species of *Hesperodiaptomus* occur in northwestern North America. A few species are found in eastern Canada and the U.S.A., and the ranges of three species extend into Siberia (Borutskii et al. 1991). The species that are morphologically closest to *H. californiensis* occur well north of its range. *Hesperodiaptomus kiseri* is found in the State of Washington and in Saskatchewan (Wilson 1959). *Hesperodiaptomus schefferi* is found in the Pribilof Islands, Alaska, and the northern Rocky Mountain States (Wilson 1959). *Hesperodiaptomus victoriaensis* has been collected in the mountains of southwestern Alberta (Anderson 1967, 1971), near Churchill, Manitoba (Hebert 1985; Boileau & Hebert 1988), and on Victoria Island, N.W.T. (Reed 1958).

Two other species of diaptomids, *Leptodiaptomus tyrrelli* and *Hesperodiaptomus novemdecimus,* occurred in large numbers together with *H. californiensis* in all three pools sampled. Many instances of co-occurring diaptomid species have been reported and have been much discussed in the published literature, including reviews by Cole (1961) and Hutchinson (1967). Of 34 examples of co-occurrence listed by Cole (1961), 10 involved congeneric species. Hutchinson (1967) observed that co-occurring diaptomid species tend to be of different sizes and suggested that these size differences may indicate non-overlapping feeding niches, and that differences in feeding would likely be found to be related to structural differences.

Several co-occurrences of species of *Hesperodiaptomus* have been reported. Wilson (1953) reported *H. wardi* (Wilson, 1953) together with *H. novemdecimus.* Anderson (1971) collected *H. shoshone* (S. A. Forbes, 1893) with *H. arcticus,* and *H. shoshone* with *H. victoriaensis.* Hammer & Sawchyn (1968) found *H. arcticus* in the same pond as *H. kiseri,* although the incidences were separated by a five-day interval. These authors noted distinct size differences between the two species, but postulated mutual exclusion between them. An especially interesting example was given by Anderson (1967), who found *H. shoshone* with *H. victoriaensis* and *L. tyrrelli* together in a pond in Alberta. There, *H. shoshone* individuals averaged 1.6 times longer than *H. victoriaensis* and preyed actively upon the much smaller *L. tyrrelli.* Anderson (1967) described the enlarged clawlike setae of the maxilliped of *H. shoshone,* which were apparently an adaptation for this predatory activity. The corresponding setae of *H. victoriaensis* were found to be unmodified, and this species apparently did not predate upon the smaller diaptomid. In the case of the Lassen County *Hesperodiaptomus* pair, the setae of the mouthparts and maxilliped of both species are unmodified. *Hesperodiaptomus novemdecimus* averaged larger than *H. californiensis* in all three ponds, and the two could be reliably sorted because of this size difference. In accordance with Hutchinson's (1967) hypothesis, we suggest that differences between these species in feeding niches are likely to exist, although we have made no direct observations.

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Orecturus amplus, a new species (Copepoda: Siphonostomatoida: Asterocheridae) from an alcyonacean in New Caledonia

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Abstract.—A new species of siphonostomatoid copepod, *Orecturus amplus,* is described from New Caledonia, where it is associated with the alcyonacean *Siphonogorgia variabilis* Hickson. The new species may be distinguished from its six congeners by its large size and by detailed features of its external anatomy.

Copepods are frequent associates of Alcyonacea (Humes 1990). Species of the order Poecilostomatoida are by far the most common copepod associates (nearly 180 species) of these cnidarians. Those of other orders are much less frequently found with soft corals (Cyclopoida, 4 species; Harpacticoida, 1 species; and Siphonostomatoida, 3 species). Three poecilostomatoids have been recorded from the alconacean *Siphonogorgia.* In Madagascar, *Acanthomolgus hians* (Humes & Ho 1968) lives with *Siphonogorgia pichoni* Verseveldt (host originally reported as *S. pendula* Studer) and *Acanthomolgus longispinifer* (Humes & Ho 1968) with *S. pichoni* (see Humes & Stock 1973). In the Moluccas (at Pulau Gomumu, south of Obi), *Acanthomolgus brevifurca* Humes, 1990, is associated with *S. variabilis* Hickson.

The relatively small number of siphonostomatoid copepods reported to date from soft corals probably reflects the lack of attention so far given to these associations. In this paper, a siphonostomatoid belonging to the genus *Orecturus,* living with *Siphonogorgia* in New Caledonia, is described.

Materials and Methods

The host alcyonacean colony was isolated immediately after collection in a plastic bag containing sea water. Sufficient 95% ethanol was later added to make approximately a 5% solution. After 2–3 hours, the soft coral was gently rinsed, and the wash water poured through a fine net (approximately 120 holes per 2.5 cm, each hole approximately 225 μm square). The copepods were then recovered from the sediment retained.

The copepods were measured and studied in lactic acid. The length of the body does not include the setae on the caudal rami. Dissections were prepared using the wooden slide method described by Humes & Gooding (1964). All drawings were made with the aid of a camera lucida.

Order Siphonostomatoida Thorell, 1859
Family Asterocheridae Giesbrecht, 1899
Genus *Orecturus* Humes, 1992
Orecturus amplus, new species
Figs. 1a–g, 2a–i, 3a–i

Type material.—7 ♀♀, 9 ♂♂ from the alcyonacean *Siphonogorgia variabilis* Hickson, in 30 m, outside Récif Mtere, near Nouméa, New Caledonia, 22°20′40″S, 166°13′55″E, 23 Jul 1971. Holotype ♀ (USNM 274207), allotype ♂ (USNM 274208), and 11 paratypes (4 ♀♀, 7 ♂♂) (USNM 274209) deposited in the National Museum of Natural History, Smithsonian Institution, Washington. Remaining paratypes in the collection of the author.

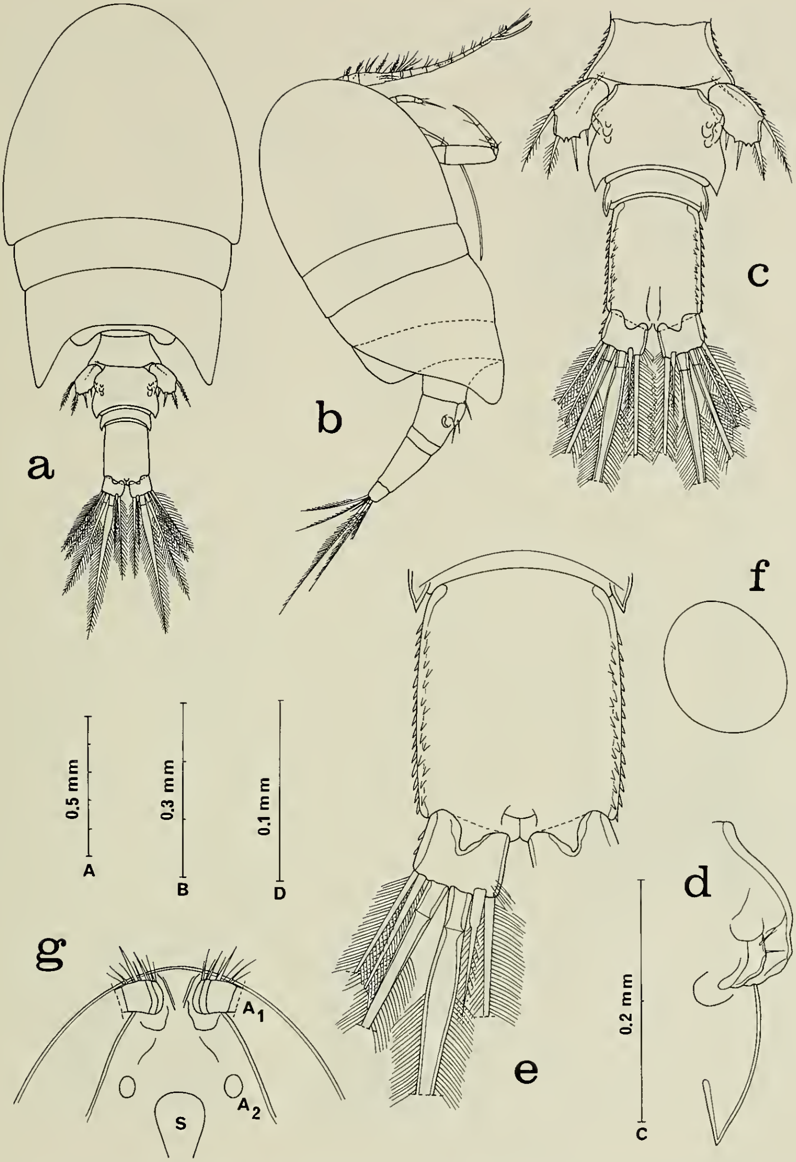

Fig. 1. *Orecturus amplus,* new species. Female. a, body, dorsal (scale A); b, body, lateral (A); c, urosome, dorsal (B); d, genital area, dorsal (D); e, anal somite and caudal ramus, dorsal (C); f, egg, ventral (B); g, rostral area, ventral (B). A_1 = antennule, A_2 = antenna, S = siphon.

Female.—Body (Fig. 1a, b) with moderately broad prosome. Length 1.54 mm (1.50–1.56 mm) and greatest width 0.80 mm (0.78–0.88 mm), based on 7 specimens in lactic acid. Greatest dorsoventral thickness 0.55 mm. Somite bearing leg 1 fused with cephalosome. Somite bearing leg 3 with posteriorly extended, narrowly rounded epimera. Somite bearing leg 4 narrow, with rounded epimera, overlapped dorsally by tergum of preceding somite. Ratio of length to width of prosome 1.38:1. Ratio of length of prosome to that of urosome 2.05:1.

Somite bearing leg 5 (Fig. 1c) 120 × 264 µm, indented laterally, with scalelike spines laterally. Genital double-somite broader

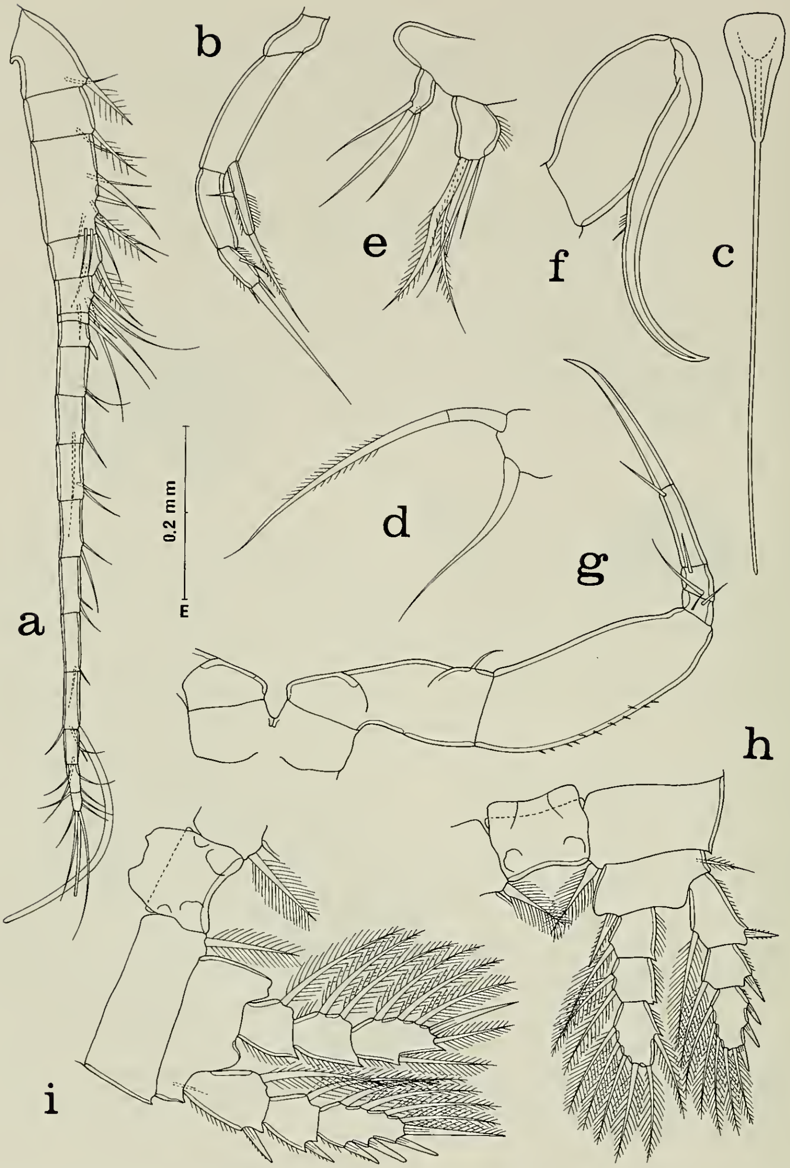

Fig. 2. *Orecturus amplus,* new species. Female. a, antennule, postero-outer (scale C); b, antenna, outer (C); c, siphon, ventral (B); d, mandible, anterior (C); e, maxillule, anterior (C); f, maxilla, posterior (C); g, maxilliped, posterior (C); h, leg 1 and intercoxal plate, anterior (E); i, leg 2 and intercoxal plate, anterior (E).

than long, 117 μm long in midline, 160 μm long including posterolateral spiniform processes, 231 μm wide; ratio 0.51:1, taking length at midline. Genital areas located dorsolaterally near indentation. Each genital area with 2 small setae (Fig. 1d). Two postgenital somites from anterior to posterior 55 × 172 μm (length including posterolateral processes) and 180 × 160 μm, longer somite with small scalelike spines (continuing on dorsal and ventral surfaces, but not shown in Fig. 1c, e).

Caudal ramus (Fig. 1e) 60 × 75 μm, wider than long, ratio 0.8:1. Dorsal seta 70

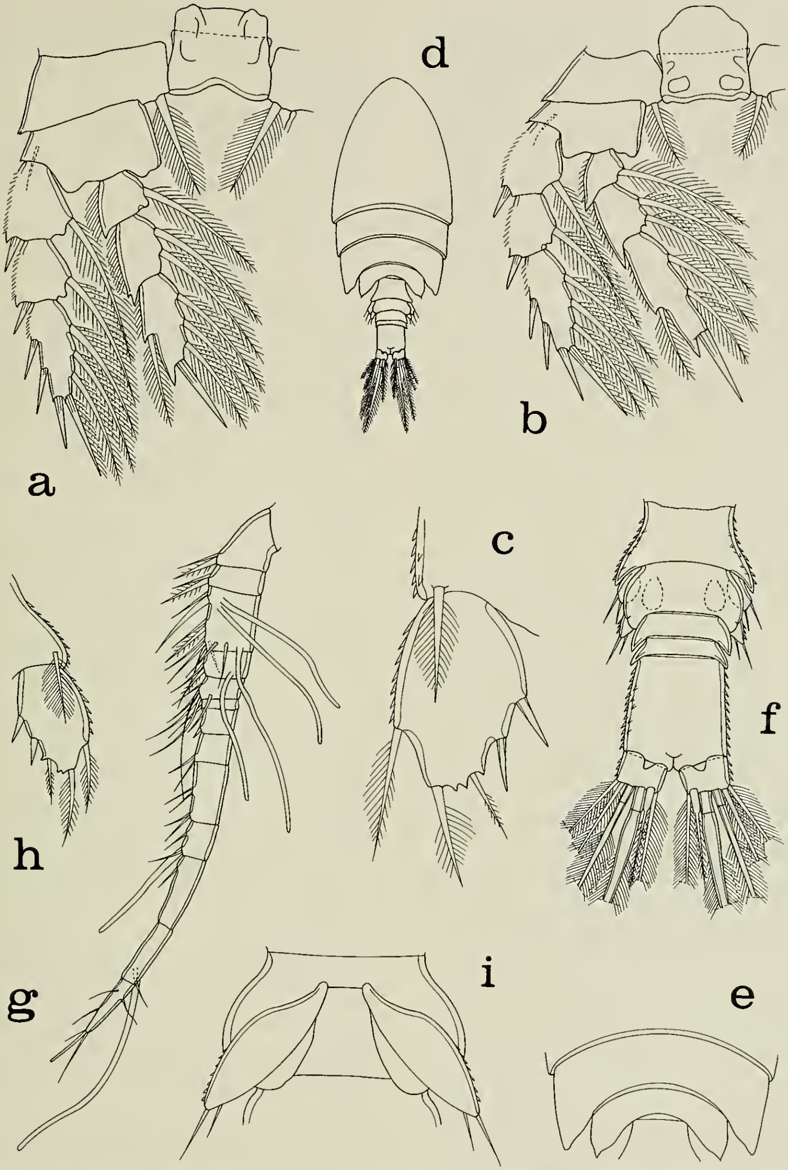

Fig. 3. *Orecturus amplus*, new species. Female. a, leg 3 and intercoxal plate, posterior (scale E); b, leg 4 and intercoxal plate, anterior (E); c, leg 5, ventral (C). Male. d, body, dorsal (A); e, somites of legs 3 and 4, dorsal (B); f, urosome, dorsal (E); g, antennule, dorsal (C); h, leg 5, ventral (D); genital somite showing leg 6, ventral (D).

μm, with elongate pedicel. Outer lateral seta 250 μm, outermost terminal seta 275 μm, innermost terminal seta 340 μm, and 2 median terminal setae 460 μm (outer) and 625 μm (inner) swollen proximally. All setae with long lateral setules. Outer margin of ramus with few scalelike spines and postero-inner corner with group of slender setules.

Dorsal surface of body without visible sensilla.

Entire egg sac not seen, but isolated egg oval (Fig. 1f), 226 × 179 μm.

Rostrum (Fig. 1g) weak. Antennule (Fig.

2a) 585 µm long, 17-segmented. Lengths of its segments (measured along their posterior nonsetiferous margins): 39 (78 µm along its anterior margin), 26, 83, 26, 25, 4, 21, 34, 36, 36, 38, 38, 39, 44, 26, 23, and 13 µm, respectively. Formula for armature: 2, 2, 10, 2, 6, 1, 1, 2, 2, 2, 2, 2, 2, 2 + 1 aesthetasc, 2, 3, and 5 + 1 aesthetasc. Enlarged seta on third segment 74 µm long. Certain setae on segments 1–4 with lateral setules. Antenna (Fig. 2b) with elongate, 1-segmented exopod 57 × 10 µm, bearing short inner seta and long terminal barbed seta 95 µm; both sides of exopod with setules. Endopod with first segment unarmed, second segment with 3 short setae and long terminal seta 120 µm long.

Siphon (Fig. 2c) 935 µm long, reaching almost to ventral edge of intercoxal plate of leg 4.

Mandible (Fig. 2d), maxillule (Fig. 2e), and maxilla (Fig. 2f) resembling those of congeners (see Humes, 1992, 1993, 1994). Maxilliped (Fig. 2g) with basis lacking inner seta but having small spinules along outer margin. Endopod 3-segmented, armed with 2,2,1; terminal claw 120 µm.

Legs 1–4 (Figs. 2h, i, 3a, b) segmented and armed as follows (Roman numerals indicating spines, Arabic numerals representing setae):

P_1	coxa 0-1	basis 1-I	exp	I-1; I-1; II,I,5
			enp	0-1; 0-2; 1,5
P_2	coxa 0-1	basis 1-0	exp	I-1; I-1; III,I,4
			enp	0-1; 0-2; 1,1,I,3
P_3	coxa 0-1	basis 1-0	exp	I-1; I-1; II,II,3
			enp	0-1; 0-2; 1,I,3
P_4	coxa 0-1	basis 1-0	exp	I-1; I-1; II,II,3
			enp	0-1; 0-2; 1,I,2

Leg 1 with inner barbed spine on basis 52 µm.

Leg 5 (Fig. 3c) placed ventrally (as shown in Fig. 1c). Suboval free segment 107 × 70 µm, ratio 1.53:1. Five setae from outer to inner 75, 65, 36, 25, and 27 µm. Two innermost setae stout, almost spinelike, and lacking setules. Other setae with lateral setules. Few scalelike spines along outer edge of free segment. Adjacent dorsal seta, here located ventrally, 52 µm with lateral setules.

Leg 6 represented by 2 small setae on genital area (Fig. 1d).

Color of living specimens red, eye red.

Male.—Body (Fig. 3d) with prosome more slender than in female. Length 0.98 mm (0.94–1.02 mm) and greatest width 0.43 mm (0.40–0.45 mm), based on 9 specimens in lactic acid. Greatest dorsoventral thickness 0.33 mm. Somite bearing leg 4 with sharply pointed epimera (Fig. 3c). Ratio of length to width of prosome 1.69:1. Ratio of length of prosome to that of urosome 2.46:1.

Somite bearing leg 5 (Fig. 3f) 73 × 127 µm including processes (length at midline 62 µm). Genital somite 60 × 86 µm including leg 6 (length at midline 65 µm). Three postgenital somites from anterior to posterior 42 × 112 µm (length at midline 26 µm), 26 × 104 µm (length at midline 16 µm), and 104 × 112 µm.

Caudal ramus 39 × 52 µm, ratio 0.75:1, resembling that of female.

Dosal surface of body without visible sensilla. Urosome with scalelike spines as in female.

Rostrum as in female. Antennule (Fig. 3g) 13-segmented, with segments 8 and 9 clearly separated (in other species these segments tending to be fused). Lengths of segments (measured along their posterior nonsetiferous margins): 21 (52 µm along anterior margin), 22, 42, 23, 13, 9, 14, 26, 48, 29, 57, 52, and 48 µm, respectively. Formula for armature: 2, 2, 10 + 3 aesthetascs, 2 + 1 aesthetasc, 6, 1, 1, 2, 4, 2, 1, 1 + 1 aesthetasc, and 5 + 1 aesthetasc. Aesthetascs on segments 3, 4, and 10 (these present in all males examined) very hyaline. Antenna as in female.

Siphon, mouthparts, and legs 1–4 like those of female.

Leg 5 (Fig. 3h) with free segment 50 × 32 µm, ratio 1.56:1, otherwise placed ventrally and similar to that of female.

Leg 6 (Fig. 3i) posteroventral flap on genital somite bearing 2 slender setae.

Color of living specimens as in female.

Etymology.—The specific epithet *amplus,* Latin meaning large, alludes to the relatively large size of this species compared to congeners.

Remarks.—*Orecturus amplus* may be distinguished by its size. None of its six congeners exceeds a length (in the female) of 1.25 mm, with their average length of only 1.11 mm. Selected features for further differentiation are as follows. In *O. bracatus* (Stock & Kleeton 1963) the genital double-somite is rectangular. In *O. excavatus* Humes, 1989, the outer side of segment 1 of the exopod of leg 1 is excavated and the posterior part of the claw of the maxilliped is swollen. In *O. finitimus* Humes, 1993, the enlarged seta on segment 3 of the antenna is longer than the segment and the basis of the claw of the male maxilliped has a low prominence. In *O. forticulus* Humes, 1993, the prosome is broad, the maxilla has an unusually stout claw, the somite bearing leg 3 has sharply pointed epimera, and the first segment of the exopod of leg 1 has an outer thornlike process. In *O. grandisetiger* Humes, 1992, the prosome is broad, the enlarged seta on segment 3 of the antennule is longer than the segment, the somite bearing leg 3 has sharply pointed epimera, and the basis of the male maxilliped has a weak inner protuberance and lacks spinules. In *O. sakalavicus* Humes, 1994, the antennule lacks an enlarged seta, the somite bearing leg 3 has sharply pointed epimera, and the basis of the male maxilliped has an inner lobe and lacks spinules. The outer spinules on the basis of the maxilliped seen in the new species are found only in *O. forticulus.*

The color of living colonies of the soft coral host, *Siphonogorgia variabilis,* was as follows: slender creamy white stems, smaller branches and twigs pale yellow, polyps lavender blue to red. The red color of *Orecturus amplus* more closely resembles that of the polyps than that of other parts of the colony, suggesting that the copepods may live on or in the polyps.

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Records of Enchytraeidae (Annelida: Oligochaeta) from west Florida. 1. *Mesenchytraeus, Cognettia, Bryodrilus, Hemienchytraeus, Henlea* and *Buchholzia*

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Abstract.—Records of eleven species of Enchytraeidae belonging to six genera are given for terrestrial habitats in Florida west of Talahassee. All are new records for the southern part of North America. A revised diagnosis of *Mesenchytraeus* is provided and a new species, *Mesenchytraeus hamiltoni,* is described which is characterised by the occurrence of secondary pharyngeal glands in V and a very short spermathecal ectal duct. Four species of *Cogettia* occurred, including two new species: *Cognettia floridae* which belongs to the group of species with three pairs of primary and two pairs of secondary pharyngeal glands and male organs in the normal position, and a species for which the description is incomplete. *Bryodrilus novaescotiae, Hemienchytraeus stephensoni* and *H. bifurcatus* are fully described and the occurrence of the widespread species *Henlea perpusilla, H. ventriculosa* and *Buchholzia fallax* is recorded.

The species recorded and described in this paper occurred in four series of collections of Enchytraeidae made in West Florida (west of Talahassee) during March 1984, April–May 1987, March 1988 and December 1993. Collection procedures and the range of habitats sampled have been described in a previous paper that also contains comments on faunal composition and ecology (Healy 1989). The enchytraeid fauna was found to be rich but patchily distributed. Among the 70–75 taxa recognised were at least 24 species believed to be new to science, a further 10 species new to North America and 18 already known from the continent but new to Florida. The large number of new species and new regional records is explained by the fact that there have been few studies of enchytraeids in North America and almost none in the Southeast. The only enchytraeids previously recorded from Florida are two species of *Grania* from the marine sublittoral on the Atlantic coast (Kennedy 1966, Coates & Erséus 1985), *Stephensoniella marina* from the marine littoral on Virginia Key (Coates 1983) and the freshwater species *Barbidrilus paucisetosus* from the Appalachicola River (Loden & Locy 1980). There are no records of terrestrial species.

This paper records details of 11 terrestrial species belonging to six of the 13 genera found in West Florida. Most of the previously known species were originally described from European populations, thus some morphological differences are to be expected in North American specimens. When Florida specimens depart from the original descriptions or those of European material as given by Nielsen & Christensen (1959), these differences are noted. A full description of *Bryodrilus novaescotiae* is given because the original description was based on a small number of fixed specimens only. *Hemienchytraeus stephensoni* and *H. bifurcatus* are also fully described, extending the known range of variability in these widespread species.

Materials and Methods

Samples were collected from a wide range of habitats, particularly moist or wet humus in woodlands or swamps, and soil from capillary zones at the edge of water bodies such as bayheads, ponds and streams. Enchytraeids were absent or in poor condition in dry soils and rare in submerged substrates where they were generally replaced by Tubificidae. The species described in this paper occurred at nine localities.

Worms were extracted from soil samples using the wet funnel method which uses light and heat from light bulbs to expel worms from samples into water-filled funnels (O'Connor 1955, Healy & Rota 1992). Some specimens of all species were examined live and measurements of live worms or their organs were made on worms lightly compressed under a cover slip. Other material was fixed in 70% ethanol or Bouin's fixative and stored in 70% ethanol. Most specimens were stained in paracarmine and whole-mounted in Canada Balsam but a few unstained mounts were also prepared.

Type specimens and other material have been deposited in the United States National Museum of Natural History, Washington D.C. (USNM) and a few specimens are in the Royal Ontario Museum (Invertebrate Zoology), Toronto (ROMIZ).

Genus *Mesenchytraeus* Eisen, 1878

Mesenchytraeus Eisen, 1878:67.
Analycus Levinsen, 1884:230.
Mesenchytraeus Eisen 1879:10, 1904:14–17; Michaelsen 1887:369–372, 1889:15–16; Čejka 1914:5; Welch 1920:42–44; Černosvitov 1937a:278; Nielsen & Christensen 1959:30–31.

Type species.—Mesenchytraeus primaevus Eisen, 1878.

Following the listing of Eisen's species *M. primaevus, M. mirabilis* and *M. falciforrnis* (Eisen 1878) as species dubia by Nielsen & Christensen (1959), Brinkhurst & Jamieson (1971) designated *Analycus* Levinsen, 1884 as the correct name for the genus on grounds of priority. However, Piper et al. (1982) re-examined Eisen's material and concluded that the specimens were undoubtedly members of *Mesenchytraeus* although their poor condition precluded the distinction of specific characters. As the original descriptions were deemed adequate, they therefore restored the name *Mesenchytraeus* designating *M. primaevus* as type species.

Diagnosis.—Medium to large worms, usually white but sometimes yellow due to colored coelomocytes or black when the epidermis is pigmented. Setae sigmoid, distinctly nodulated or with slight swellings. Head pore at or near the apex of the prostomium. Clitellum well developed, sometimes extends over several segments. Paired pharyngeal glands on septa at 4/5 and 5/6, secondary pharyngeal glands, when present, ventral in two to five segments. Transition between esophagus and intestine gradual. Peptonephridia absent. Esophagus and intestine without diverticula or appendages. Dorsal vessel originates in, or more usually behind, clitellum. Coelomocytes of one type, nucleate, rather small for the size of the worm, round, oval or spindle-shaped. Nephridia with poorly developed interstitial tissue, allows the coils of the canal to be seen clearly, preseptale consisting of a nephrostome on a short or long neck, postseptale with two or three lobes. Brain rather short, often broader than long, its anterior border indented or cleft. Paired seminal vesicles usually present, sometimes extending within the egg sac into post-clitellar segments. Sperm funnel small, barrel-shaped or cylindrical. Sperm duct often enlarged to form an atrium just before it enters penial bulb. Atrial glands (prostates) and penial glands present or absent. Egg sac present, often extends through several segments behind clitellum. Spermathecae simple or with diverticula, free or fused to esophagus.

Remarks.—The above diagnosis is a

modified version of those given by Eisen (1878, 1879, 1904), and Nielsen & Christensen (1959), and takes into account more recent descriptions. Nodulated setae were considered diagnostic by Nielsen & Christensen but were not mentioned by Eisen, either in his generic diagnoses or in any of his detailed species descriptions. Subsequent reviews of the genus (e.g., Michaelsen 1887, 1889; Čejka 1914, Welch 1920, Černosvitov 1937a) similarly omitted mention of the character. Re-examination of the material described in Eisen's 1878 paper by Piper et al. (1982) confirmed the presence of noduli in all three species and it must be assumed that the character was overlooked by early workers. The nodulus may be very weak, however, and may be represented by little more than a slight swelling, as in the new species described below, making it difficult to recognise for an inexperienced worker. A nodulus is unusual in enchytraeids and is present in only one other genus. However, reliance should not be placed on this character when constructing or using keys to genera. Other modifications of existing diagnoses concern the postseptal regions of the nephridia, which Nielsen & Christensen describe as bilobed but which frequently have three lobes, and the egg sac, which Eisen describes as single and median but which may extend backward as two distinct sacs. Eisen (1904) described the penial bulb as a muscular cushion containing radiating muscular strands, which in some species are powerful and usually contain internal glands (penial glands), but the bulb structure is variable and the whole structure may be quite compact. Although not always present, an atrium, formed by expansion of the sperm duct at the entrance to the penial bulb, sometimes with attached glands, is unique in the Enchytraeidae. None of the characters proposed by Eisen (1878, 1879) as grounds for erecting the new genus has proved to be useful; these are: the presence of sperm balls or spermatophores in the coelom (not recorded in any other enchytraeid genus but only present in some *Mesenchytraeus* species), brain deeply divided in front (not unique to *Mesenchytraeus,* indentation sometimes shallow), and an unusually short vas deferens (usually short but not always exceptionally so). Cardiac glands (Herzkörper of Michaelsen), mentioned by early workers, are internal structures in the dorsal vessel, not easily detected in whole mounts. In practice, the most reliable character that distinguishes *Mesenchytraeus* is the nephridium with its free nephrostome (also found in some other genera), poorly developed interstitial tissue and lobed postseptale. In live worms, the nephridia have a very distinctive appearance that makes *Mesenchytraeus* specimens instantly recognisable.

Distribution.—Eisen (1904) described 18 species of *Mesenchytraeus* from western parts of North America (mainly Alaska and California) and a further ten species have been described from western regions by other workers; in contrast, only three species are recorded from the eastern part of the continent (Tynen 1975). The genus also appears to be well represented in Siberia (Nurminen 1973a, Piper et al. 1982, Timm & Popchenko 1978, Timm 1994) while only eleven species are recognised in Europe. Very few species have been found in the tropics. The genus thus appears to have its present centre of distribution in northern regions of the western Nearctic and eastern Palearctic. The poor representation in West Florida, where only one species was at all frequent, supports this view.

North America, South America, Greenland, Europe, Spitzbergen, Siberia, Japan, Antarctic, ?Africa.

Mesenchytraeus hamiltoni,
new species
Fig. 1

Material examined.—Holotype: USNM 170722 whole mounted specimen from edge of "sewage pond", University of West Florida, Pensacola, collected by author, December 1993. Paratypes from the type lo-

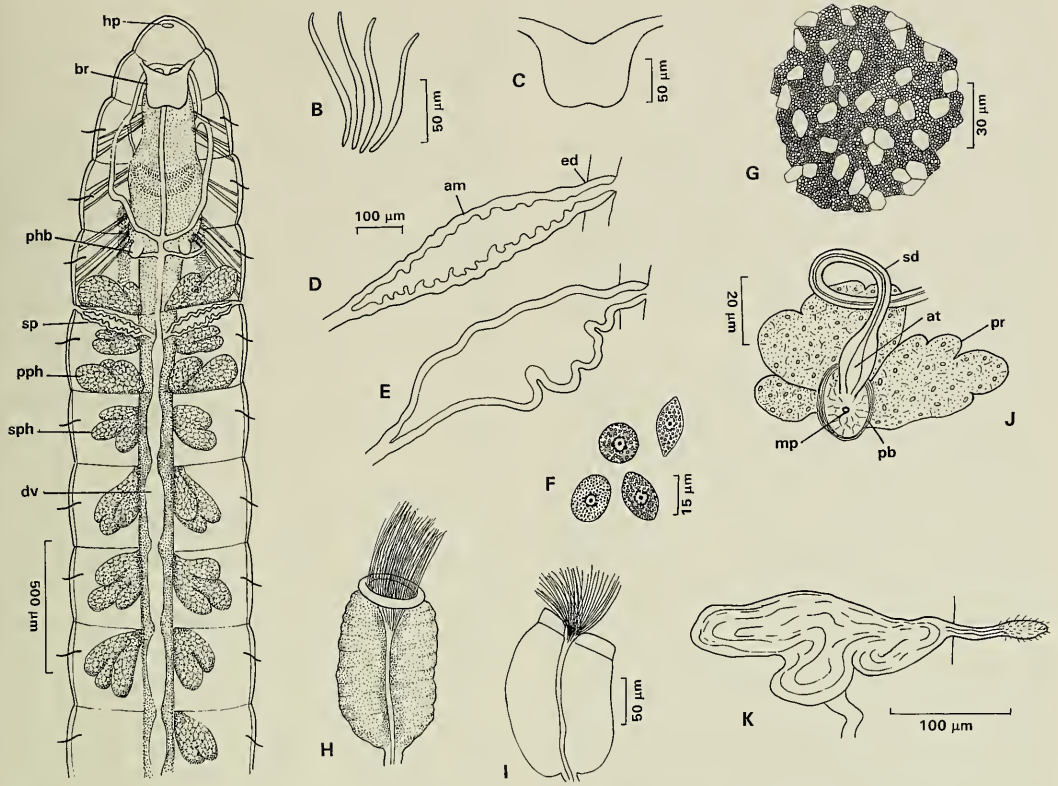

Fig. 1. *Mesenchytraeus hamiltoni,* new species. A, anterior segments, dorsal view; B, dorsal setal bundle; C, brain; D, spermatheca of live worm, contracted; E, spermatheca of live worm, expanded; F, coelomocytes; G, dorsal clitellar gland cells and clear interspaces; H, sperm funnel, live specimen; I, sperm funnel, fixed specimen; J, male pore and associated structures; K, nephridium. am ampulla, at atrium, br brain, dv dorsal vessel, ed ectal duct, hp head pore, mp male pore, pb penial bulb, phb pharyngeal bulb, pph primary pharyngeal gland, pr prostate, sd sperm duct, sp spermatheca, sph secondary pharyngeal gland.

cality: USNM 170723–170726, two stained and two unstained whole mounts, one with clitellum partly removed. Other material: seven whole mounts in author's collection. Approximately 16 live mature specimens examined.

Type locality.—Wet or saturated peaty sand with moss and plant roots at edge of a pond receiving clean water from a sewage treatment plant, water level constant. pH 4.5–5.3.

Etymology.—The species is dedicated to Professor Paul Hamilton of the University of West Florida who introduced me to many interesting and rewarding localities.

Description.—Medium to large, white, yellowish or pink worms; live specimens 18–30 mm, 0.7 mm in diameter. Fixed specimens often much contracted, mature individuals measuring 8–22 mm with a prominent clitellum up to 1.2 mm in diameter. Segments in mature specimens 55–86 ($\bar{X}$ = 66, *SD* 7.9, n = 11), 55–75 in submature ones. Setae sigmoid with nodulus poorly developed or absent, without ental hook (Fig. 1B), 108–120 μm in the preclitellar region, 120–144 μm in posterior segments. Lateral bundles with three or four setae, ventral bundles with 3–12 in preclitellar segments, 3–11 behind the clitellum, setae about equal in length within bundle. Setae absent dorsally in XII and XIII, occasionally present ventrally in XII, reduced in number or absent ventrally in XIII. Cutaneous glands in two or three rows at about the level of the setae, or scarcely visible. Clitellum extends from ½XI to ¾ or all of XIII with numerous small gland cells containing coarse granules, irregularly scattered with clear interspaces, that mask internal organs in live as well as stained specimens (Fig. 1G). Gland cells may be almost continuous ventrally in fully mature individuals. Head pore at, or near, tip of prostomium.

Primary pharyngeal glands on 4/5 and 5/6 free dorsally, either unlobed or with two or three lobes; secondary glands, each with several lobes, situated ventrally in V, VI, VII and usually in VIII (Fig. 1A). A few specimens had either one or two glands in IX and one individual possessed a lobed gland unilaterally in X (Fig. 1A). Two small bulbs on dorsal posterior border of the pharynx in IV (Fig. 1A). Chloragocytes small, brown, present from IV, form a dense layer from VIII, 12–16 cells across the intestine in the preclitellar region in mounted specimens. Esophagus merges with intestine without increase in diameter, intestine enlarges behind origin of dorsal vessel. Coelomocytes 14–30 μm, oval or spindle-shaped, with rather coarse granules and a weakly staining nucleus (Fig. 1F). Dorsal vessel originates in XI–XIII with dilatations in VII–XII and conspicuous branches in II and III (Fig. 1A); bifurcation anterior to brain. Blood faintly or distinctly red. Brain about as broad or slightly broader than long, about 80 μm in length, truncated or slightly indented posteriorly, deeply indented on its anterior border (Fig. 1C). Nephridial nephrostome elongated, on a long neck, postseptale with two or three lobes; efferent duct arises mid-ventrally (Fig. 1K). First nephridia at 6/7, occasionally at 5/6.

Testes large and spongy in mature worms, appear brown by transmitted light in living specimens. Seminal vesicles paired, confined to XI or extend into X. Sperm funnels small, barrel-shaped, 120–160 μm in length, about 1.5 times as long as wide, with a raised collar about as wide as the funnel in fixed specimens, appearing slightly narrower in live worms (Fig. 1H, I). Sperm duct 14–16 μm wide, about ten times length of funnel, loosely coiled in XII. Male openings irregular or semicircular slits. Each sperm duct widens distally to form a thick-walled, fusiform atrium that opens centrally into penial bulb; three large, slightly lobed glands attached to bulb (Fig. 1J). Two egg sacs develop asymmetrically on 11/12 as pouches, each containing a string of oocytes and eggs, reaching to XVIII on one side. Ovarian tissue diffuse, extending back in egg sacs which develop before sperm funnels and ducts. Up to five mature eggs present at a time. Spermathecae simple, without diverticula, each consists of an elongated ampulla that tapers entally to merge with esophagus in V and ectally to a short ectal duct, only a little longer than wide, scarcely longer than thickness of body wall (Fig. 1D, E). Ampullae expand and contract and occasionally pulsate. When contracted, wall becomes rugose or folded internally (Fig. 1D). Only small amounts of sperm, arranged lengthwise, in ampulla. Spermathecae develop early and are fully formed in specimens only half the final size and in which there are no signs of male organs or oocytes.

Remarks.—Among the ten or so described species of *Mesenchytraeus* with spermathecae attached to the esophagus in V, but which lack diverticula, *M. hamiltoni* is unique in the shortness of the ectal duct of its spermatheca and in the presence of secondary pharyngeal glands in V. These features are deemed sufficient to characterise the species although details of structures associated with the male opening, often an important diagnostic character in the genus, have not been described for most of the species with which it might be compared. *Mesenchytraeus hamiltoni* most resembles *M. glandulosus* (Levinsen, 1884) which has five pairs of secondary pharyngeal glands but has a spermathecal ectal duct equal in length to one third of the ampulla, lacks secondary pharyngeal glands in V and has a nephridial funnel without a neck. The number of pharyngeal glands was variable for individuals of the same size and stage of maturity.

Although the species was plentiful at the type locality and at several other sites, mature specimens were rare. None was found in March 1984, only four in April–May 1987, three in March 1988 and seven in December 1993. A low proportion of adults in populations is common in the genus (personal observation).

Habitat.—*Mesenchytraeus hamiltoni* was common in the Pensacola region and was sometimes the dominant enchytraeid in wet substrates. It occurred in a variety of habitats including woodland leaf litter in valleys and swamps, *Sphagnum* and pitcher plant (*Sarracenia*) bogs, and saturated soils at the edge of water bodies where the highest densities occurred. At the latter sites they were often accompanied by Tubificidae. The pH range was 3.9–5.8.

Distribution.—In and around the campus of the University of West Florida, Pensacola; Blackwater Forest, at the edge of a swamp; Avalon Peninsula, edge of a pitcher plant (*Sarracenia*) bog; Lakewood, among *Sphagnum* and grassroots at edge of lake. Not found in the east of the study area.

Mesenchytraeus sp.

Material examined.—Seven live, immature specimens.

Remarks.—A somewhat yellowish species was present at several hardwood forest sites but no fully mature specimens were available for a definitive identification. Specimens had two pairs of primary and two pairs of secondary pharyngeal glands and spermathecae communicating with the esophagus in V, each with a pair of elongated diverticula. The species resembles *M. beumeri* (Michaelsen, 1886) in general appearance.

Habitat and distribution.—In hardwood leaf litter. Occasional at the University of West Florida, Pensacola and in Torreya State Park; common at Tall Timbers Forest Research Station.

Genus *Cognettia*
Nielsen & Christensen, 1959

Cognettia species are recognised by sigmoid setae, without nodulus, in bundles of two or three; nephridia with preseptale consisting of funnel only and an antero-ventral or mid-ventral origin of the efferent duct; absence of peptonephridia; absence of esophageal and intestinal diverticula; dorsal vessel originating in or behind clitellum; a simple penial bulb and a simple spermatheca, not attached to the oesophagus. Testes, ovaries and male pores may be displaced forward by up to four segments.

Distribution.—The only record of *Cognettia* in North America is for *C. glandulosa* from Montreal, Canada (Nurminen 1973b). The genus has proved so far to be characteristic of wet, acid soils in cold or cold-temperate lands and members are usually the dominant enchytraeids in tundra and coniferous forests of northern Europe. However, the discovery of four species in Florida shows that *Cognettia* species can survive in a warm climate while the presence of two new species suggests that North America, like Europe, may have its own endemic species.

Canada, Greenland, Europe, Spitzbergen, Siberia, Japan, Ecuador, Antarctic.

Cognettia floridae, new species
Fig. 2

Material examined.—Holotype: USNM 170727, stained whole mount, Edward Ball Nature Trail, University of West Florida, Pensacola, a hardwood, bayhead swamp, collected by the author April 1987. Paratypes from the type locality and other sites in the University of West Florida: USNM 170728–170732, two stained and two unstained whole mounts. Other material: ROMIZ 13242–13243, stained whole mounts; 11 whole mounts in the author's collection; 42 live specimens examined.

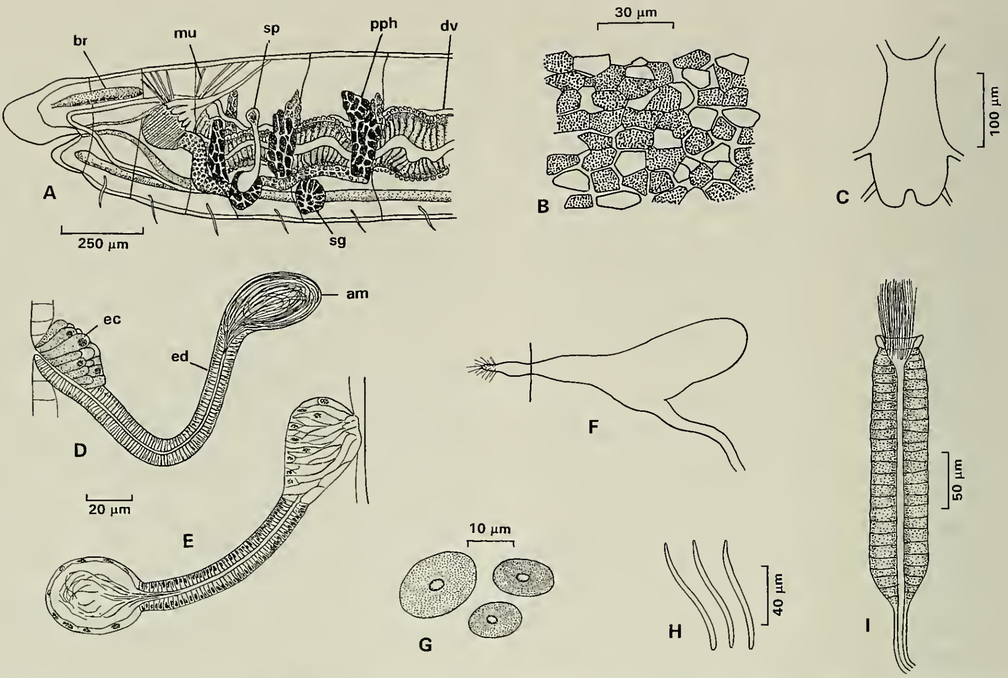

Fig. 2. *Cognettia floridae,* new species. A, anterior segments, lateral view; B, dorsal clitellar gland cells and clear interspaces; C, brain; D, spermatheca of live worm; E, spermatheca of fixed specimens; F, nephridium; G, coelomocytes; H, setae; I, sperm funnel, live worm. am ampulla, br brain, dv dorsal blood vessel, ec ectal glands, ed ectal duct, mu muscle; pph primary pharyngeal gland, sg secondary pharyngeal gland, sp spermatheca.

Type locality.—In moist, wet or saturated sandy humus under *Taxodium* and hardwood trees in a partly tidal, freshwater bayhead swamp; some areas subject to periodic flooding. pH 3.9–4.7.

Etymology.—Named after the State of Florida, genitive case.

Description.—Live specimens greyish-white, 7–9 mm, fixed specimens 5–9 mm, diameter 0.5–0.52 mm, 0.56 mm at clitellum. Segments (29)39–46 ($\bar{X}$ 40.9, SD = 3.6, n = 23). Setae without ental hook (Fig. 2H), 80–96 µm in preclitellar region, 80–104 µm in posterior segments, three per bundle in all regions, occasionally only two, setae absent in XII. Cutaneous gland cells small, in numerous rows or more or less scattered. Clitellum prominent in live worms, extending over XII–XIII with squarish gland cells arranged in transverse rows. In stained mounts, the gland cells, which are packed with coarse granules, are irregularly scattered with clear interspaces, absent mid-ventrally (Fig. 2B). Head pore at 0/1.

Three pairs of primary pharyngeal glands, all free dorsally, without ventral lobes, and two pairs of compact secondary glands, situated ventrally in V and VI (Fig. 2A). Esophagus merges gradually with intestine from 6/7. Chloragocytes present from IV, forming a dense layer from VI, 10–12 across intestine in preclitellar region in compressed specimens. Dorsal vessel arises at 13/14, occasionally in XIV or XV, anterior vessel bifurcates at level of 0/1. Blood colorless in specimens from drier habitats, faintly or distinctly red in those from wet substrates. Coelomocytes round or oval, finely granular with a prominent nucleus (Fig. 2G), 14–32 µm long, about a quarter of length of setae. Nephridial nephrostome on a short neck, long efferent duct arises antero-ventrally or mid-ventrally

(Fig. 2F). First nephridium at 6/7. Brain 160–200 μm long, 1.5–2 times longer than wide, deeply incised posteriorly (Fig. 2C).

Seminal vesicle unpaired, dorsal, confined to XI. Sperm funnels small, cylindrical, in live worms about 100 μm long, four or five times longer than wide, equal to about ¼–⅓ diameter of live worm (Fig. 2I). In fixed specimens, length usually about ¼ of worm diameter. Collar slightly narrower than funnel. Sperm duct long and narrow, diameter 6 μm, coiled in XII, opens through a compact penial bulb, greatest diameter about 90 μm, which occupies ⅙ to ⅕ of the diameter of clitellum in mounted specimens. One, or usually two, eggs present at a time. Spermathecae confined to V. Ectal ducts thick-walled, about four times length of ampullae, each with a mass of fused, elongate cells on anterior face, near opening (Fig. 2D, E). Ampulla dorsal to oesophagus in V, thin-walled, 35–50 μm long, 1.2 times longer than wide, with most of sperm arranged lengthwise and extending into proximal part of ectal duct in most specimens (Fig. 2D, E).

Remarks.—*Cognettia floridae* belongs to a group of species that comprises *C. cognettii* (Issel, 1905), *C. lapponica* Nurminen, 1965, *C. hibernica* Healy, 1975 and *C. zicsii* Dózsa-Farkas, 1989 all of which reproduce sexually and have reproductive organs in the normal position for Enchytraeidae. It resembles *C. lapponica, C. hibernica* and *C. zicsii* in having three pairs of primary pharyngeal glands and two pairs of secondaries and spermathecae confined to V but it is unique in the asymmetrical ectal swellings on the spermathecal ducts.

Habitat.—The species was common in and around the campus of the University of West Florida and plentiful at two other localities. It was found in a range of substrates including sandy peat and peaty sand, *Sphagnum,* coniferous and broad-leaved leaf litter, finely divided humus and among roots of aquatic plants at the edge of water bodies. All sites were wet, saturated or flooded, with pH levels 3.9–4.5, among the lowest for the region. Mature individuals were common.

Distribution.—Pensacola, campus of the University of West Florida; Avalon Peninsula, pitcher plant (*Sarracenia*) bog; Lakewood, edge of a lake. Not found in the eastern part of the study area.

Cognettia sp.
Fig. 3

Material examined.—Two live mature specimens collected in April 1984 were available for the following description but both were damaged during examination and no further mature individuals could be found. The remaining material consists of one stained, whole-mounted, submature specimen, USNM 170732, three stained whole mounts of immature specimens USNM 170733–170735 and ten whole mounts of immatures in the author's collection. Approximately 30 live, immature individuals were also examined.

Description.—Medium sized, rather slender worms, creamy white, internal organs partly masked by abundant coelomocytes in live worms. Length of live, mature specimens 10–12 mm; live, non-fragmenting immatures reach 20 mm. Maximum length of fixed immature specimens 12 mm, diameter 0.28–0.37 mm. Segments 50 and 58 in the mature specimens but reach 64 in immatures. Setae without ental hook, 68–84 μm in all regions, three ventrally, three or sometimes two laterally. Setae absent from IX or X in mature individuals. Clitellum only slightly raised, extends over IX–½X (over X–½XI in submature specimen), gland cells irregularly scattered or partly in transverse rows (Fig. 3D). Male pores in X or XI. Cutaneous glands small, in numerous rows or scarcely visible. Head pore at, or just anterior to 0/1.

Five pairs of unlobed, primary pharyngeal glands in large individuals but fifth pair often small, developing unilaterally or absent (Fig. 3G). Only four pairs in mature worms. Anterior glands may be united dor-

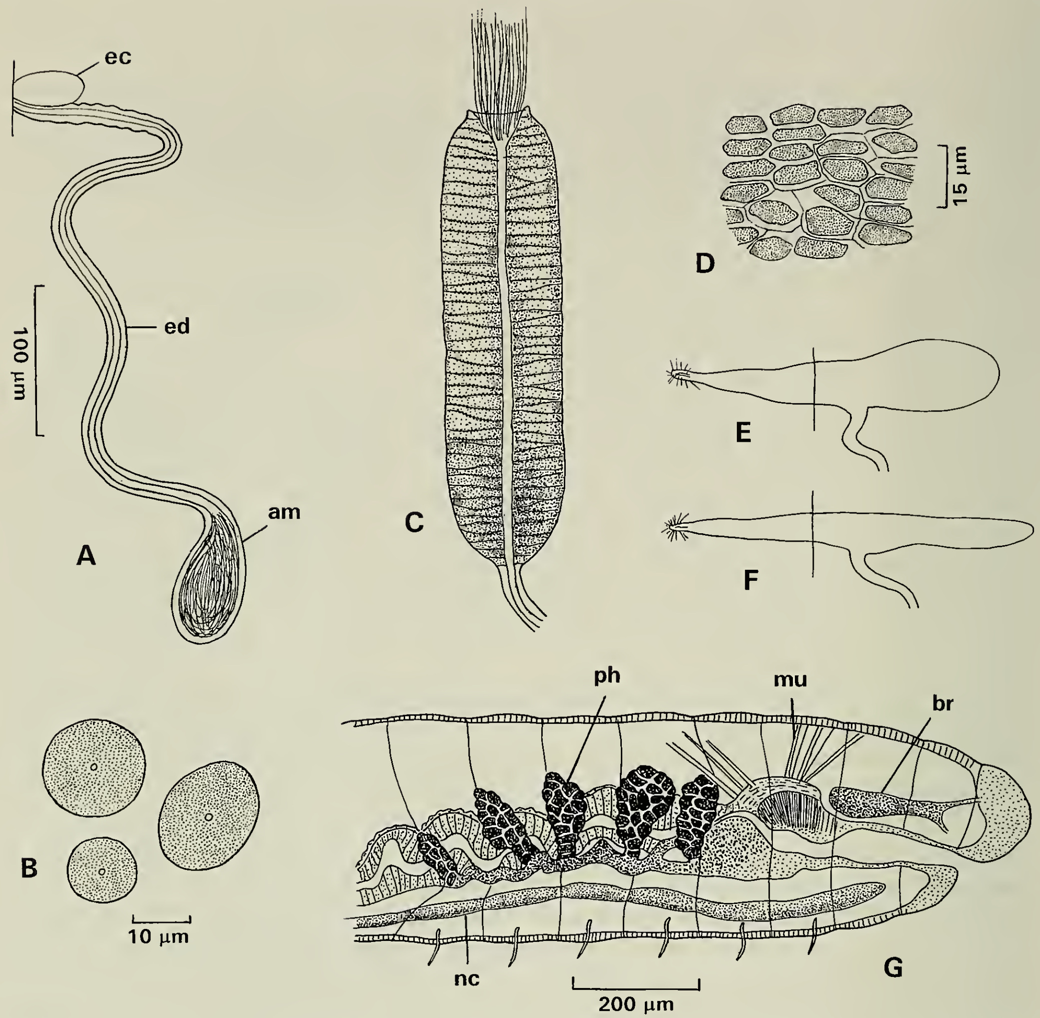

Fig. 3. *Cognettia* sp. A, spermatheca, live worm; B, coelomocytes; C, sperm funnel, live worm; D, clitellar glands; E, preclitellar nephridium; F, postclitellar nephridium; G, anterior segments, lateral view. am ampulla, br brain, ed ectal duct, eg ectal gland, mu muscle, ph pharyngeal gland, nc ventral nerve cord.

sally while posterior ones are usually free. Secondary pharyngeal glands absent. Esophagus merges gradually with intestine. Chloragocytes present in a dense layer from behind last pair of pharyngeal glands i.e., in VIII or IX, 10–14 across the intestine in compressed specimens. Dorsal vessel from XIV or XV, anterior bifurcation just behind 0/1. Blood colorless or faintly red. Coelomocytes 20–30 µm, round or oval with a sharp outline, packed with fine granules that make them appear brown by transmitted light in living worms (Fig. 3B). They are usually very abundant, often so densely packed as to mask internal organs. Nephridia with free nephrostome and elongate preseptale, efferent duct long, arising antero-ventrally or mid-ventrally (Fig. 3E, F). Brain about 1.5 times longer than broad with a truncate or sinuous posterior border.

Seminal vesicle present, unpaired. Sperm funnels cylindrical, about four times longer than wide, each with narrower, scarcely raised, collar (Fig. 3C). Sperm ducts long and narrow, opening at compact penial bulbs. Spermathecal ectal ducts long, slender, without swellings, leading to ovoid ampullae in VII (Fig. 3A). One large ectal gland anterior to each spermathecal opening.

Remarks.—The above description is incomplete owing to the shortage of mature specimens but the distinctive appearance of live individuals made them easily recognisable in samples, even as immatures, and there seems little doubt that this is a new species. Many worms were regenerating anterior or posterior segments and the species obviously reproduces principally by fragmentation; sexual individuals were rare in the population. The species is close to *C. sphagnetorum* (Vejdovský, 1878) which reproduces in the same way and which also has four or five pairs of primary pharyngeal glands and no secondary glands. *Cognettia sphagnetorum,* however, has a chamber containing a ring of sperm at the junction between the ectal duct of the spermatheca and the ampulla and more anterior male openings (in VIII or IX). Other *Cognettia* with displaced reproductive organs, namely *C. glandulosa* (Michaelsen, 1888), *C. paxi* (Moszyński, 1938) and *C. anomala* (Černosvitov, 1928), all have secondary pharyngeal glands. While there are no important diagnostic differences between immature forms of *C. sphagnetorum* and the present species, the abundant coelomocytes with sharp outline and densely granular cytoplasm give the Florida species a distinctive appearance.

Habitat and distribution.—University of West Florida, Pensacola, in the drier parts of a bayhead swamp and in an adjoining ravine with hardwoods. Common in moist, but not wet, leaf litter and humus, pH 3.6–4.5, above the zone subject to periodic flooding.

Cognettia ?sphagnetorum (Vejdovský, 1878)

Pachydrilus sphagnetorum Veydovský 1878: 304.
Cognettia sphagnetorum Nielsen & Christensen 1959:42–43, figs. 28, 29; Kasprzak 1986:124–125, figs. 332–334; Chalupský 1992:142, fig. 10.

Material examined.—Two stained, whole-mounted immature specimens in the author's collection. Three live immature specimens examined.

Remarks.—The absence of mature individuals makes a definitive identification impossible, but specimens resembled *C. sphagnetorum* from Ireland in general appearance although they had only four pairs of pharyngeal glands. Nielsen & Christensen (1959) give five pairs for Danish material, except in mature individuals, but I have found in Irish populations that the fifth pair is often absent in fragmenting individuals. Fragmentation is the normal method of reproduction in *C. sphagnetorum* and sexual individuals are always rare. Material from Florida included one specimen with a developing clitellum and one which appeared to be a juvenile, with only 20 segments, although according to Christensen (1959) the species does not seem to be capable of producing viable eggs.

Habitat and distribution.—Lakewood, among grass roots and leaf litter at the edge of a lake, pH 4.2–4.4. Europe, Iceland, Spitzbergen, Antarctic. (Some of these records are based on immatures only.)

Cognettia ?glandulosa (Michaelsen, 1888)

Pachydrilus sphagnetorum var. *glandulosus* Michaelsen, 1888:483.
Marionina glandulosa Issel 1905:455–456, fig. 3.
Enchytraeoides glandulosus Černosvitov 1928:16–17, Pl. 1, figs. 10, 11.
Cognettia glandulosa Nielsen & Christensen 1959:43–44, fig. 30; Kasprzak 1986: 125–126, figs. 335–337.

Material examined.—USNM 170736–170737, two stained, whole-mounted immature specimens; two whole mounts in the author's collection; five live, immature individuals examined.

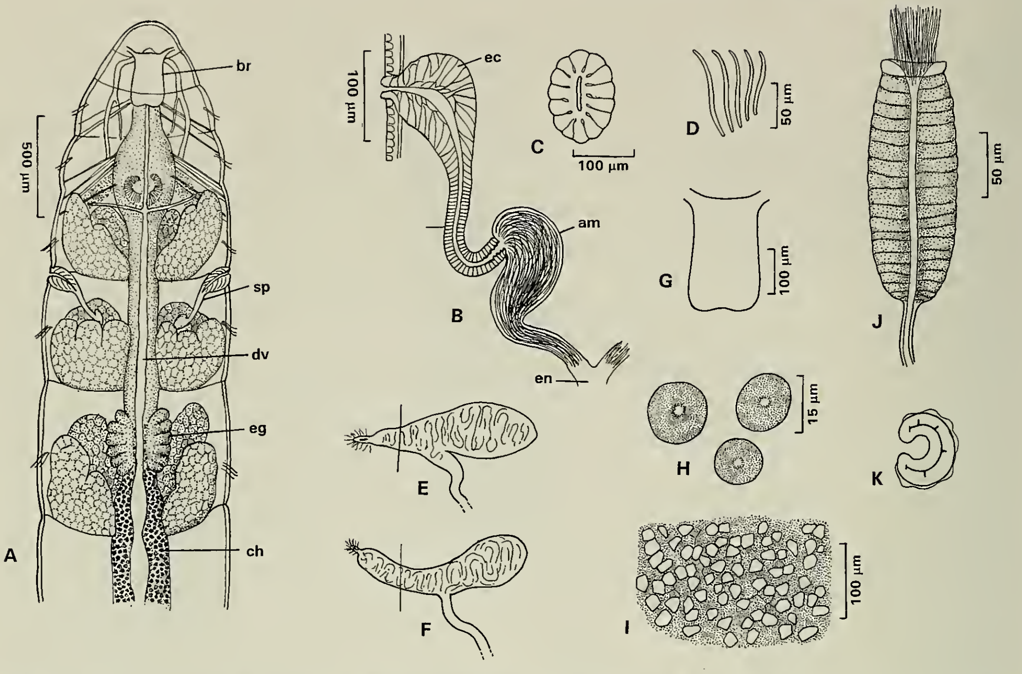

Fig. 4. *Bryodrilus novaescotiae.* A, anterior segments, dorsal view; B, spermatheca, live worm; C, spermathecal pore, surface view; D, setal bundle; E, preclitellar nephridium; F, postclitellar nephridium; G, brain; H, coelomocytes; I, clitellar glands, dorsal view; J, sperm funnel, live worm; K, male pore, ventral view. am ampulla, br brain, ch chloragocytes, dv dorsal blood vessel, ed ectal duct, ec ectal glands, en ental duct, eg esophageal gland, sp spermatheca.

Remarks.—The distinctive feature of this species is the presence of five pairs of primary and five (occasionally four) pairs of secondary pharyngeal glands. Immature specimens are commonly identified on the basis of this character alone. The spermatheca is also distinctive. No sexual individuals were found, however, during this survey, thus a positive identification is not possible. Specimens resembled *C. glandulosa* from Ireland in general appearance. The presence of regenerating fragments indicated that individuals were reproducing by fragmentation.

Habitat and distribution.—Ponce de Leon, leaf litter on floodbank of stream issuing from limestone, pH of litter 5.34. Canada, Greenland, Iceland, Europe, Siberia, Antarctic.

Genus *Bryodrilus* Ude, 1892

Diagnostic characters of the genus are sigmoid or curved setae, without nodulus, of different sizes within a bundle; four esophageal diverticula in VI; peptonephridia and intestinal diverticula absent; dorsal vessel originates within or behind the clitellum; coelomocytes of uniform size and shape; preseptale of nephridium consists of funnel only, efferent duct arises anteriorly, near the septum ("*Henlea* type") or medially; compact penial bulb; simple spermathecae whose ental ducts usually unite before communicating with the dorsal wall of the esophagus.

Distribution.—So far confined to the northern Holarctic, the majority of species being recorded from North America and Siberia. Alaska, Canada, Greenland, Europe, Siberia.

Bryodrilus novaescotiae
Bell, 1962
Fig. 4

Bryodrilus novaescotiae Bell, 1962:169–171, Pl. iv, figs. 1–9.

Material examined.—Three stained whole mounts USNM 170746–170748; three stained whole mounts ROMIZ 13241, 13244–13245, 17 whole mounts in the author's collection. Approximately 30 live specimens examined. Type material not located.

Description of new material.—Medium to large species, white or yellowish due to color of chloragogen tissue and abundant coelomocytes. Length variable; live specimens 10–20 mm, reach 30 mm when stretched; fixed specimens 8–16 mm, diameter 0.7–0.8 mm, slightly wider at clitellum. Segments (37)45–64 ($\bar{X}$ = 54.2, *SD* = 5.5, *n* = 19). Setae sigmoid, without ental hook, three or four in lateral bundles, five or six (occasionally seven) in anterior ventral bundles, four to six ventrally behind clitellum (Fig. 4D). Setae diminish in size from outside of bundle to mid-line and measure 50–100 μm in preclitellar region, 112–128 μm in posterior segments. Cutaneous gland cells in about ten rows anteriorly, more noticeable at level of setae, eight or nine rows per segment behind clitellum. Clitellum extends over XII and ¼–¾ XIII, only slightly raised, with numerous small, coarsely granular, irregularly scattered gland cells and polygonal interspaces (Fig. 4I). Ventrally, gland cells nearly continuous. Head pore a transverse slit just anterior to 0/1.

Three pairs of lobed pharyngeal glands, all free dorsally and with ventral lobes (Fig. 4A). Four esophageal glands in VI, closely applied to the esophagus, situated dorso-laterally and ventro-laterally, each with five to seven regular lobes (Fig. 4A), apparently solid, no internal canals seen. Chloragocytes small, average 10–15 in number across intestine in compressed specimens, form a dense layer from 6/7 at point where gut widens gradually. Coelomocytes numerous, round or oval, finely granular, nucleus not visible in live worms but distinct when stained, diameter (16)20–42 μm (Fig. 4H). In live individuals, coelomocytes appear brown by transmitted light. Dorsal vessel originates at 11/12 or sometimes 12/13, with segmental dilatations in VI–XI, anterior bifurcation at 0/1. Blood colorless. Nephridia with small, free nephrostome and elongate preseptale, postseptale with long, narrow efferent duct that arises antero-ventrally in preclitellar region, mid-ventrally in posterior segments (Fig. 4E, F). First nephridium at 6/7. Brain usually about 1.5 times longer than wide but sometimes shorter with a sinuous posterior border and straight or indented anterior border (Fig. 4G).

Testes small, oval and compact with a smooth outline. Seminal vesicle unpaired, confined to XI. Sperm funnels cylindrical or taper distally, each with a distinct collar of about same width as funnel (Fig. 4J), length in live specimens 150–180 μm, three or four times longer than wide, up to five times longer when stretched, equal to ¼ to ⅓ of diameter of worm. In mounted specimens, funnel has a smooth outline and is usually bent into a semicircle. Sperms duct long and narrow, coiled in XII, about 6 μm in diameter; each opens through a large but compact penial bulb, about 60 μm in longitudinal diameter but sometimes smaller. In fixed specimens, bulb occupies about ⅓ of diameter of clitellum. Male openings semicircular slits (Fig. 4K). One egg present at a time. Spermathecae large, more or less confined to V (Fig. 4B). Ectal duct of spermatheca composed of two parts roughly equal in length, a stout, thick-walled section communicating with one side of ampulla, and a large, bulbous, asymmetrical mass of cells surrounding a narrow chamber that opens to the outside through a straight or curved slit at 4/5, surrounded by a protruding ring of large cells forming a rosette at the surface up to 190 μm across (Fig. 4C). Ampulla thin-walled, roughly pear-shaped in live specimens but contracting to become more spherical when fixed. Ampullae taper entally, ental ducts usually unite just before communicating with esophagus at 5/6 or in anterior part of VI (Fig. 4B), but occasionally communicate separately. Ampullae and ental ducts contain abundant sperm, mostly arranged lengthwise.

Remarks.—The distinctive character of *B. novaescotiae* is its spermathecae. The large swellings near the openings of the ectal ducts are not present in any other member of the genus. Bell (1962) also considered the solid esophageal glands to be unique as they are hollow in other species. His specimens differed chiefly in the form and dimensions of the spermathecae, each of which had a large, hemispherical chamber in the ectal bulb, a smaller "spherical" ampulla and a longer common ental duct. He mentioned two ectal glands in addition to the mass of fused cells around the orifice, but these are not shown in his figure (Bell 1962, fig. 3). Bell also noted a hemispherical chamber within the penial bulb which could not be detected in mounted specimens from Florida. Other differences in Bell's specimens are a shorter brain, about half as long as wide, irregular-shaped coelomocytes (possibly resulting from poor fixation) and nephridia with a large preseptale and an efferent duct that arises terminally but is folded back to give the impression of leaving subterminally or even near the septum. This latter character cannot be considered significant since in sectioned material it can be difficult to tell whether the distal portion of the nephridial duct is folded inside or outside the sheath of the postseptale. Bell did not mention lobes on the esophageal glands, which are not present in other known species of *Bryodrilus,* the dimensions of the sperm funnel, or the presence of a seminal vesicle.

Habitat and distribution.—University of West Florida, Pensacola, in drier parts of a hardwood swamp and an adjoining wooded ravine, mainly above the level of periodic flooding. Soil a moist, spongy humus with numerous fine roots, pH 3.5–4.5. Canada (Nova Scotia).

Genus *Hemienchytraeus* Černosvitov, 1934

Hemienchytraeus species possess a median, unpaired, bifurcated peptonephridium arising from the dorsal wall of the pharynx, which is unique in the Enchytraeidae. Other useful characters are setae in pairs; absence of esophageal or intestinal diverticula; nephridia with large preseptale enclosing the nephrostome; long sperm ducts usually coiled into a spirals; small, compact penial bulbs and free spermathecae each of which has an ectal duct without glands at the opening and a simple ampulla without diverticula.

Distribution.—*Hemienchytraeus* species were the most abundant and widespread enchytraeids in West Florida, especially in moist or wet habitats. Preliminary sampling in Peninsular Florida (unpublished) indicates that the same is true there. The genus is mainly tropical; only one species is recorded from Europe and is uncommon. Europe, India, Japan, Africa, South America.

Hemienchytraeus stephensoni (Cognetti, 1927)
Fig. 5, A–I

Enchytraeus cavicola Stephensen, 1924 (non Joseph 1880):127–129, Pl. 6, figs. 1–4.

Enchytraeus stephensoni Cognetti, 1927:4.

Enchytraeus myrmecophilus Černosvitov, 1930a:85–89, figs. 1–9.

Enchytraeus rangoonensis Stephensen, 1931:177–179, fig. 1.

Hemienchytraeus stephensoni (*E. cavicola* = *E. stephensoni* + *E. myrmecophilus* + *E. rangoonensis*) Černosvitov, 1934:298–304, figs. 1–11.

Hemienchytraeus stephensoni Černosvitov 1939:92–93, figs. 43–49; Christoffersen 1979:40–46, figs. 1–23; Nakamura 1984: 32–33, Fig. 1B, C, F; Dózsa-Farkas 1989:200–202, figs. 24–33.

Material examined.—Five stained, whole mounts, USNM 170741–170745, four stained, whole mounts ROMIZ 13239–13240, 13246–13247; 30 stained, whole mounts in the author's collection. Approximately 50 live specimens examined.

Description of new material.—Small to

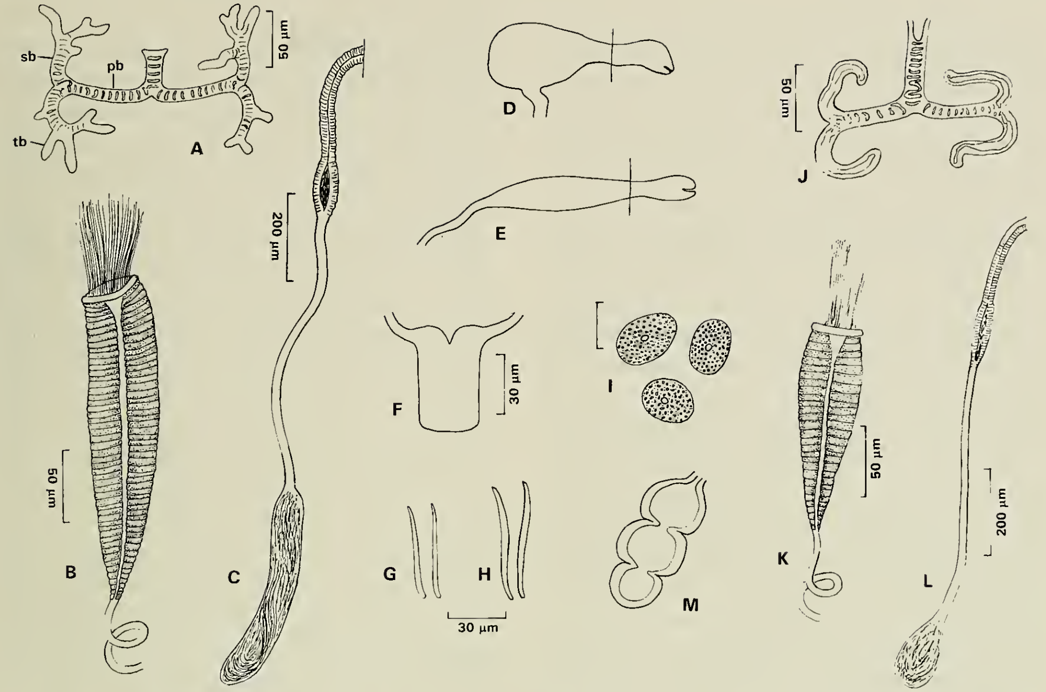

Fig. 5. *Hemienchytraeus stephensoni.* A, peptonephridium; B, sperm funnel, live. worm; C, spermatheca; D, preclitellar nephridium; E, postclitellar nephridium; F, brain; G, anterior setal bundle; H, posterior setal bundle; I, coelomocytes. *Hemienchytraeus bifurcatus.* J, peptonephridium, K, sperm funnel, live worm; L, spermatheca. *Buchholzia fallax.* M, esophageal gland in IV. pb primary branch, sb secondary branch, tb tertiary branch.

medium-sized worms, live specimens rather transparent, with a prominent clitellar region due to presence of large eggs. Live specimens 8–10 mm, fixed specimens 6–9 mm, diameter 0.2–0.3 mm, 0.24–0.38 mm at clitellum. Segments 36–48 ($\bar{X}$ = 44.1, *SD* = 2.7, *n* = 29). Setae two per bundle, occasionally three, with weak ental hook. Setae absent in XII. In anterior region setae straight or slightly curved and rather small, 32–40 µm long, more curved, thicker and longer in posterior half of worm, 50–62 µm in terminal segments (Fig. 5G, H). Cutaneous gland cells small and inconspicuous, in about four rows per segment. Prostomium with numerous dark-staining gland cells. Clitellum over XII–½XIII, gland cells small, arranged in more or less regular transverse rows, especially in ventral region and on anterior and posterior borders of clitellum. Glands may be absent mid-ventrally. Head pore near tip of prostomium. Some specimens were in mucus tubes encrusted with particles of organic matter.

Three pairs of pharyngeal glands, all united dorsally and with ventral lobes. Peptonephridium arises from dorsal side of pharynx in III, proximal portion of variable length, thick-walled with a coiled or sinuous lumen, primary and secondary branches narrower but also with coiled lumina (Fig. 5A). Each secondary branch divides into three to five thin-walled, finger-like processes. Entire peptonephridium confined to IV. Chloragocytes from V, form a dense layer from VII, 11–13 cells across intestine in preclitellar region in compressed specimens. Transition between esophagus and intestine gradual with enlargement behind pharyngeal glands. In all specimens collected from the Pensacola region in 1993, a section of the intestine behind the clitellum, usually between XIV–XVI and XXVIII–XXX, was enlarged and brown in colour. In other specimens, the brown region was reduced or absent. Coelomocytes sparse, of various sizes and shapes, but mainly round, 8–18 μm, almost hyaline in live individuals, faintly granular with a distinct nucleus in fixed specimens (Fig. 5I). Dorsal vessel originates in XIII, usually with isolated, yellow, dendritic cells on surface of vessel (seen in live worms); anterior bifurcation at 0/1. Blood colorless. Nephridia with large, ovoid preseptale that encloses a dorsally directed nephrostome, postseptale of variable shape, usually ovoid in preclitellar segments where duct arises mid-ventrally and elongated in posterior segments where duct is sub-terminal or terminal (Fig. 5D, E). First nephridium at 6/7. Brain about 1.5 times longer than wide, deeply indented or even cleft on its anterior border, posterior border sinuous or straight (Fig. 5F).

Testes compact. Small, paired seminal vesicles usually present in XI. Sperm funnels funnel-shaped, somewhat flattened, 190–360 μm long, 40–112 μm wide, somewhat longer than diameter of worm, generally six to eight times longer than wide in live specimens, with collar about same width or slightly narrower than rest of funnel (Fig. 5B). Funnels taper to spirally coiled ducts 5–6 μm in diameter, which open at small, compact penial bulbs, longitudinal diameter 54–82 μm. Male pores curved slits. One to three large eggs present at a time, contained in an egg sac that extends to 14/15 or rarely 15/16. Spermathecae with long, thick-walled ectal ducts, 12–18 μm in diameter, outer surface rough, which swell to form sperm-containing chambers in V or VI, continue as smooth, thin-walled tubes, and terminate in thin-walled, cylindrical ampullae in VI–IX (Fig. 5C). Length of spermathecae variable; ampullae may be twice or several times longer than wide, swollen and occupying up to 2½ segments when mature.

Remarks.—*Hemienchytraeus stephensoni* is a very variable species, hence the number of nominal species synonymised by Černosvitov (1934). The variability has been commented on by Černosvitov (1939), who noted differences in the length of the basal part of the peptonephridium and in the form and complexity of the septal (pharyngeal) glands in South American specimens. Christoffersen (1979) distinguished four types among Brazilian material from a single locality that differed in body length and width, setal length, pharyngeal glands, form of the peptonephridium, origin of dorsal vessel, number and shape of nephridia, form of the penial bulbs, length of sperm funnels and length of spermathecae and ampullae. He concluded that *H. stephensoni* is a complex of cryptic species. Two extreme forms were recognised among West Florida material that differed in lengths of setae, sperm funnels, spermathecal ampullae and the proximal section of the peptonephridium and in the form of the pharyngeal glands, but intermediates were also found. Size and segment number and dimensions of setae and sperm funnel are within the range of specimens from South America (Christoffersen 1979, Dózsa-Farkas 1989) and Japan (Nakamura 1984), but specimens differ in having both secondary and tertiary branches to the peptonephridium and in the presence of seminal vesicles. No individuals were found with more than two secondary branches on each side of the peptonephridium, as in material from Lake Titicaca (Černosvitov 1939) and Ecuador (Dózsa-Farkas 1989). In spite of Christoffersen's ability to recognise distinct types within a region, and the differences between material from Florida and South America, I believe *H. stephensoni* to be one variable species with a wide ecological tolerance and a wide geographic range.

Habitat and distribution.—*Hemienchytraeus. stephensoni* was by far the most common enchytraeid in the region and was recorded from all localities and most kinds of inland habitat.

Pensacola, woodland, swamp, edge of a pond, floodbank of a river and boggy area, Avalon Peninsula, pitcher plant (*Sarracenia*) bog; Ponce de Leon, woodland at edge of a stream; Lakewood, edge of a lake; Marianna, woodland on limestone and bank of a river; Torreya State park, woodland on limestone; Port St. Joseph, edge of roadside ditch. pH range 3.6–7.2.

Mainly tropical. South America (Argentina, Paraguay, Brazil, Bolivia, Ecuador), India, Burma, Central Africa, Japan. Recorded from almost every conceivable terrestrial habitat including woodland, grassland, tree bark, anthills, bat guano and the marine littoral zone. New for North America.

Hemienchytraeus bifurcatus
Nielsen & Christensen, 1959
Fig. 5J–L

Hemienchytraeus bifurcatus Nielsen & Christensen 1959:45, figs. 23–27.

Hemienchytraeus bifurcatus Nakamura 1984:31–32, fig. 1A, D, E.; Kasprzak 1986:178, figs. 639–643.

Material examined.—Three stained, whole mounted specimens USNM 170746–170748; one stained whole mount ROMIZ 13248; seven stained whole mounts in the author's collection. Approximately 28 live specimens examined.

Description of new material.—Medium to small worms, live specimens 4–6 mm, transparent when viewed microscopically, with a prominent clitellar region due to presence of rather large eggs. Fixed length 4–6 mm, diameter 0.3–0.4 mm, 0.3–0.45 mm at clitellum. Segments (25)29–44 ($\bar{X}$ = 35.2, SD = 4.9, n = 20). Setae straight or slightly curved with a weak ental hook, two per bundle throughout, absent in XII, 32–58 μm. Cutaneous glands small, indistinct. Clitellum over XII-½XIII with small gland cells arranged in more or less transverse rows or sometimes irregularly, smaller or absent in mid-ventral region. Head pore near tip of prostomium. Some specimens were in mucus tubes with adhering debris and soil.

Three pairs of pharyngeal glands, all lobed and united dorsally. Peptonephridium arises from mid dorsal region of pharynx in III, proximal section of variable length, branching dichotomously into two primary and four secondary branches (Fig. 5J). Proximal part of unpaired section hollow and contractile in live specimens, distal section and primary branches stout with a coiled or sinuous lumen, secondary branches thin-walled with a wide lumen. Entire peptonephridium confined to IV. Chloragocytes from V, forming a dense layer from VII. Esophageal-intestinal transition gradual, gut expands behind pharyngeal glands. Coelomocytes sparse, of various shapes and sizes, dominant type round or oval, 10–14 μm, nucleated, granular. Dorsal vessel originates in XIII or XIV, anterior bifurcation at 0/1. Blood colorless. Nephridial preseptale large, postseptale egg-shaped with postero-ventral efferent duct in preclitellar region, more elongated with terminal or subterminal duct behind clitellum. Nephridia starting at 4/5 or 5/6, absent X–XVI. Brain rectangular, about 1.5 times longer than wide, deeply indented or even cleft on its anterior border, more or less truncated posteriorly.

Small, paired seminal vesicles usually present, sometimes only developed on one side. Sperm funnels funnel-shaped, three or four times longer than broad in live worms, 100–150 μm in length, equal to ⅓ or ½ diameter of worm, with a collar equal to or slightly narrower than rest of funnel (Fig. 5K). Funnels taper to long, spirally-coiled ducts in XII, open at small, compact penial bulbs, about 32 μm across. One to three large eggs present at a time, egg sac extending to XIV. Spermathecae long, each consists of a fairly stout, thick-walled ectal duct, without glands at the orifice, duct swells to form a sperm-containing chamber in V or VI and then extends as a thin-walled tube to an ovoid or spherical ampulla situated in any of segments VI–IX, usually in VII (Fig. 5L).

Remarks.—This species, like the previous one, is very variable, especially in size, form of the nephridia and lengths of spermathecae and sperm funnels. The different dimensions of the reproductive organs are not related to stage of maturity, for individuals with sperm in the ampulla may have long or short spermathecae and either short or long sperm funnels. Danish specimens (Nielsen & Christensen 1959) differed in having a brain indented posteriorly, nephridia with terminal efferent ducts, coelomocytes with refringent granules, no seminal vesicle and a sperm funnel only 2–3 times longer than wide. A longer sperm funnel was also reported in Japanese specimens (Nakamura 1984).

The species is similar in general appearance to *H. stephensoni* but is generally smaller and has somewhat more granular coelomocytes, more noticeable in live specimens. The two species often occurred together and although the form of the peptonephridium is quite different, this was sometimes difficult to see clearly. Mature individuals could be reliably distinguished by the greater dimensions of the spermathecal ampulla and sperm funnel in *H. stephensoni,* as noted by Nakamura (1984).

Habitat and distribution.—Not as abundant, nor as widespread as *H. stephensoni.* Pensacola, woodland leaf litter at the University of West Florida, grass cuttings at Scenic Hills golf course; Avalon Peninsula, pitcher plant (*Sarracenia*) bog; Ponce de Leon, woodland soil and leaf litter; Marianna, woodland soil and leaf litter on limestone. pH range 3.9–6.9. Denmark, France, Japan, India. New for North America.

Genus *Henlea* Michaelsen, 1889

The principal diagnostic characters of the genus are straight or slightly curved setae, usually of unequal size within a bundle, the outer ones longer, esophagus expands abruptly into the intestine (with the possible exception of the sub-genus *Hepatogaster*), esophageal appendages present, intestinal diverticula present or absent, a preclitellar origin of the dorsal vessel, usually in VIII or IX, and nephridia with free nephrostome and anterior origin of the efferent duct, often described as "*Henlea* type" but not unique to that genus.

Cosmopolitan: E and W of North America, S America, Europe, Siberia, Africa, Antarctic.

Henlea perpusilla Friend, 1911
aug. Černosvitov 1937b

Henlea perpusilla Friend, 1911:466–467.
Henleanella perpusilla Friend, 1913a:89.
Henlea bisetosa Friend, 1914:135.
Henlea inusitata Friend, 1913a:83–84.
Henlea minima Friend, 1913a:84.
Henlea nivea Černosvitov, 1930b:88, figs. 3–6.
Henlea perpusilla Friend 1913b:270–271, figs. 34–35; Černosvitov 1937a:194–196, figs. 2–5; Nielsen & Christensen 1959: 58–59, figs. 46, 47; Kasprzak 1986:256–257, figs. 992–996.

Material examined.—Two stained, whole mounts USNM 170749–170750; two stained whole mounts in the author's collection. Live specimens examined, 27.

Remarks.—The large number of synonyms that are now recognised reflects a wide variation in size and morphology (Černosvitov 1941, Nielsen & Christensen 1959), which is partly explained by the existence of different cytotypes (Nielsen & Christensen 1959). Size of the live specimens (6–8 mm) and segment number (30–33) of Florida material are within the range of European specimens.

Habitat and distribution.—Common in Marianna State Park, deciduous woodland on limestone, sandy humus, sandy alluvial deposits and humus with limestone fragments; Tall Timbers Research Station, live oak forest, dark, sandy loam and leaf litter. pH range 5.5–7.1. Absent from the west of the study area. Canada (Cornwallis Is., Prince of Wales Is., Devon Is., Rocky Mountains), Greenland, Europe, Lebanon, Siberia, Japan, Antarctic, Bolivia.

Henlea ventriculosa
d'Udekem, 1854

Enchytraeus ventriculosus d'Udekem, 1854: 863, figs. 1, 4, 6–9.
Henlea multispinosa Friend, 1913a:85.
H. (*Udekemiana*) *ventriculosa* Černosvitov, 1930b:75.
Henlea groenlandica Černosvitov, 1929: 146, figs. 1, 2.
H. (*Udekemiana*) *groenlandica* Černosvitov, 1930b:75.
Fridericia stewarti Stephenson, 1909:109.
Henlea ventriculosa Michaelsen, 1889:31–32, 1900:69–70; Nielsen & Christensen 1959:62, figs. 50, 53, 57; Kasprzak 1986: 264–265, figs. 1028–1030.

Material examined.—Two stained, whole mounts USNM 170751–170752; three stained, whole mounts in the author's collection. Five live specimens examined.

Remarks.—Size, 5–8 mm when fixed, and segment number (38–44) of Florida individuals are within the range of European specimens but the spermathecae have shorter ectal ducts, about equal to the length of the ampullae, while each ental duct is longer than the combined lengths of ampulla and ectal duct. In addition, there are several small glands at the ectal opening. Danish specimens lacked these glands, the ectal duct was longer and the ental duct shorter (Nielsen & Christensen 1959). In spite of these differences, the species could be identified with confidence by the characteristic gut diverticula.

Habitat and distribution.—Marianna State Park, deciduous woodland on limestone, rotting wood, leaf litter, humus with limestone fragments. pH range 5.3–6.7. Canada (Cornwallis Is., Prince of Wales Is.), USA (Massachusetts, N. Carolina), Europe, Siberia, Tibet, Japan, New Zealand, S. America.

Genus *Buchholzia* Michaelsen, 1887

The genus is recognised by the following unique combination of characters: sigmoid setae, decreasing in size within bundles toward the dorsal and ventral midlines of the body; hollow esophageal appendages in IV; transition between esophagus and intestine abrupt with one or two dorsal diverticula at 7/8; anteclitellar origin of the dorsal vessel in the region of the intestinal diverticula; and small, hyaline, anucleate coelomocytes in addition to the normal kind.

So far, confined to the northern hemisphere but not recorded from Asia. Canada, Europe, N. Africa.

Buchholzia fallax Michaelsen, 1887
(Fig. 5M)

Buchholzia fallax Michaelsen, 1887:374–376, pl. 21, fig. 4A–E.
Buchholzia fallax Beddard, 1895:334–335; Michaelsen 1900:72–73; Černosvitov 1928:9; Ude 1929:57–58; Nielsen & Christensen 1959:65, figs. 59–61; Wilcke 1967:72, fig. 6A, B; Kasprzak 1986:117–118, figs. 294–298, table 8.

Material examined.—Two stained, whole mounts USNM 170753–170754; ten whole mounts in the author's collection. Live specimens examined, 18.

Remarks.—Distinguished from *B. appendiculata* (Buchholz, 1862), which was recorded from Montreal by Nurminen (1973b), by the presence of one, rather than two, intestinal diverticula and only three instead of four pairs of pharyngeal glands, and by having male organs in the usual position for enchytraeids. All specimens examined are small, 4–7 mm compared with 12–14 mm for specimens from Denmark (Nielsen & Christensen 1959). Segments 30–38 (Danish material 37–42). A seminal vesicle is usually present, stated to be absent by Nielsen & Christensen and not mentioned by Michaelsen (1887). The pulsating esophageal appendages in IV are of a different shape from those figured by Nielsen & Christensen (1959:143, fig. 60); they are elongate with partial cross walls dividing the cavity into three compartments (Fig. 5M), rather than rosette-like. The small, secondary cavities in the spermathecal ampulla, figured by Michaelsen, could not be seen and have not been mentioned by other authors. Some specimens were inside mucus tubes encrusted with rings of soil particles.

Habitat and distribution.—Common in Marianna State Park, deciduous woodland on limestone. A few in a similar habitat in Torreya State Park. pH range 5.5–7.1. Absent from the west of the study area. Europe, N. Africa. New for North America.

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Artacama valparaisiensis, a new species of Terebellidae (Annelida: Polychaeta) from subtidal soft bottoms of Valparaiso Bay, Chile

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Abstract.—A new species of terebellid, *Artacama valparaisiensis*, is described from Valparaiso Bay, Central Chile. The species closely resembles *A. crassa* Hartman, 1967, from the South Shetland Islands, Antarctica, but can be distinguished on the basis of the following morphological criteria: shape and number of proboscidial papillae, size and number of the branchial filaments, relative size of lobe at the upper edge of uncinal ridges in abdominal parapodia and presence of constrictions in the limbate setae.

Systematics of the Terebellidae was reviewed recently by Holthe (1986). According to his review, *Artacama* Malmgren, 1866, with eight valid species is the only genus in subfamily Artacaminae. McHugh (1995) has carried out a cladistic analysis of the Terebellidae in which she shows that *Artacama* is the sister taxon of a large clade within the Amphitritinae. The Artacaminae has therefore been synonymized with the Amphitritinae, which is diagnosed by the presence of double rows of uncini on posterior thoracic segments. The character that identified the Artacaminae, a peristomium modified on its ventral side to form a conspicuous proboscis-like organ adorned with papillae, is considered an autapomorphy for the genus *Artacama* (McHugh 1995). Only two species of *Artacama, A. crassa* Hartman, 1967 and *A. proboscidea* Malmgren, 1866, have been reported from southeastern Pacific, in antarctic and subantarctic waters (Rozbaczylo 1985). From 1978 to 1980 an extensive research program on benthic communities at Valparaiso Bay, Central Chile, was carried out by Dr. José Stuardo (presently at Universidad de Concepción) and Dr. Héctor Andrade (presently at A & A Tecnolab S.A., División Ambiental). Three areas with different particle size (sand, sandy-mud and sandy-silt), organic matter and other biochemical components were sampled, from 34 to 59 meters depth. Samples from these areas have been studied by Stuardo et al. (1981) regarding their biochemical and granulometric composition. They showed that among the three sampled areas there were differences in proteins, lipids and organic matter; the sandy-mud area showed the highest values and sandy area the lowest values. Among the abundant polychaetes collected during that program numerous individuals of *Artacama* were found. These differed from the other known species reported for the genus, and consequently are described as a new species.

Specimens of the new species were compared with the holotype of *A. crassa* deposited in the National Museum of Natural History, Washington, D.C. (USNM 55569) and a specimen of *A. proboscidea* from Western Canadian Arctic (USNM 41132) identified by E. & C. Berkeley.

Type and paratype specimens of the new species are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Sala de Sistemática, Departamento de Ecología, Pontificia Universidad Católica de Chile, Santiago (SSUC); and Museo de Zoología, Universidad de Concepción (UCCC).

Materials and Methods

Polychaetes were collected at Valparaiso Bay, Central Chile. Samples were taken monthly, from November 1979 to October 1980, with a 0.1 m^2 Van Veen dredge at three areas with different particle size (sand, sandy-mud and sandy-silt), from 34 to 59 meters depth. Polychaetes were fixed in 10% formalin and preserved in 70% ethanol. Figures were prepared by means of a drawing tube on a Wild M-5 microscope. Scanning electron microscopic (SEM) observations and photographs were obtained using a JEOL JSM-25SII microscope.

Artacama valparaisiensis, new species

Figs. 1, 2

Material examined.—Central Chile: Valparaiso Bay, off Punta Osas, ca. 32°59′20″S, 71°33′56″W, 44 m, H. Andrade, coll., 9 Jul 1979, holotype (USNM 170005), and 14 paratypes (USNM 170006); 4 Sep 1979, 8 paratypes (UCCC 23169–23176), and 14 paratypes (SSUC 6719).

Description.—Holotype incomplete with 52 setigers, measuring about 60 mm long, width about 9 mm at thorax. Body (Fig. 1a) thick anteriorly and colorless in alcohol, with first 8–11 segments enlarged, tapers posteriorly to a narrow pygidial end. Total length of one of the largest complete specimens, is 104 mm including proboscis, width 12 mm at thorax and 4 mm at abdomen, and consists of 102 setigerous segments; 17 thoracic setigers and 85 abdominal setigers. Large, ovoid and papillose proboscis (Fig. 1a) extends forward from buccal segment below mouth. Prostomium (Fig. 1b) is small folded, bilobed structure, with small oral aperture immediately below. Eyes absent. Small, horseshoe-shaped tentacular lobe on dorsal side of peristomium, with a dorsal indentation and numerous tentacles, short and clubbed, most of which are broken. Proboscis covered overall with numerous, conical and minute, papillae (Fig. 1c) arranged in about ninety longitudinal rows. Lateral lappets absent on segments 2–4. Three pairs of long filiform branchiae on segments 2–4; each branchia is a tuft of approximately 50 equal-length filaments arising from basal stump. Nephridiopores, in form of short tubes, number five pairs; the best developed are on segment 3 below second pair of branchiae, in line with the more posterior notopodia; smaller ones are on segments 6, 7, 8 and 9, between notopodia and uncinal ridges, postero-ventral to notopodia. Ventral glandular pads present on first 10 setigers. Thorax with fixed number of setigers; seventeen bundles of notosetae starting on segment 4; uncini first present from the second setiger (fifth segment); occur in single rows on first six uncinal ridges, then in double rows from setigers 8 to 17, oriented "fang to fang." Thoracic notopodia (Fig. 1d) with triangular lamellae, postsetal lobe larger than presetal; 40–50 long, pointed setae decreasing in length from dorsal to ventral part of notopodia, laterally winged, with one or two constrictions (Fig. 1e). Thoracic neuropodia with avicular uncini with a large fang surmounted by four or five alternating rows of many small teeth (Fig. 2a, b). Abdomen with numerous segments bearing parapodia (Fig. 1g, h) with flaplike tori and dorsally large, subcircular membrane which increase in size towards the posterior end; uncini in single rows restricted to ventral margin; abdominal uncini resemble thoracic but main fang is longer and thinner and have six or seven alternating rows of teeth (Figs. 1f, 2c, d).

Posterior end tapers to terminal pygidium (Fig. 1i), with terminal anus, with crenulate sides.

Geographical distribution.—Known only from Valparaiso Bay, Chile.

Remarks.—*Artacama valparaisiensis* new species resembles, most closely, *A. crassa* Hartman, 1967 and *A. proboscidea* Malmgren, 1866. However *A. valparaisien-*

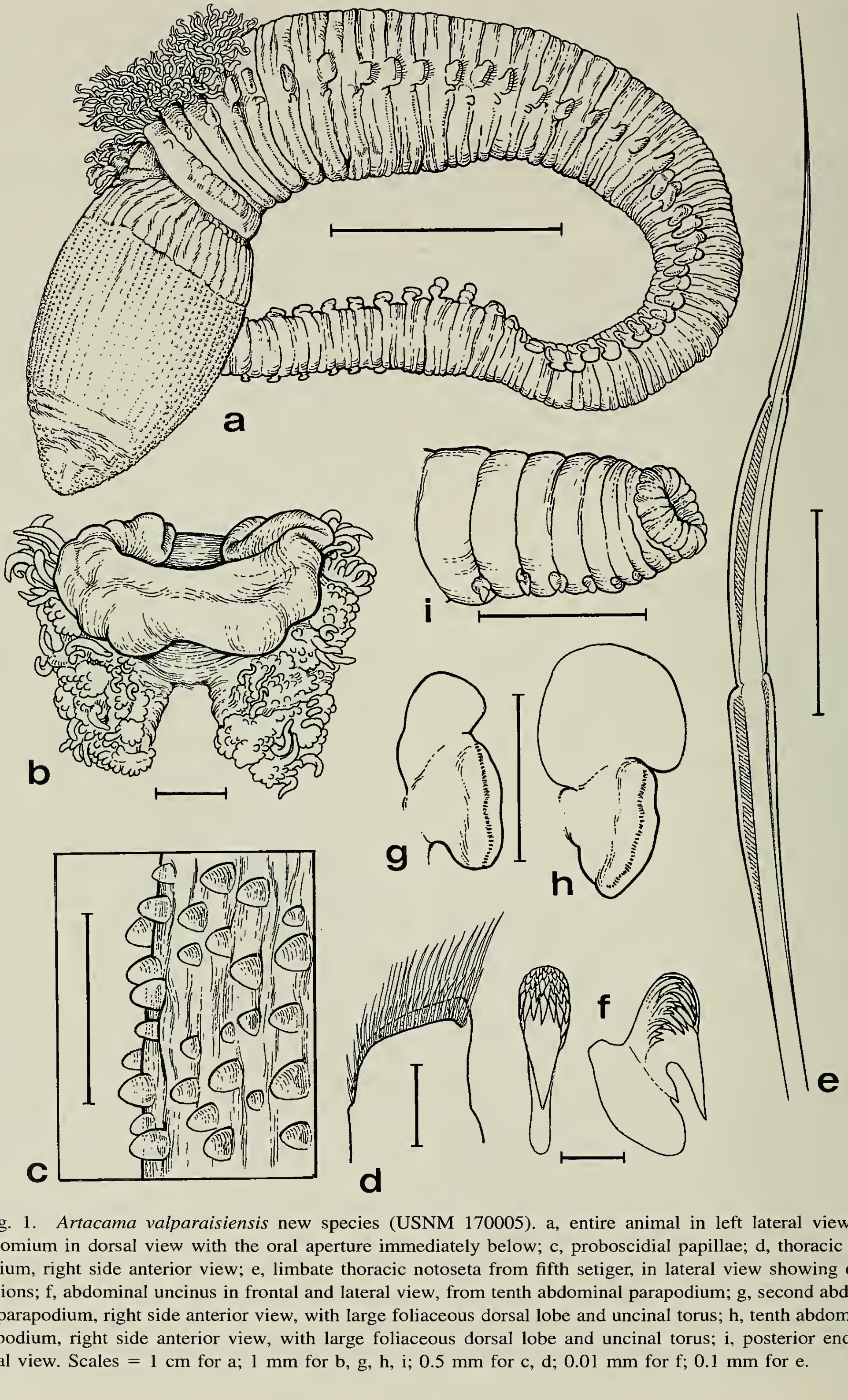

Fig. 1. *Artacama valparaisiensis* new species (USNM 170005). a, entire animal in left lateral view; b, prostomium in dorsal view with the oral aperture immediately below; c, proboscidial papillae; d, thoracic parapodium, right side anterior view; e, limbate thoracic notoseta from fifth setiger, in lateral view showing constrictions; f, abdominal uncinus in frontal and lateral view, from tenth abdominal parapodium; g, second abdominal parapodium, right side anterior view, with large foliaceous dorsal lobe and uncinal torus; h, tenth abdominal parapodium, right side anterior view, with large foliaceous dorsal lobe and uncinal torus; i, posterior end, in lateral view. Scales = 1 cm for a; 1 mm for b, g, h, i; 0.5 mm for c, d; 0.01 mm for f; 0.1 mm for e.

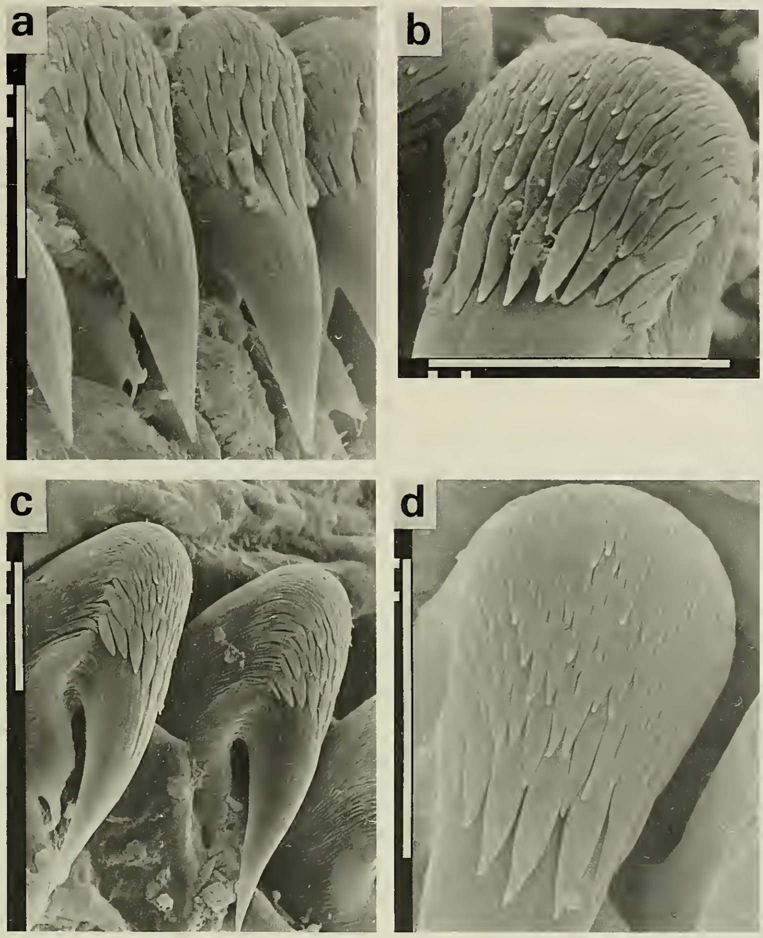

Fig. 2. *Artacama valparaisiensis* new species, SEM micrographs: a, thoracic uncini in lateral view from the first uncinigerous segment (fifth thoracic segment); b, detail of the upper part of an uncinus of thoracic segment 11 (first segment with double rows of uncini); c, abdominal uncini in lateral view from the fourth abdominal segment; d, detail of the upper part of an uncinus of the fourth abdominal segment. Scales = 0.01 mm for a–d.

sis differs from *A. crassa* in that papillae of the proboscis are more abundant, conical, and smaller; the number of branchial filaments is higher (ca. 50 in each branchiae) and each filament is longer and thinner; presence of constrictions in the limbate setae; thoracic notopodia with postsetal lamellae longer than presetal lobe, while in *A. crassa* both lobes are short; abdominal parapodia with the uncinigerous tori longer and the dorsal membrane comparatively smaller. On the other hand, *A. proboscidea* shows fewer branchial filaments, shorter and thicker than those of *A. valparaisiensis.* Papillae of the proboscis of *A. proboscidea* are bigger and fewer than in *A. valparaisiensis.* Dorsal membrane of abdominal parapodia of *A. valparaisiensis* is bigger than those of *A. proboscidea.* Absence of constrictions in the limbate setae of *A. proboscidea.* McIntosh (1885) described *A. challengeriae* from several localities off Kerguelen Islands, 46–202 m; Hartman (1959) considers this species similar to *A. proboscidea.* Description of *A. challengeriae* is so general and vague that it is difficult to compare it with *A. valparaisiensis.* Nevertheless, from figures (Pl. LI. fig. 6; Pl.

XXVIIIA. figs. 23a, b, 24, 25) in McIntosh (1885) can be established that *A. challengeriae* differs from *A. valparaisiensis* at least in that the former has proboscidial papillae bigger an fewer; edges of limbate setae are entire, without constrictions; ventral margin of uncini presents an ondulating outline while in *A. valparaisiensis* has a uniform and slight convexity the same as in *A. crassa* and *A. proboscidea.*

Etymology.—The specific name *valparaisiensis* refers to the type locality, Valparaiso Bay.

Ecological remarks.—*Artacama valparaisiensis* was more abundant between May and September, with densities of 100 indiv./m^2 in May and 250 indiv./m^2 in September. The species showed the highest density in the sandy-mud area (30–250 indiv./m^2), the second one was the sandy-silt area (5–100 indiv./m^2); at the sandy area the species was extremely rare. In the sandy area few specimens of small size were found only in May and September while in the sandy-mud and sandy-silt areas numerous specimens of different size were found throughout the sample period. This pattern of distribution appears to be correlated with the different organic matter content of sediments in the sites sampled (Stuardo et al. 1981). In the population studied it was possible to distinguish adult females by the presence of eggs in the coelomic cavity. Maximum egg size was 165 μm diameter.

Acknowledgments

We thank Dr. Jose Stuardo, Departamento de Oceanología, Universidad de Concepción, who made specimens available for sudy and Dr. Héctor Andrade, A & A Tecnolab S.A., División Ambiental who furnished information about collecting. We specially thank Clara Yañez for her skill and patience in producing the illustrations used in this paper and José Morillas for the scanning electron photomicrographs. We thank Dr. Kristian Fauchald of the National Museum of Natural History, Washington, D.C., for the loan of specimens for comparison. The manuscript was greatly improved by the valuable comments and suggestions provided by Dr. Christopher J. Glasby and an anonymous reviewer who also provided valuable bibliography.

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Review of *Hermilepidonotus* Uschakov, 1974, and two species of polynoid polychaetes (Lepidonotinae)

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Abstract.—The genus *Hermilepidonotus* Uschakov, 1974, and type species *Lepidonotus robustus* Moore, 1905, are reviewed, and compared with the closely related *Lepidonotus helotypus* (Grube, 1877), based on examination of types and available new material.

Under *Lepidonotus helotypus* (Grube, 1877), from China, Seidler (1924:56) included *Lepidonotus robustus* Moore, 1905, from the Gulf of Alaska. This was followed by Annekova (1937), from the North Japan Sea, by Hartman (1938), from Alaska, and by Uschakov (1950, 1955), from the Okhotsk Sea. On further study, *L. robustus* was considered to be distinct from *L. helotypus,* by Hartman (1948) and by Uschakov (1974). Based mainly on a characteristic pharynx, the latter author referred *L. robustus* to the new genus *Hermilepidonotus.* The close similarity of these two Pacific Ocean boreal species is the basis for adding *L. helotypus* to *Hermilepidonotus.* The two species are more fully described herein and some new records are presented. In addition to the specimens deposited in the National Museum of Natural History, Smithsonian Institution (USNM), types and additional material were obtained on loan or in exchange from the following sources: the former British Museum (Natural History), London (BMNH), now renamed the Natural History Museum, London, through J. D. George and A. I. Muir; National Science Museum, Tokyo (NSMT), through M. Imajima; Zoological Institute Academy of Science, Leningrad (ZIASL), through P. V. Uschakov; Zoologisches Museum, Berlin (ZMB), through G. Hartwich; and Zoologisches Staatsmuseum, Hamburg, through G. Hartmann-Schröder.

Family Polynoidae Kinberg, 1856
Subfamily Lepidonotinae Willey, 1902
Genus *Hermilepidonotus* Uschakov, 1974, emended

Type species.—*Lepidonotus robustus* Moore, 1905, by monotypy and original designation.

For: *H. robustus* (Moore, 1905) and *H. helotypus* (Grube, 1877), new combination.

Diagnosis.—Body elongate-oval, with 26 segments. Prostomium lepidonotoid, bilobed, with 3 antennae and 2 palps; ceratophore of median antenna in anterior notch, lateral antennae inserted terminally on anterior extensions of prostomium, on same level as median antenna; 2 pairs of eyes on posterior half of prostomium. First or tentacular segment not distinct dorsally; tentaculophores lateral to prostomium, each with aciculum, few setae on inner side, and pair of dorsal and ventral tentacular cirri, similar to antennae. Elytra and large elytrophores 12 pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23. Elytra large, suboval, leaving middorsum uncovered, without fringes of papillae, thick, soft, with micropapillae on (*H. robustus*) or with microtubercles and conical macropapillae (*H. helotpyus*). Dorsal cirri on non-elytrigerous segments, with cylindrical cirrophores and smooth styles; dorsal tubercles bulbous inflated areas. Second or buccal segment with first pair of elytrophores, biramous parapodia, and long ventral buccal cirri lateral to ventral mouth. Eversible muscular pharynx with 2 pairs of chitinous hooked jaws and border papillae; [about 15 pairs (13–17, in *H. helotypus*) or border papillae plus numerous branched, threadlike papillae, in *H. robustus*)]. Parapodia biramous, with small conical notopodia on anterodorsal sides of large neuropodia; neuropodia with subequal presetal and postsetal lobes, with smaller, truncate supraacicular parts and longer, diagonally truncate subacicular parts. Notosetae slender, with spinous rows, short, with blunt tips and longer, with fine tips. Neurosetae stout, with long spinous regions and long, bare, entire tips. Ventral cirri short, subulate. Nephridial papillae beginning on segment 8. Pygidium with anal ridge and pair of anal cirri.

Hermilepidonotus robustus
(Moore, 1905)
Fig. 1

Lepidonotus robustus Moore, 1905:544, pl. 36:figs. 32–35.—Hartman, 1948:12.

Lepidonotus helotypus.—Seidler, 1924:56 (part).—Annenkova, 1937:145, pl. 1:fig. 1, pl. 3:fig. 14.—Hartman, 1938:109.—Uschakov, 1950:157; 1955:128, fig. 19, A–E; 1965:107, fig. 19, A–E.—Chlebovitsch, 1961:165. Not Grube, 1877.

Hermilepidonotus robustus.—Uschakov, 1974:458, figs. A–H (synonymy); 1982: 112, pl. 33, 1–8.—Buzhinskaja, 1985:82.

Material examined.—Alaska: Shelikov Strait, 88–119 m, from hermit crab, *Albatross* sta 4291, 15 Aug 1903, holotype of *L. robustus* (USNM 5523). Virgin Bay, T. Kincaid, collector, 1 specimen (USNM 32311). Coal Harbor, Unga Island, 1872, W. H. Dall, collector, 1 specimen (USNM 18652). Kodiak Island, W. J. Fisher, collector, 1 specimen (USNM 18867). Aleutian Islands, R. C. McGregor, collector, 1 specimen (USNM 18904). Canoe & Cold Bays, 27–73 m, Sep & Oct 1940, 4 specimens (USNM 21318–21320; ZIASL, ident. by Hartman, 1948).

Bering Sea: West Black Hill, 18 m, 27 Jul 1957, Weber, collector, 1 specimen (USNM 32310).

Okhotsk Sea: 16 Aug 1947, P. V. Uschakov, collector, 1 specimen (USNM 43574, from ZIASL, as *L. helotypus* by Uschakov, 1950).

Description.—Length of holotype 37 mm, width with setae 17 mm, 26 segments. Lengths of specimens examined 13–40 mm, widths 7–16 mm. Uschakov (1974) reported lengths to 65 mm, widths with setae to 20 mm. Body elongate-oval, flattened dorsoventrally. Segments multiringed (wrinkled), with pigmented transverse bands. Large oval elytra leaving middorsum uncovered, without fringes of papillae. Elytra rather thick, soft, of gelatinoid texture, with pigmented network on median and posterior areas, colorless on anterior and lateral areas; surfaces with slightly raised, bulbous, white spots with small "papillae" (thickened cuticle?) in center and scattered micropapillae (Fig. 1J; Moore 1905, pl. 36:fig. 32; Uschakov 1974, figs. C, D; 1982, pl. 33,3). Dorsal cirri on non-elytrigerous parapodia with cylindrical cirrophores, bulbous basally, on posterodorsal sides of notopodia, with styles long, cylindrical, with filamentous tips, and extending beyond neurosetae; dorsal tubercles forming slightly inflated areas (Fig. 1G; Moore 1905, pl. 36: fig. 35; Uschakov 1974, fig. B; 1982, pl. 33, 2).

Bilobed prostomium with stout ceratophore of median antenna in anterior notch, style rather short, with filamentous tip; lateral antennae with ceratophores formed of anterior extensions of prostomium, equal in length and lateral to ceratophore of median antenna, with styles slightly shorter; palps stout, tapering, slightly longer than antennae; anterior pair of eyes in region of greatest width of prostomium, larger than posterolateral pair; tentaculophores with few (0–7) slender setae on inner sides; dorsal and ventral tentacular cirri similar to median antenna (Fig. 1A; Uschakov 1974, fig. A; 1982, pl. 33, 1).

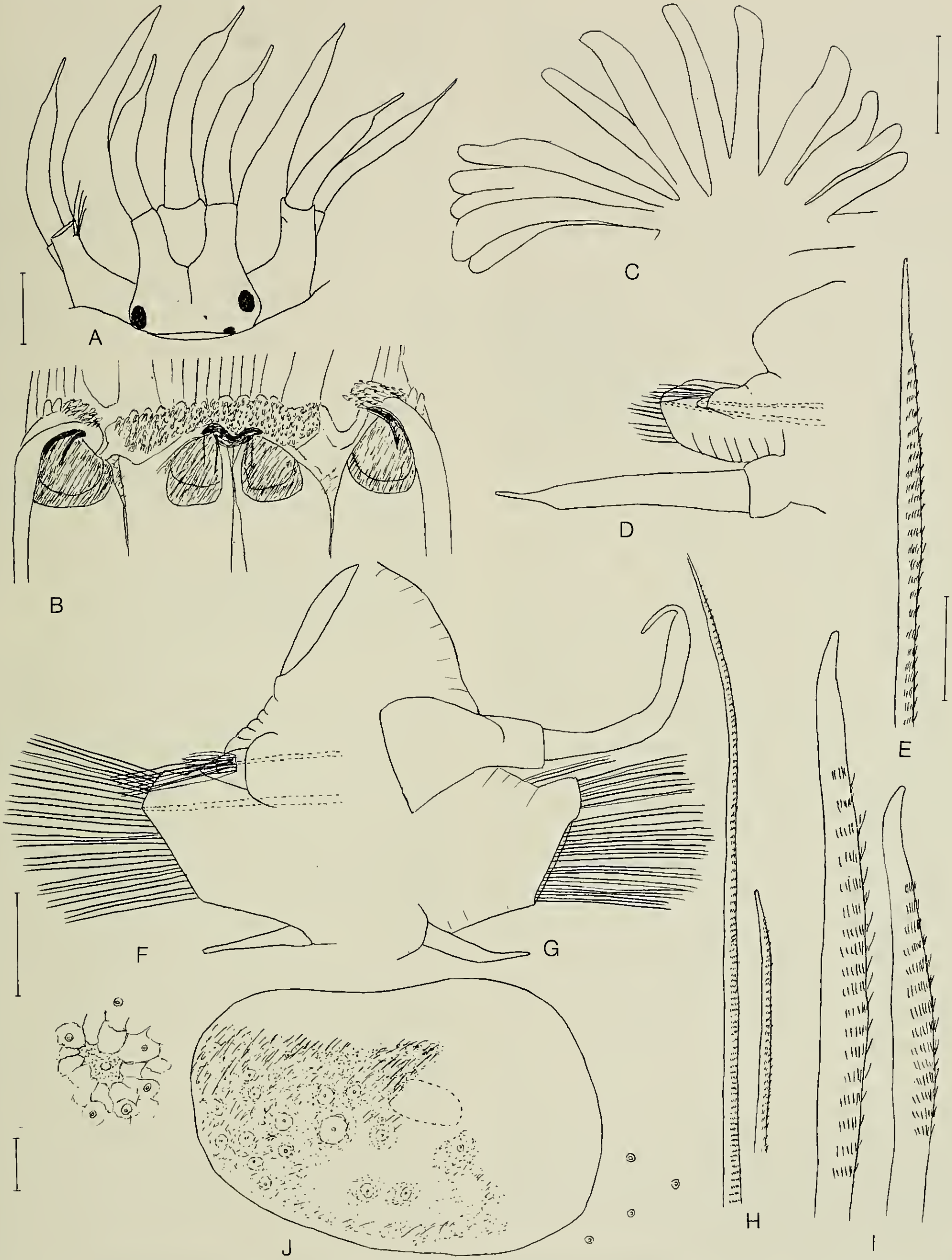

Fig. 1. *Hermilepidonotus robustus,* A, D–J, holotype of *Lepidonotus robustus* (USNM 5523); B, C, pharynx from specimen from Aleutian Is. (USNM 18904): A, Dorsal view of anterior end, posterior pair of eyes partially hidden by segment II; style of left dorsal tentacular cirrus missing; setae lacking on right tentaculophore; B, Muscular pharynx removed from body and cut open midventrally and flattened, showing left and right ventral jaws on outside and dorsal pair of jaws in middle, and distal pharyngeal papillae; C, Pharyngeal branched papillae; D, Right elytrigerous parapodium from segment II, anterior view, acicula dotted; E, neuroseta from same; F, Right middle elytrigerous parapodium, anterior view, acicula dotted; G, Right middle cirrigerus parapodium, posterior view; H, Short and long notosetae from same; I, Short lower and longer upper neurosetae from same; J, Right middle elytron, with detail of micropapillae and pigmented network. Scales = 1.0 mm for A, B; 0.2 mm for C; 1.0 mm for D, F, G; 0.1 mm for E, H, I; 1.0 mm for J.

Segment II without nuchal fold, with large bulbous elytrophores, biramous parapodia, and long ventral buccal cirri, lateral to ventral mouth, similar to tentacular cirri (Fig. 1D; Uschakov 1974, fig. A; 1982, pl. 33, 1). Notosetae similar to following segments; neurosetae more slender than following, with long spinous regions and long tapered bare tips (Fig. 1E). Eversible muscular pharynx with 2 pairs of large hooked jaws and numerous border papillae enclosing numerous branched, threadlike papillae, forming thick brush (Fig. 1B, C; Uschakov 1974, figs. F, G, H; 1982, pl. 33, 6–8).

Biramous parapodia with small subconical notopodia on anterodorsal bases of larger neuropodia; smaller supraacicular part of neuropodia truncate and larger subacicular part diagonally truncate (Fig. 1F, G; Moore 1905, pl. 36:fig. 35; Uschakov 1975, fig. B; 1982, pl. 33, 2). Notosetae forming close tuft, slender, with close transverse rows of fine teeth, some shorter, with blunt tips, and some longer, tapering to slender tips and extending beyond tips of neuropodia (Fig. 1F, H; Moore, 1905 pl. 36:figs. 34, 35). Neurosetae stout, dark golden color, forming dense bundles arranged in horizontal rows; 2 supraacicular and 7 subacicular (Moore 1905), with long spinous regions (13–20 rows), supraacicular longer than subacicular ones, all with long, slightly hooked, bare tips (Fig. 1F, I; Moore 1905, pl. 36:fig. 33; Uschakov 1974, figs. B, E, 1982, pl. 33, 2, 5). Ventral cirri short, subulate, extending to lower tips of neuropodia (Fig. 1F, G). Nephridial papillae beginning on segment 8, on inflated areas and directed between parapodia. Pygidium with anus on middle of segments 25–26, with pair of anal cirri.

Distribution.—Gulf of Alaska, Bering Sea, Aleutian and Kurile Islands, North Japan and Okhotsk Seas, in 0–210 meters.

Hermilepidonotus helotypus
(Grube, 1877), new combination
Fig. 2

Polynoe (*Lepidonotus*) *helotypus* Grube, 1877:49.

Polynoe (*Lepidonotus*) *gymnonotus* Marenzeller, 1879:112, pl. 1:fig. 3.

Lepidonotus gymnonotus.—McIntosh, 1885: 64, pl. 10:fig. 4, pl. 17:fig. 5, pl. 9A:figs. 2, 3.

Lepidonotus holotypus.—Seidler, 1924:56, figs. 12, 13 (synonymy, part, not *L. robustus* Moore).—Fauvel, 1933:8.—Monro, 1934:358.—Not Annenkova, 1937: 145 (=*H. robustus*)—Hartman, 1938:109 (part, not *H. robustus*).—Not Uschakov, 1955:128 (=*H. robustus*).—Uschakov & Wu, 1959:10, 28–29; 1965:157; 1979:17 (English translation).—Imajima & Hartman, 1964:25 (synonymy).—Imajima & Gamô, 1970:2, fig. 4.—Rho & Song, 1974:77, figs. 12–16; 1975:98.—Uchida, 1982:3, figs. 4–7.—Jae, Lee, & Noh, 1987:2, pl. 1A–D.

Lepidonotus (*Lepidonotus*) *helotypus.*—Uschakov, 1982:106, pl. 30, 1–7).

Material examined.—China: Chefóo, Grube, collector, syntype of *P.* (*L.*) *helotypus* (ZMB 1074). China, C. Ping, collector, 2 specimens (BMNH 1925.5.5.11; USNM 50910, ident. Monro, 1934).

Japan: off Kobé, 15–91 m, *Challenger* Expedition, 2 Jul 1873, 3 specimens (BMNH 1885.12.1.46; 1921, 5,1,169, as *L. gymnonotus* by McIntosh). Kobé, Gordon & Smith, collectors, 3 specimens (ZMB Q1858). Kokodate Bay, 2–25 m, *Albatross* sta 3656, 3657, 19 Sep 1895, 11 specimens (USNM 23749, 50911, 50912). Hokodate, Hilgendorf, collector, 2 specimens (ZMB 2091, as *P.* (*L.*) *gymnonotus*). South Japan, N. Schedel, collector, 5 specimens (ZMH V-526, as *L. gymnonotus* by Augener). Formosa or Japan, Laberer, collector, 5 specimens (ZMB 211, as *L. gymnonotus*). Hayama, Miura Peninsula, May 1966, Imajima, collector & identified, 1 specimen (USNM 544770, from NSMT).

Description.—Length of syntype (ZMB 1074) 50 mm, width with setae 16 mm, segments 26. Imajima & Hartman (1964) reported lengths to 63 mm, widths to 20 mm. Body elongate-oval, flattened dorsoventral-

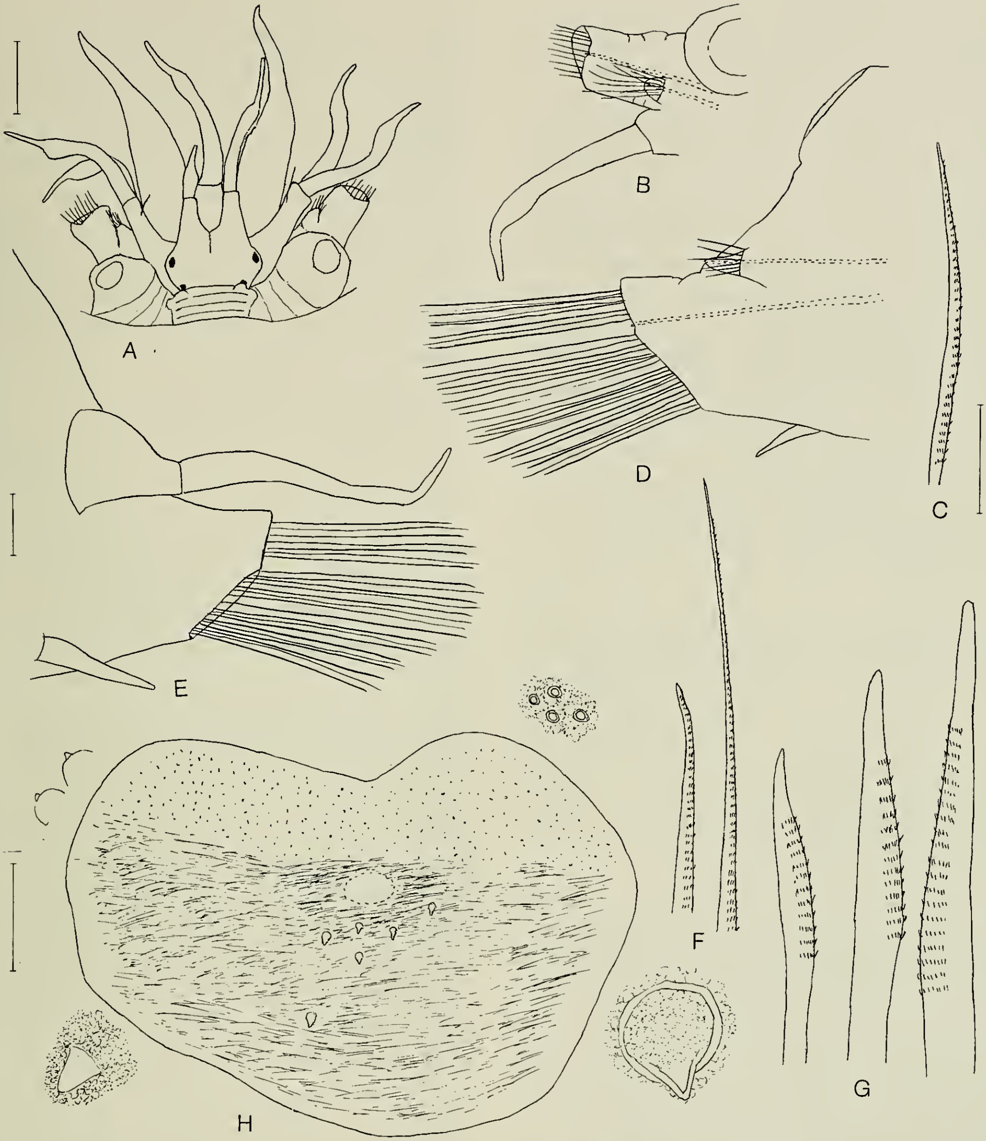

Fig. 2. *Hermilepidonotus helotypus,* specimen from Hokodate, Japan (USNM 50912); A, Dorsal view of anterior end, left lateral antenna small, regenerating; B, Right elytrigerous parapodium from segment II, anterodorsal view, acicula dotted; C, Neuroseta from same; D, Right middle elytrigerous parapodium, anterior view, acicula dotted; E, Right middle cirrigerous parapodium, posterior view; F, short and long notosetae from same; G, Lower, middle and upper neurosetae from same; H, Right middle elytron, with detail of conical macropapillae and microtubercles among cellular network. Scales = 1.0 mm for A; 0.5 mm for B, D, E; 0.1 mm for C, F, G; 1.0 mm for H.

ly. Segments multiringed, with transverse colored bands on posterior parts of segments, matching elytra in color. Large oval elytra overlapping and leaving middorsum uncovered, without fringes of papillae (McIntosh 1885, pl. 10:fig. 4). Elytra rather thick, soft, with pigmented network, except for anterior fourth and over scar of attachment to elytrophore; numerous microtubercles in cellular network of colorless area;

surface of posterior pigmented area with projecting whitish conical macropapillae, variable in number and arrangement, from almost lacking to numerous (10–50, by Uschakov 1982) (Fig. 2H; McIntosh 1885, pl. 17:fig. 5; Uchida 1982, fig. 5A, C–J; Uschakov 1982, pl. 30, 2). Dorsal cirri on nonelytrigerous segments with cylindrical cirrophores, bulbous basally, on posterodorsal sides of notopodia, with styles long, cylindrical, with tapered tips and extending to tips of neurosetae; dorsal tubercles bulbous, inflated (Fig. 2E; Uchida 1982, fig. 6C).

Bilobed prostomium with stout ceratophore of median antenna in anterior notch, style with subterminal enlargement and filamentous tip; lateral antennae with ceratophores formed of anterior extensions of prostomium, slightly shorter than ceratophore of median antenna; palps stout, tapering, longer than antennae; anterior pair of eyes in region of greatest width of prostomium, slightly larger than posterolateral pair; tentaculophores with aciculum and slender seta on inner side, and dorsal and ventral tentacular cirri, similar to median antenna (Fig. 2A; Uchida 1982, figs. 5A, B, 6A; Uschakov 1982, pl. 30, 1).

Segment II with slightly developed nuchal fold, with large bulbous elytrophores, biramous parapodia, and long ventral buccal cirri, similar to tentacular cirri (Fig. 2A, B; Uchida 1982, fig. 5B). Notosetae similar to following segments; neurosetae more slender than following, with long spinous regions and slender entire tips (Fig. 2C). Eversible pharynx with 13–17 pairs of marginal papillae (Uschakov 1982, pl. 30, 7).

Biramous parapodia with small conical notopodia on anterodorsal sides of large neuropodia; neuropodia with subequal presetal and postsetal lobes; smaller supraacicular part of neuropodia truncate and larger subacicular part diagonally truncate (Fig. 2D, E; Uchida 1982, fig. 6B, C). Notosetae forming small bundle, thin, with long spinous regions, some short, with blunt tips and some long, tapering to fine tips (Fig. 2F; Uchida 1982, fig. 7E, F). Neurosetae numerous, stout, dark reddish amber-colored, with long spinous regions, supraacicular ones with longer spinous regions than subacicular ones, all with rather long, slightly hooked, entire tips (Figure 2G; Uchida 1982, fig. 7I–K). Ventral cirri short, subulate, not extending to lower tips of neuropodia (Fig. 2D, E; Uschakov 1982, pl. 30, 4). Nephridial papillae beginning on segment 8. Pygidium with anus medial to parapodia of segment 25, with pair of anal cirri medial to dorsal cirri of last 2 segments, directed posteriorly.

Distribution.—Yellow Sea, China, South Japan, Korea, Kurile Islands, in 0–108 meters.

Remarks.—Uschakov referred *Lepidonotus robustus* to the new genus *Hermilepidonotus,* based mainly on the unusual structure of the pharynx, with numerous threadlike papillae forming a thick brush. Specimens of *Lepidonotus,* and the majority of other polynoids, have the pharynx with 9 pairs of large marginal papillae. *Lepidonotus helotypus,* referred herein to *Hermilepidonotus,* has more numerous border papillae (13–17 pairs) than the 9 pairs in other species of *Lepidonotus.* Also, the neuropodia of the two species of *Hermilepidonotus* differ from those of other *Lepidonotus* species in having subequal presetal and postsetal lobes (Figs. 1F, G, 2D, E) and lacking the larger presetal conical acicular process as found in species of *Lepidonotus.*

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The Antarctic genus *Callozostron* and its relationship to *Primnoella* (Octocorallia: Gorgonacea: Primnoidae)

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Abstract.—Specimens of the gorgonacean genus *Callozostron* obtained in Antarctic waters during operations conducted by the U.S. Antarctic Research Program reveal that *Callozostron horridum* Kükenthal, 1909, is a junior synonym of *Callozostron mirabile* Wright, 1885. *Callozostron carlottae* Kükenthal, 1909, is confirmed as a valid species, and two new species, *Callozostron diplodiadema* and *Callozostron acanthodes* are described. All species are illustrated by stereoscopic scanning electron micrographs (SEM). The genus *Primnoella* Gray, 1858, is restricted to the "Compressae" species group, and polyps and sclerites of *Primnoella australasiae* (Gray, 1850), type species of the genus, are illustrated by SEM for the first time. A new genus, *Convexella,* is established for the "Convexae" species group of *Primnoella,* and polyps of *Primnoella magelhaenica* Studer, 1879, type species of *Convexella,* from a wide bathymetric and geographic range are illustrated by SEM to show morphological variation within the species.

During biological operations of the U.S. Antarctic Research Program (USARP), several deep-water dredge and trawl tows in Antarctic waters have yielded specimens of the three species of *Callozostron* so far described, *C. mirabile* Wright, 1885, *C. carlottae* Kükenthal, 1909, and *C. horridum* Kükenthal, 1909. This material shows that *C. horridum* cannot be maintained as a species separate from *C. mirabile,* and that a species distinct from *C. carlottae* remains to be described, in addition to a new species having a branched colony unlike any known heretofore. These are here described respectively as *Callozostron diplodiadema* and *C. acanthodes,* new species.

Operations of USARP in the Patagonian region and on Burdwood Bank have obtained numerous colonies attributable to *Primnoella magelhaenica* Studer as reported by Thomson & Ritchie (1906, as *magellanica*) from the *Scotia* cruise and by Broch (1965) from the *Brategg* expedition. These show sufficient variation to accommodate both *Primnoella magelhaenica* and *P. flagellum* as described by Studer (1879) from the same geographical area. The largest colonies are superficially almost indistinguishable from specimens of *Callozostron diplodiadema* new species and *C. carlottae* Kükenthal, obscuring but not eliminating the distinction between *Primnoella* and *Callozostron.*

Preparation of samples.—In general, sclerites, intact whorls and isolated polyps were prepared according to methods described elsewhere (Bayer & Stefani 1989: 450–451). However, in order to determine the arrangement of opercular and circumopercular sclerites, single polyps were individually macerated in Sodium hypochlorite solution and observed under the dissecting microscope during the process in order to distinguish opercular from circumopercular scales, and the isolated sclerites washed one by one by tranferring them through a series of drops of distilled water, drying, and mounting in sequence on SEM stubs.

Callozostron P. Wright, 1885

Callozostron P. Wright, 1885:691.—Studer [& Wright], 1887:48.—Wright & Studer, 1889:48.—Versluys, 1906:124.—Kükenthal, 1912:331; 1915:152; 1919:449; 1924:306.—Bayer, 1981:936 (in key only).—Bayer & Stefani, 1989:455 (in key only). (Type species: *C. mirabile* Wright & Studer, 1889, by subsequent monotypy.)

Diagnosis.—Flagelliform, unbranched or sparsely branched primnoids with tall, cylindrical polyps standing almost vertically from the axis, arranged in whorls; bases of polyps may be partially fused to form unbranched polyp leaves; opercular scales of nearly uniform size, distinctly differentiated from marginal scales; at least 4 marginal scales with very long, slender apical spine; body completely covered by scales. No irregular, tuberculate sclerites in walls of longitudinal stem canals.

Remarks.—In my key to octocoral genera (Bayer 1981:936), *Callozostron* is not distinguished from *Ainigmaptilon,* in both of which the polyps partially fuse to form pennatulacean-like "polyp-leaves." However, the spiculation of the polyps differs in the two genera. All nominal species of *Callozostron* have 8 well-differentiated smaller opercular scales within a ring of large marginal scales bearing long apical spines. In *Ainigmaptilon* the distalmost 8 scales are larger than the marginals, which are not well differentiated from the body scales below. Those of *A. antarcticum* (Molander) are triangular, with a broadly pointed apex (Molander 1929: fig. 22a) reminiscent of the opercular scales of *Primnoella gracilis* Molander (1929: fig. 18a), and those of *A. virgularoides* (Molander) are lancet-shaped with a short apical spine. In *A. edisto* Bayer (1950: fig. 2a) they bear long, smooth spines, and in *A. haswelli* Dean they have a strong, serrated apical spine (Thomson & Rennet, 1931: pl. 13, fig. 1). The 8 distalmost polyp scales of *A. antarcticum* and *A. virgularoides* converge over the infolded tentacles in a manner similar to those of *Primnoella gracilis* Molander, but in *A. haswelli* and *A. edisto* these scales cannot fold over the tentacles because of their long apical spines. Molander (1929), Carlgren (1943) and Bayer (1950) call these sclerites "Deckschuppen" or "opercular scales" whether or not they have long spines but, in fact, there is no functional "operculum" as in *Callozostron.*

In the examples so far reported, the axis of *Ainigmaptilon* terminates basally in a funnel-shaped expansion which encloses a quantity of mud that served to anchor the colony in soft substrate, whereas in those cases that are known, the axis of *Callozostron* terminates in a small, discoidal holdfast for attachment to solid substrate.

Most records of *Ainigmaptilon* are from shallow or moderate depths: *wallini*: 75 m; *antarcticum,* 125 m; *haswelli*: 517–549 m; *edisto*: 182 m; USNM records of *antarcticum*: 88–526 m; *edisto*: 182–662 m.

Except for one doubtful record, specimens of *Callozostron* have been taken at much greater depths, usually below 1000 m and mostly between 2000 and 3000 m.

Accordingly, there seems to be no doubt that both *Callozostron* and *Ainigmaptilon* should be treated as valid genera separable on the basis of differences in the opercular and circumopercular scales as mentioned above.

In the discussion of his new genus *Lycurus* (= *Ainigmaptilon*), Molander (1929: 70) pointed out the similarities of the genus to *Primnoella gracilis* and suggested that it may have arisen from such a form. A strong morphological similarity also exists between *Callozostron* and certain *Primnoella* species including *P. magelhaenica* Studer and *P. flagellum* Studer.

In *Callozostron carlottae* Kükenthal and *C. diplodiadema* new species, the basal fusion of adjacent polyps is minimal (see Figs. 9, 11, and Kükenthal 1912:334, fig. 43), inviting comparison with *Primnoella magelhaenica* Studer, in which the polyps are not appressed to the axis and often (but not always) stand out almost vertically (see Figs. 21, 23, 27, and Broch 1965: pl. 1, fig. 1). *Primnoella magelhaenica* has distinctly pointed marginal scales that surround and overlap the opercular scales proper. In this respect, the polyps of *P. magelhaenica* are similar to those of *C. carlottae,* differing most conspicuously in the absence of strongly developed apical spines on the scales of three whorls surrounding the operculum, which is poorly differentiated from, and partially covered by, the marginal (circumopercular) sclerites.

Key to species of *Callozostron*

1(2). Colonies dichotomously branched, polyps arranged in whorls. Whorls composed of up to 6 polyps. Apex of opercular scales prolonged as a narrow spine. Marginal spines smooth, about 7× as long as height of basal part . . . . *acanthodes,* new species

2(1). Colonies flagelliform, sometimes bifurcate but not repeatedly branched, polyps arranged in whorls that may be densely crowded. Apex of opercular scales more or less acutely pointed but not prolonged as a narrow spine.

3(4). Whorls sometimes densely crowded and more or less obscured, composed of as many as 12 or even more polyps; polyps about 3 mm tall exclusive of marginal spines; marginal spines smooth, slender, 4–6, commonly 4, developed only on the marginal transverse row of body scales, 2–3× as long as the height of the wide basal part . . . . *mirabile*

4(5). Colonies flagelliform or bifurcate. Whorls distinct, composed of 8–9 polyps; polyps about 2 mm tall exclusive of marginal spines; marginal spines stout, with raised longitudinal ridges, about 24, developed on 3 transverse rows of body scales, about 2× as long as height of basal part . . . . *carlottae*

5(1). Colonies flagelliform. Whorls distinct, composed of up to 14 polyps; polyps about 2 mm tall exclusive of marginal spines; marginal spines slender, smooth, about 16, developed on 2 transverse rows of distal body scales, about 5× as long as height of basal part . . .*diplodiadema,* new species

Callozostron mirabile Wright, 1885
Figs. 1, left; 2–6

Callozostron mirabile Wright, 1885:691, figs. 234, 235.—Wright & Studer, 1889: 48, pl. 10, figs. 1–5; pl. 20, fig. 1.—Versluys, 1906:124.—Kükenthal, 1912:328–333 *passim*; 1919:450; 1924:306.—Schimbke, 1915:22.

Callozostron horridum Kükenthal, 1909:49; 1912:331, figs. 38–42, pl. 22, figs. 12, 13; 1919:451; 1924:307.—Schimbke, 1915: 23.

Material.—Antarctica, Oates Coast: 64°59′S, 160°36′E, 2836–2864 m, USNS *Eltanin* sta. 1957, 7 Feb 1967; one colony USNM 78662. South Atlantic Ocean, between South Orkney Islands and Palmer Peninsula: 63°03′S, 49°11′W, 2653–2941 m, USNS *Eltanin* sta. 529, 3 Mar 1963; 2+ colonies USNM 77377 (SEM 1159). South Atlantic Ocean, off South Georgia Island: 56°04′S, 33°59′W, 3239–3138 m, USNS *Eltanin* sta. 722, 8 Sep 1963, 5+ colonies USNM 77378 (SEM 1160, 1166, 1167, 1622, 1623). South Atlantic Ocean, off South Georgia Island: 54°00′S, 33°40′W, 2718–2663 m, USNS *Eltanin* sta. 723, 9 Sep 1963. 1 colony USNM 77381. South Atlantic Ocean, off South Sandwich Islands: 57°22′36″S, 26°34′00″W, 2248–2402 m, R/V *Islas Orcadas* sta. 51, 26 May 1975, 1+ colony USNM 82876 (SEM 1624, 1625). South Atlantic Ocean, off South Sandwich Islands: 57°39′24″S, 26°26′42″W, 415–612 m, R/V *Islas Orcadas* sta. 52, 26 May 1975, 1+ colonies USNM 77339 (probably a contaminant from sta. 51). South Pacific Ocean, off Antipodes Island, New Zealand: 49°40′S, 178°56′E, 952–1336 m, USNS *Eltanin* sta. 1852, 3 Jan 1967, 3+ colonies USNM 77402. Scotia Sea: 60°02′S, 49°14′W, 3819–3876 m, USNS *Eltanin* sta. 545, 7

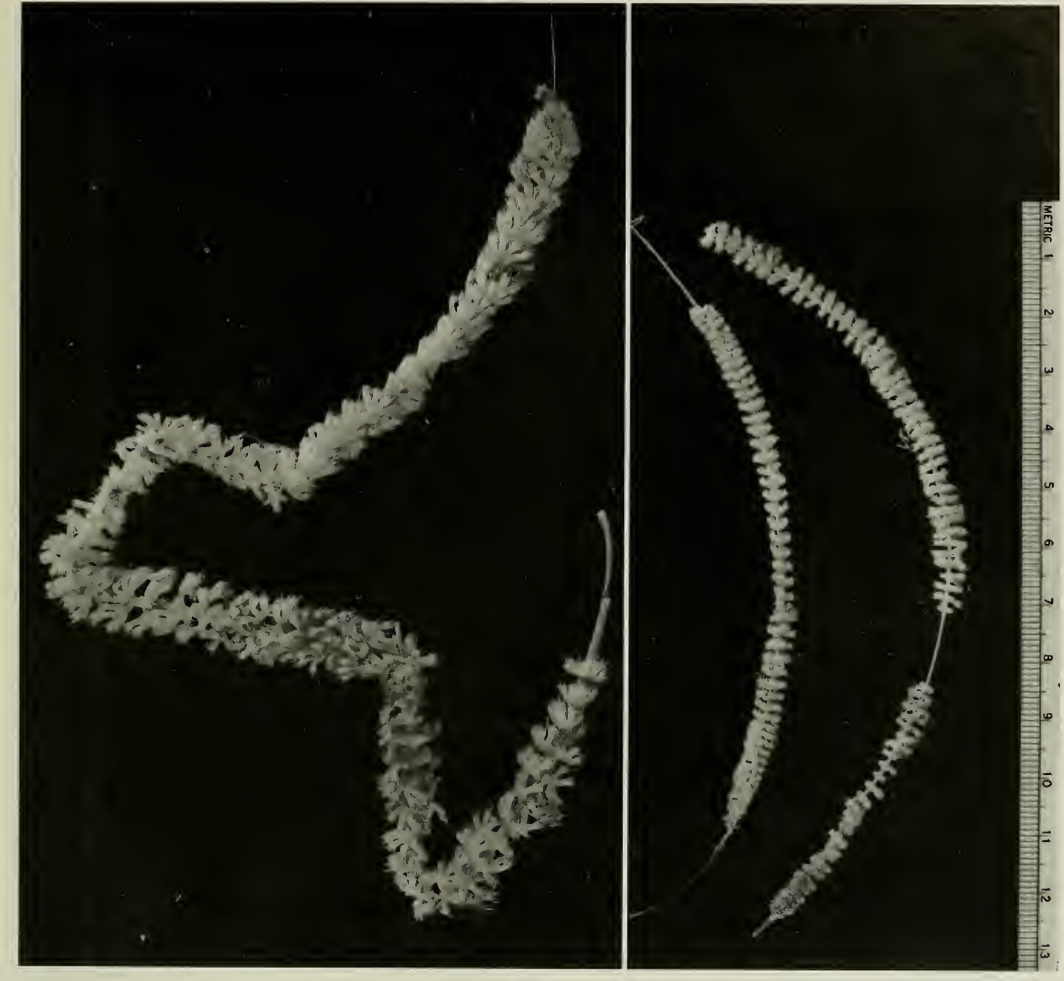


Fig. 1. Left, *Callozostron mirabile* Wright, USNM 82876. Colony with axis still in place but broken; Right, *Callozostron diplodiadema* new species, USNM 77386. Two incomplete colonies (syntypes).

Mar 1963, 1 incomplete colony ripped from axis and broken, USNM 85294 (SEM 1630–1634).

Diagnosis.—*Callozostron* with up to 12 or more polyps in whorls that may be obscured by close crowding. Long, slender apical spine developed on 4–6 marginal scales of polyps.

Remarks.—The distalmost whorl in a colony may consist of as few as 4 polyps (Fig. 3), but this number quickly increases proximad. Fully developed polyps (Fig. 2, top) are about 3 mm tall excluding the 4–6 long, marginal spines (Fig. 2, bottom), which usually are more or less broken, and indistinctly united by their bases into groups of a few individuals (Fig. 2, top). In contraction, eight distalmost polyp scales fold over the retracted tentacles as a conical operculum (Fig. 4). The marginal scales of immature polyps (Fig. 5) do not have the long apical spine present on fully developed individuals (Figs. 2, 4). Sclerites (Fig. 6) are of the generalized primnoid type: thin, rounded scales with finely dentate margins, smooth externally and covered with closely set complex tubercles internally, those of the polyp body (Fig. 6c) larger than those

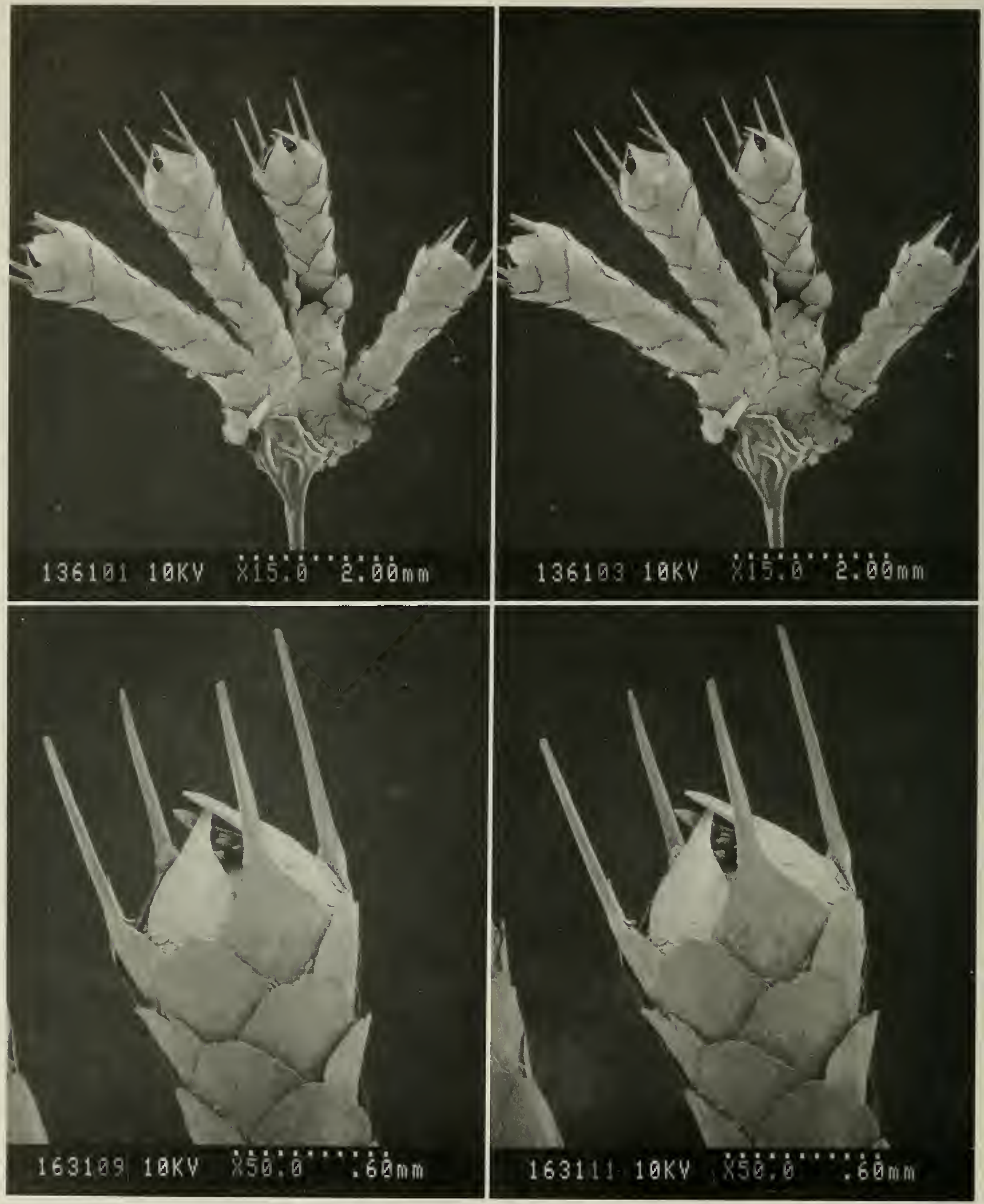


Fig. 2. *Callozostron mirabile* Wright, USNM 85294. Top, Four polyps from a whorl; Bottom, Detail of oral end of polyp with four marginal scales prolonged into spines. Stereoscopic pairs (SEM 1631).

of the coenenchyme (Fig. 6d); the opercular scales are of the usual roughly triangular shape, thin, with a broad, shallow apical groove. Four to six of the marginal scales are unusual in having an exceptionally long, thin, fragile, apical spine (Fig. 6b).

The present material provides evidence that the coenenchyme and polyps of the

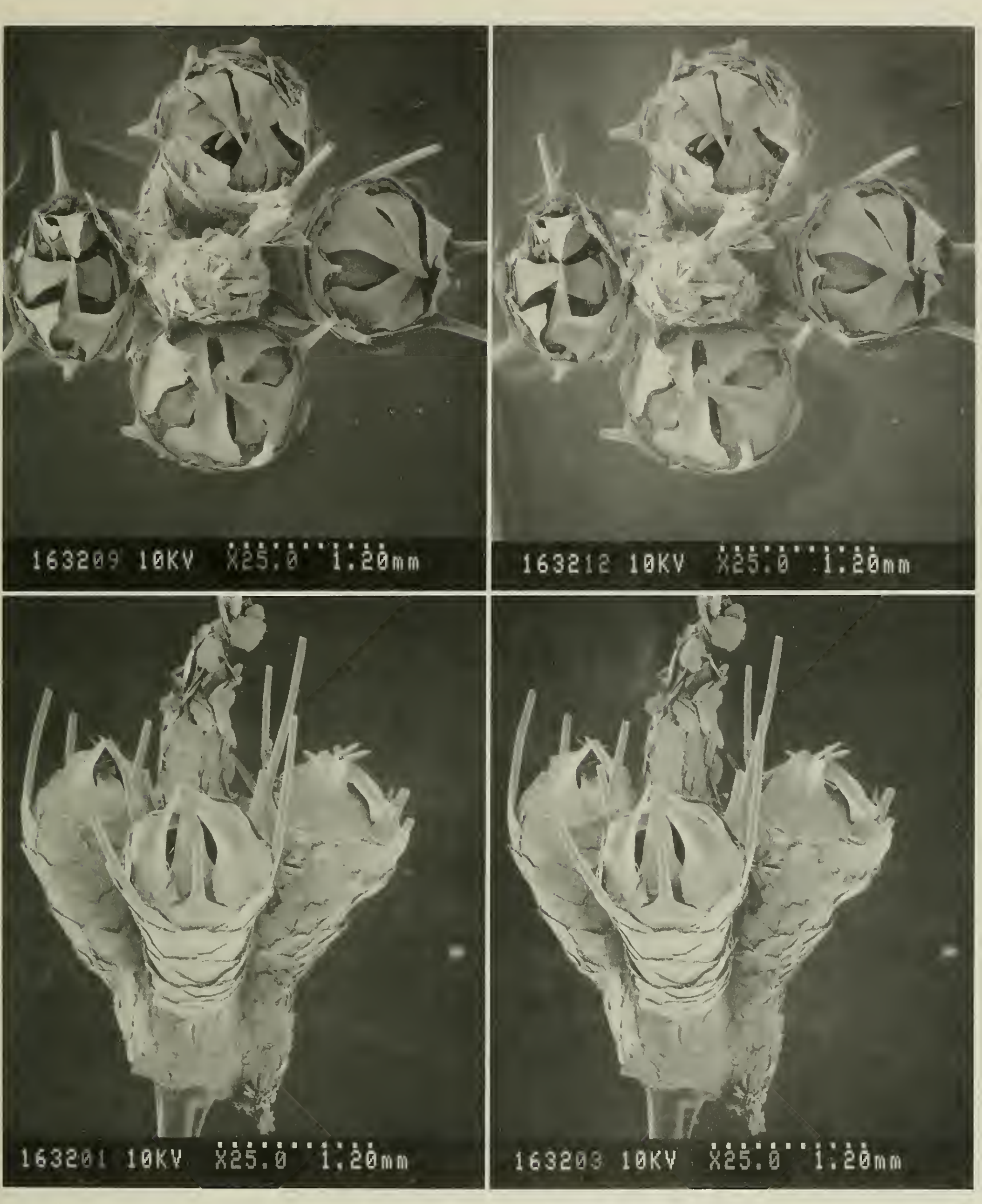


Fig. 3. *Callozostron mirabile* Wright, USNM 85294; whorl with only four polyps, from distal end of colony. Top, Oral view; Bottom, Side view. Stereoscopic pairs (SEM 1632).

original type specimen may have been stripped from the axis during collection and the whorls tightly compressed together as shown in the original figures. Some of the specimens here reported are similarly damaged. Some have a well-developed axis (Fig. 1), and some have been stripped off of the axial skeleton during collection. Furthermore, as specimens of *Callozostron carlottae* Kükenthal, *Primnoella magel-*

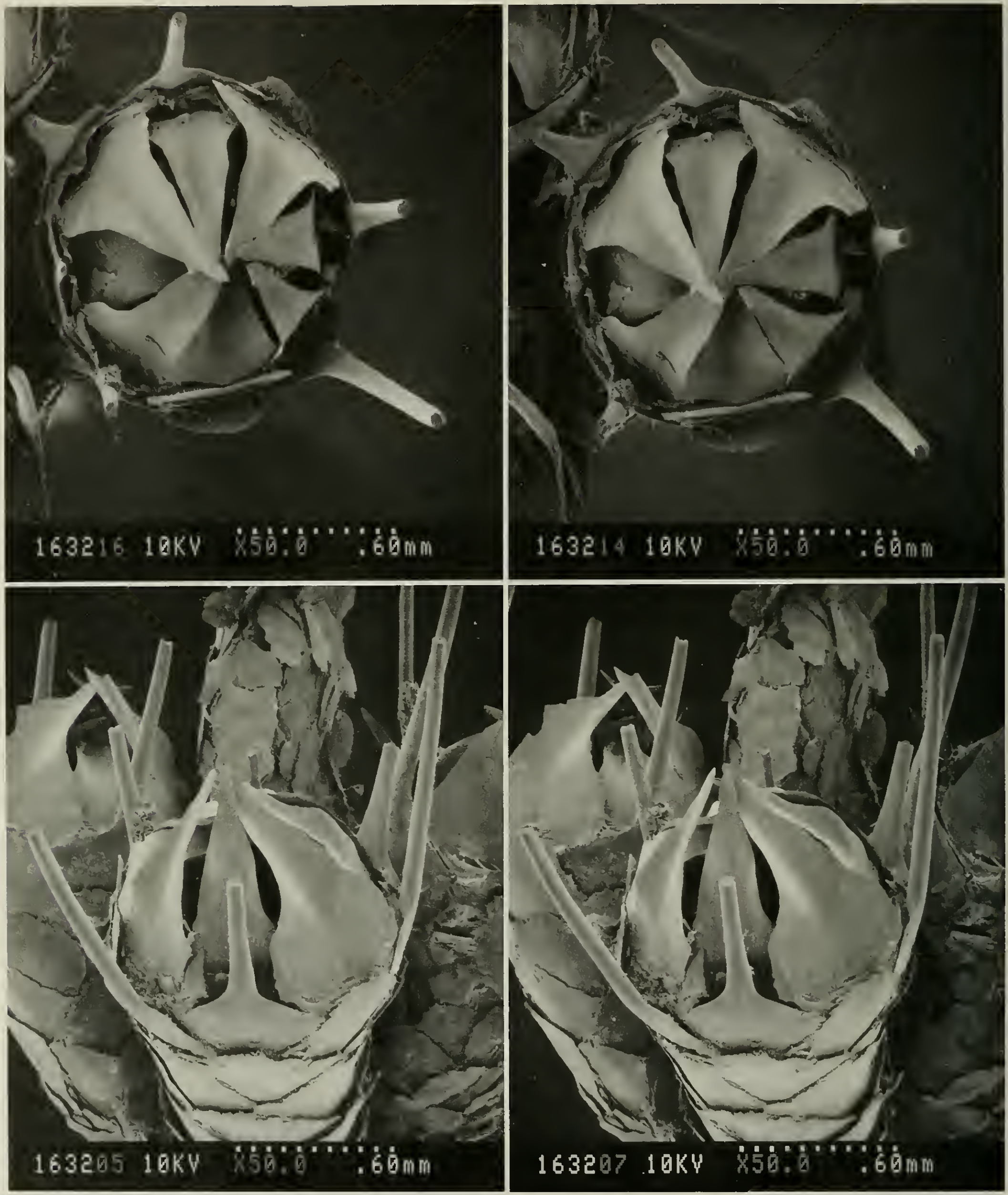


Fig. 4. *Callozostron mirabile* Wright, USNM 85294. Top, Oral view of polyp showing opercular scales in closed position; Bottom, Oblique view of polyp with opercular scales in closed position. Stereoscopic pairs (SEM 1632).

haenica Studer, and *Ophidiogorgia paradoxa* Bayer have been similarly stripped from their supporting axes, this circumstance seems not to be rare among unbranched primnoids.

Callozostron mirabile appears to be widely distributed around Antarctica. The type locality is off the Leopold & Astrid Coast of Princess Elizabeth Land at 65°42′00″S, 79°49′00″E in 3036 m. It also

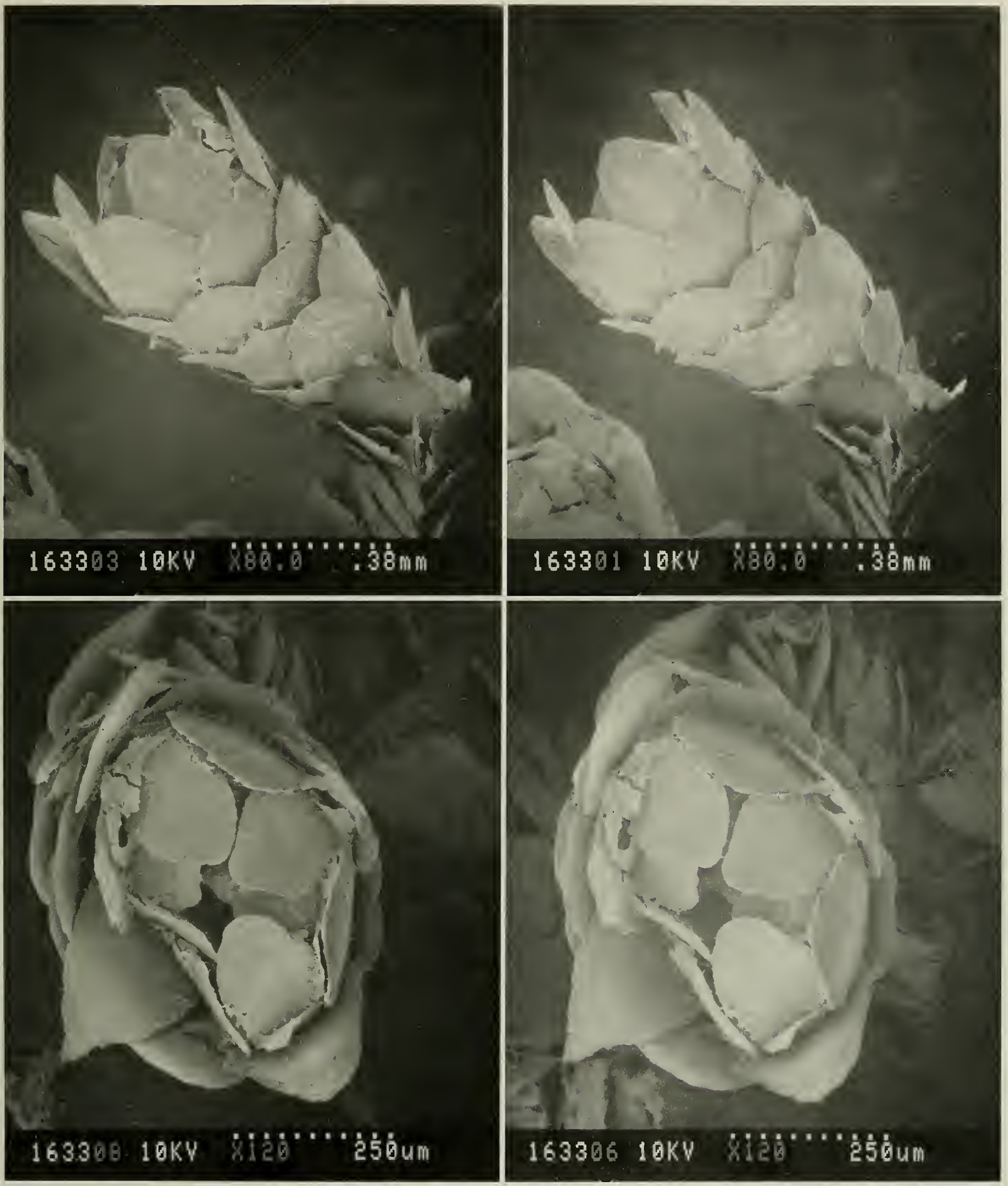
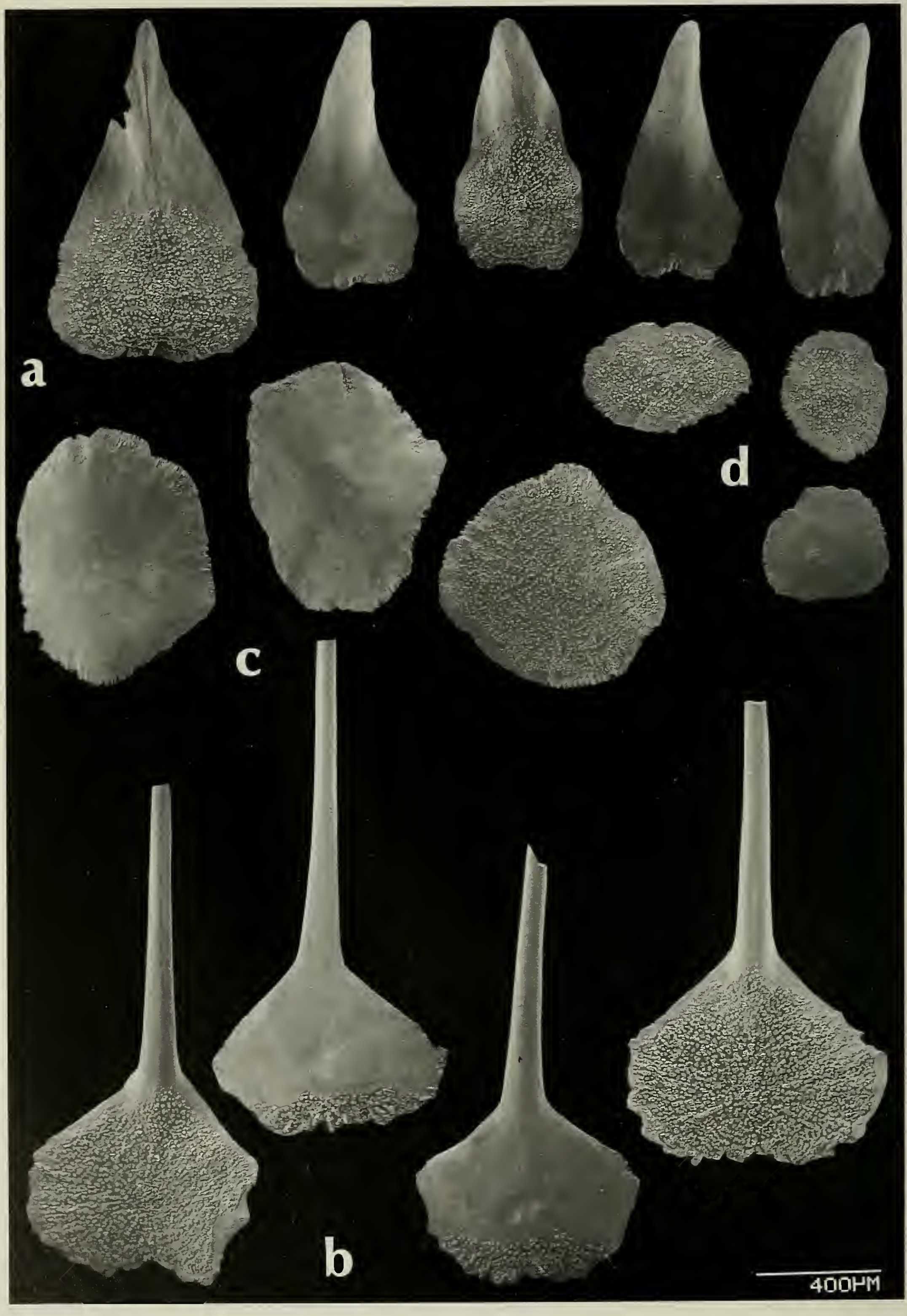


Fig. 5. *Callozostron mirabile* Wright, USNM 85294. Lateral and oral views of young polyp before differentiation of marginal and opercular scales. Stereoscopic pairs (SEM 1633).

has been taken by USNS *Eltanin* in the vicinity of the Balleny Islands off Wilkes Land, 64°59′S, 160°36′E, in 2536–2864 m; off the Antipodes Is., New Zealand, at 49°40′S, 178°56′E, in 952–1336 m; by R/V *Islas Orcadas* at 2 stations in the Scotia Sea at 2653–2941 m and 3819–3876 m, and 2 stations off South Sandwich Is. at 224–2402 m and 415–462 m. The unusually shallow depth of the specimen from sta. 52 (USNM 77339) is suspect, because it immediately followed sta. 51 of the same date


a
c
d
b
400µM

in 2248–2402 m (USNM 82876) and probably was obtained with the same Blake trawl. The probability of contamination in sta. 52 of fragments from sta. 51 must be considered sufficiently strong to discount the anomalous bathymetric record.

Callozostron carlottae Kükenthal, 1909
Figs. 7, top; 8–10

Callozostron carlottae Kükenthal, 1909:49; 1912:334, figs. 43–47, 53, 54, pl. 22, figs. 14–17; 1919:451; 1924:307, fig. 168.—Schimbke, 1914:25.

Material.—Antarctic Ocean, off South Orkney Islands: 61°04′S, 39°55′W, 2355–2897 m, USNS *Eltanin* sta. 1545, 11 Feb 1966. 2 bifurcate colonies lacking holdfast, and 1 simple branch, USNM 77387. (SEM 1626, 1627.)

Diagnosis.—Flagelliform or bifurcate *Callozostron* with polyps in whorls of 8 or 9, having 2 rings of 8 scales (marginal and submarginal) surrounding the operculum, most or all with a stout apical spine; basal fusion of polyps negligible.

Comparisons.—This species superficially resembles *Callozostron diplodiadema* new species, but the polyps are shorter and the spines of the marginal and submarginal scales are shorter, stouter, distinctly tapered and prismatic in section.

Remarks.—The specimens here recorded agree with the type material of *C. carlottae* insofar as the ambiguities of the original description allow, except in growth form. The type specimen (Kükenthal 1912) was flagelliform and showed no evidence of branching, but two of the three colonies in the present collection are bifurcate immediately above the holdfast (Fig. 7, top) and the third is a single flagelliform branch that could be half of a bifurcate colony. Superficially, an unbranched colony would closely resemble a stout colony of *Primnoella magelhaenica* Studer, 1879 (cf. Figs. 20, 21).

Polyps are arranged in regular whorls (Fig. 8, top) of 9 (in the original type material mostly 8, but 9 in the median whorls, an insignificant difference); their overall height in the present material (Fig. 9) is about 2.5 mm (2.3–2.7 mm), of which a little more than 0.5 mm consists of the projecting marginal spines, compared with 1.2 mm overall as given by Kükenthal (1912: 335). The discrepancy may be explained by a difference in the way measurements were made but this cannot be verified as neither magnification nor scale accompanies Kükenthal's illustrations (1912: figs. 43, 53). In shape, the polyps (Fig. 9) are strikingly similar to Kükenthal's drawing (1912: fig. 43), with a double ring of strong spines surrounding the operculum (Fig. 8, bottom). Basal fusion of polyps is no more than occurs in *Primnoella magelhaenica* (cf. Fig. 24).

The sclerites are of the usual primnoid form, but somewhat thicker than in *Callozostron mirabile*. The body scales are broadly oval (Fig. 10c), and the opercular scales (Fig. 10a) diminish in size toward the adaxial side more than is the case in *mirabile*. The apical spine of the marginal and submarginal scales is marked by a few smooth longitudinal ridges (Fig. 10b). Although Kükenthal stated that numerous warts cover the surface of the lower part of the marginal scales, it is not clear whether he referred to the outer surface, the inner surface, or both. In primnoids, the inner surface of sclerites is invariably covered with complex warts, but the outer surface varies according to species and/or location. His illustration of a marginal scale (1912: fig. 44) appears to show the inner surface, leaving the nature of the outer surface un-

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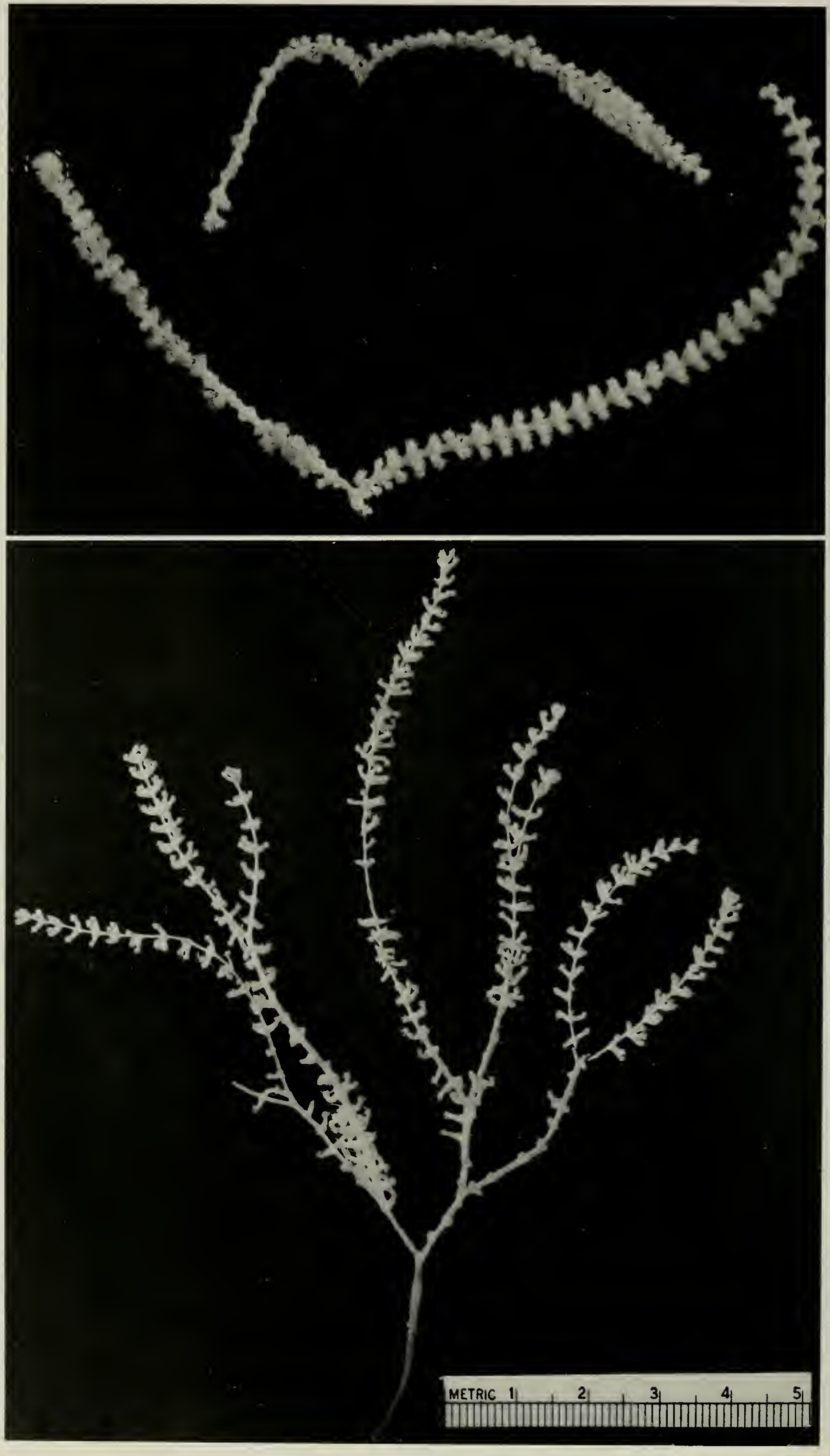
Fig. 6. *Callozostron mirabile* Wright, USNM 85294. Sclerites (SEM 1634). a, Opercular scales; b, Marginal scales; c, Body scales; d, Coenenchymal scales.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specified. In the present material, the outer surface of the proximal part of both marginal and opercular scales is covered with simple granules (Fig. 10a, b) while that of the body scales is smooth except for the proximal edge (Fig. 10c).

Callozostron diplodiadema, new species

Figs. 1, right; 11–14

Material.—Scotia Sea, SW of South Georgia Island: 55°01′S, 39°55′W, 2886–3040 m, USNS *Eltanin* sta. 1537, 8 Feb 1966. 7+ colonies USNM 77386. (SEM 1628, 1655–57.)

Diagnosis.—Flagelliform *Callozostron* with polyps in distinct whorls of up to 14, having 2 rings of 8 scales (marginal and submarginal) surrounding the operculum, each with a long, smooth apical spine; basal fusion of polyps negligible.

Description.—The material consists of 7 incomplete colonies still with supporting axial skeleton, the longest of which is 19 cm in length lacking holdfast (Fig. 1, right), and 10 pieces of various size stripped off the axis during collection. It is likely that at least some of these pieces occupied naked spaces on some of the damaged colonies. One colony with axis nearly or quite intact apically is 9.7 cm long and attached by a small discoidal holdfast to a flat black pebble. The polyps stand almost perpendicular to the axis and are arranged in regular whorls (Figs. 11, 12), mostly of 9–12 but initially of 4 and ultimately as many as 14. Where the coenenchyme remains undisturbed on the axis, 4–5 whorls occur in 1 cm of length, but where artificially compressed along the axis or completely stripped from it, 7 whorls may be closely crowded in 1 cm of length.

The polyps are about 2 mm tall exclusive of the operculum and marginal spines (Fig. 12, bottom), only the basal part of their bodies fused together, the free distal half about 0.5 mm in diameter widening distally to about 0.8 mm at the level of the circumoperculum. The marginal (circumopercular) and submarginal scales each have a long, smooth, somewhat curved apical spine (Fig. 14b), together forming crown of 16 spines surrounding the operculum (Fig. 13, top). The operculum (Fig. 13, bottom) is composed of 8 tall, triangular scales of about equal size, with somewhat convex sides (Fig. 14a). The opercular scales are vertically aligned with the circumopercular and following longitudinal rows of body scales. The distal margin of some of the scales in the transverse row beneath the submarginals may be more or less acutely pointed but not produced as a spine (Fig. 14c). The abaxial and adaxial longitudinal rows of body scales consist of 5–6 scales each, including the spinous submarginals and circumoperculars. Their outer surface is smooth and glossy, the inner surface covered by complex tubercles where embedded in the body wall (Fig. 14d). The coenenchymal sclerites (Fig. 14e) are rounded scales smaller than those of the polyps. The tentacles are devoid of sclerites. No irregularly tuberculate sclerites are present in the walls separating the longitudinal stem canals.

Comparisons.—This species superficially resembles *C. carlottae* but the polyps are taller and the spines of the marginal and submarginal scales are much longer, smooth, cylindrical or elliptical in cross section.

Etymology.—Greek διπλόος, double + διάδημα, diadem, crown. Noun in apposition.

Callozostron acanthodes, new species

Fig. 7, bottom; 15–17

Material.—East of North Island, New Zealand, 38°24′S, 178°53′E, 1354–1995 m,

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Fig. 7. Top, *Callozostron carlottae* Kükenthal, two bifurcate colonies, USNM 77387; Bottom, *Callozostron acanthodes*, holotype, USNM 94575.

Fig. 8. *Callozostron carlottae* Kükenthal, USNM 77387. Top, Part of branch showing two whorls of polyps (SEM 1626); Bottom, Oral view of polyp (SEM 1627). Stereoscopic pairs.

USNS sta 1712, 5-foot Blake trawl 40 minutes at depth, 28 May 1966. One colony with branches detached, USNM 94575. (SEM 1594, 1595, 1603, 1617, 1618.)

Diagnosis.—Dichotomously branched *Callozostron* with tall, slender polyps arranged in widely spaced whorls commonly of 5, sometimes 6, rarely isolated; usually

4 whorls in 1 cm; individuals often partly united basally as pairs. Marginal scales with extremely long, slender spine, vertically aligned with opercular scales; apex of opercular scales prolonged as a slender, acute spine.

Description.—The holotype colony (Fig. 7, bottom) is sparsely dichotomously branched in one plane, 11 cm tall lacking the holdfast and perhaps the uppermost terminal twig; undivided terminal twigs to 5 cm in length. The axis is calcified, light brown with little or no luster in the main stem, cylindrical, smooth, 0.9 mm in diameter, becoming paler distad; in the terminal branches it is cream white with moderate pearly luster, proximally about 0.5 mm in greater diameter, flattened in the plane of branching, tapering distad to an extremely fine tip.

The polyps are situated in widely spaced whorls of 3–6, commonly 5 (Fig. 15); usually 4 whorls in 1 cm except at the tips of branches where there may be 5. The distalmost whorl consists of 2–4 polyps, new polyps arising within whorls proximad. Nowhere in the colony is there any evidence of new whorls of polyps originating between fully developed whorls, indicating that growth is exclusively terminal. Rarely a single polyp occurs in the location of a whorl.

Fully developed polyps (Fig. 15, bottom) are about 2.5 mm tall and 0.5 mm in diameter, nearly cylindrical, somewhat flared immediately below the tentacles, and inclined slightly distad. Adjacent polyps may be proximally somewhat fused to form pairs (Fig. 16, top). They are covered by roughly fanshaped scales aligned in more or less distinct longitudinal rows consisting of about 10 scales. The body scales (Fig. 17a) are externally smooth, internally sculptured with scattered complex tubercles; their distal free margins are irregularly serrate. Several of the marginal scales (Fig. 17b) have an extremely long, slender apical spine that may exceed 3 mm in length; the spine usually is smooth, but in some cases shows traces of widely scattered, low, simple granules. Owing to their extreme delicacy, none of the marginal scales were preserved with spine intact, so their greatest length cannot be determined. The operculum (Fig. 16, bottom) consists of eight ovate scales with the distal margin smooth and apically extended as a smooth, slender spine (Fig. 17c).

The coenenchyme is thin, covered by small, externally smooth, rounded scales (Fig. 17d).

Comparisons.—*Callozostron acanthodes* new species differs sharply from previously known species by its openly dichotomous branching, the wide spacing of the whorls, and the conspicuous apical spine of the of the opercular scales.

Etymology.—Greek ακανθώδης, thorny.

Remarks.—This species is assigned to the genus *Callozostron* because of the regular verticillate arrangement of the polyps, clear differentiation of opercular from marginal scales, spinelike apical projection of the marginal scales, and regular rows of body scales. The branched colonial form is not considered an exclusive character as it is here shown that colonies of *C. carlottae* may be bifurcate. The polyps bear some resemblance to those of *Mirostenella* Bayer, 1988, but are proportionally much taller, with several but not all of the marginal scales furnished with a strong apical spine.

Discussion.—If the tendency toward proximal fusion of polyps in *Callozostron acanthodes* is disregarded, the species cannot be aligned with any valid genus recognized in the keys of Kükenthal (1915, 1919, 1924), and Bayer (1981). No genus having verticillate polyps with 8 marginal scales vertically aligned with the 8 opercular scales, as in *Mirostenella,* had been described. Although the sclerites of the polyps of *Plumarella* meet these qualifications, the polyps of that genus are not arranged in whorls. In *Mirostenella,* all 8 marginal scales have an acute apex or short spine; in *Callozostron,* as few as 4 or as


162705 5.0KV X20.0 1.50mm
162707 5.0KV X20.0 1.50mm
162713 5.0KV X30.0 1.00mm
162715 5.0KV X30.0 1.00mm

many as 8 marginal scales are prolonged as spines, but when all 8 are spinous (*carlottae, diplodiadema*), the next one or two circles of body scales below the marginals also are spinous.

Primnoella Gray

Primnoella Gray, 1858:286; 1870:49.—Studer [& Wright], 1887:51 (part).—Wright & Studer, 1889:87 (part: B. "Carinatae").—Versluys, 1906:48, 52 (part: Carinatae).—Kükenthal 1907:210.—Aurivillius, 1931:267.—Deichmann, 1936: 162.—Bayer, 1956:F220 (part); 1981:936 (part; in key only).—Broch, 1965:20 (part).—Bayer & Stefani, 1989:455 (part; in key only).

Primnoella "Compressae" Kükenthal, 1908:13; 1912:311; 1915:148; 1919:384; 1924:279.

Type species.—*Primnoa australasiae* Gray, 1850, by monotypy.

Diagnosis.—Flagelliform, unbranched or sparsely branched primnoids with polyps arranged in whorls, directed strongly upward, often appressed to axial cortex but never adnate; opercular scales decreasing in size toward axis, distinctly differentiated from, and more or less overreached by, marginal (i.e., "circumopercular") scales; body of polyps compressed, with two longitudinal abaxial rows of wide imbricating scales, outer lateral and inner lateral rows reduced in size and numbers; adaxial surface either naked except for at most a few small scales below the marginals, or with small, delicate scales arranged in two more or less complete longitudinal rows. Surface of coenenchyme covered with rounded or polygonal scales; walls of longitudinal stem canals with irregular, tuberculate sclerites.

Remarks.—The genus *Primnoella* Gray, 1858, was based upon *Primnoa australasiae* Gray, 1850, syntypes of which are still preserved dry in The Natural History Museum, London (Reg. nos. BMNH 1850.1.21.1, 6 and 10; 1983.3.2.13 and 14).

Species groups within Primnoella sensu lato.—As heretofore defined, the genus *Primnoella* comprises two groups of species having polyps of distinctly different morphological types with respect to form and spiculation. In one group including the type species, designated "Carinatae" by Wright & Studer (1889:87) and later "Compressae" by Kükenthal (1908:13), the polyps are directed strongly upward, more or less closely appressed to the coenenchyme, with two longitudinal rows of large abaxial scales, reduced outer and inner lateral scale rows, and their adaxial surface more or less naked and mostly devoid of sclerites below the marginals. In the other group, designated "Convexae," which includes *P. magelhaenica,* the polyps are curved inward less strongly if at all, there are four longitudinal rows of abaxial scales and well developed inner lateral and adaxial rows of scales so their adaxial surface is completely covered by sclerites.

Although the polyps of some species of the Convexae group of *Primnoella* have fewer scales in the adaxial sclerite rows than in the abaxial rows, the adaxial side of the body nevertheless is completely covered by scales even if it is somewhat shorter than the abaxial side. There is no naked or nearly naked adaxial tract like that of all species of the Compressae group. Therefore, species of the Convexae group are separated from those of the Compressae group by a morphological discontinuity much more distinct and consistent than that separating many other related genus-group taxa in this and other families of Gorgonacea. This discontinuity justifies the recognition of the

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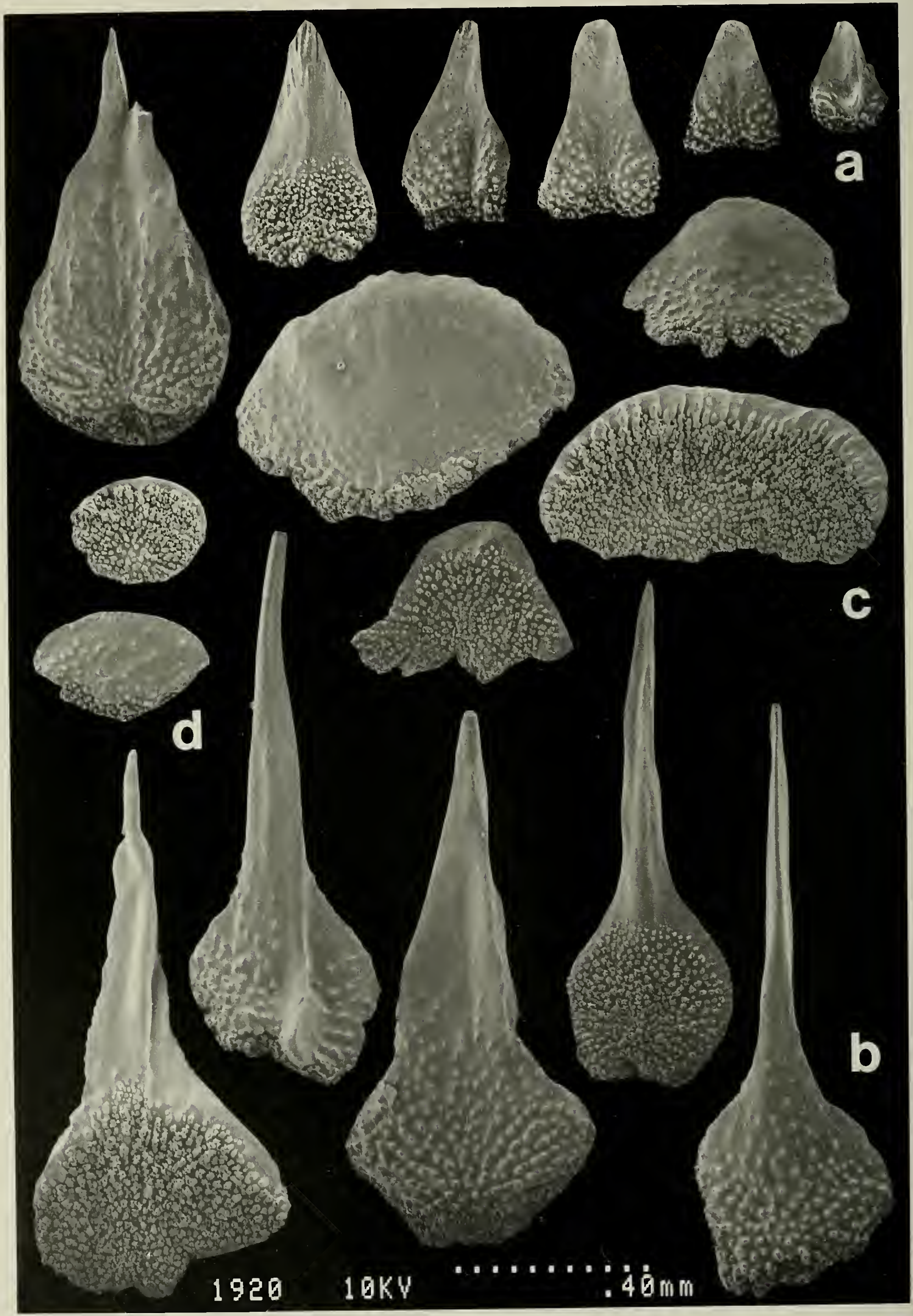
Fig. 9. *Callozostron carlottae* Kükenthal, USNM 77387. Part of one whorl. Top, Three polyps seen from below; Middle, Three polyps seen from above; Bottom, Detail of two polyps. Stereoscopic pairs (SEM 1627).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Convexae group of species as a genus distinct from the Compressae group.

Inasmuch as no genus-group name has heretofore been established for any species of the Convexae group, the name *Convexella* is now proposed for them as a distinct taxon, with *Primnoella magelhaenica* as type species.

Distribution of Primnoella "Compressae."—The genus *Primnoella* as now restricted is most richly represented in Antarctic and sub-Antarctic waters, with relatively few species in temperate and tropical waters of the Atlantic, Pacific and Indian oceans. It is represented in the northern hemisphere by only one species, *P. polita* Deichmann, 1936.

Species.—Kükenthal (1924:280) assigned 7 species to the "Compressae" group: *P. scotiae* Thomson & Ritchie, 1906; *compressa* Kükenthal, 1908; *biserialis* Wright & Studer, 1889; *australasiae* (Gray, 1850); *delicatissima* Kükenthal, 1909; and *grandisquamis* Wright & Studer, 1889. To these may now be added *P. polita* Deichmann, 1936. As demonstrated below, *Caligorgia* (sic) *gracilis* Thomson & Mackinnon can also be assigned to *Primnoella* rather than to *Callogorgia.*

Primnoella australasiae (Gray, 1850)
Figs. 18, 19

Primnoa australasiae Gray, 1850a:146, Radiata pl. 2, figs. 8, 9; 1850b:510.

Primnoella australasiae.—1858:286; 1859: 483; 1870:50.—Wright & Studer, 1889: 88, pl. 18, figs. 1, la; pl. 21, fig. 15.—Versluys, 1906:52.—Thomson & Mackinnon, 1911:688, pl. 61, fig. 1.—Kükenthal, 1919:401, pl. 41, figs. 62, 63.

Material examined.—D'Entrecaseaux Channel, between Tasmania and Bruce's Island. (Gray, teste Joseph Millingin, F. L. S. Syntypes, The Natural History Museum, London, register nos. 1850.1.21.1, 6 and 10; 1983.3.2.13 and 14 (SEM 1936-1938). D'Entrecasteaux Channel (43°17′S, 147°15′E), near Kinghorne Point, Bruny Island, Tasmania, 15 m, coll. A. J. Blackman, 1979. One colony, USNM 58926 (SEM 485, 487). Bluff Harbor, South Island, New Zealand (46°34′S, 168°20′E), coll. Dr. E. Kershner, January 1875. 30 colonies, dry, USNM 4505 (SEM 505).

Discussion.—Robust, flagelliform colonies up to 1 m tall have 5–8 whorls of 13–15 strongly appressed polyps of the "Compressae" type in 1 cm of axial length. Only the two abaxial sclerite rows are fully visible and contain 10–14 scales each; the outer lateral rows each consist of about the same number of scales but they are smaller and because of their position only their edes are visible. The inner lateral rows each contain at least 5 or 6 scales, still smaller than those of the outer lateral rows. The walls of the longitudinal stem canals are filled with irregularly tuberculate sclerites of extremely diverse shape.

The dry specimens here reported from Bluff Harbor, New Zealand (Fig. 19, right) resemble Gray's type material (Fig. 18) from D'Entrecasteaux Channel, Tasmania. The colonies are attached by discoidal holdfasts to the dead shells of pectinid bivalves, as many as 7 to a single shell, and reach a height of approximately 1 m. In some colonies, the proximal 3 or 4 scales of the abaxial rows are somewhat larger than those located more distally, and there is evidence that this may be related to the presence of eggs or embryos in the gastrovascular cavities. Although this condition was not noticed in the type specimens (Fig. 18), it was not specially looked for among the numerous dry specimens.

The polyps of the topotypic colony from

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Fig. 10. *Callozostron carlottae* Kükenthal, USNM 77387. Sclerites (SEM 1920). a, Opercular scales; b, Marginal scales; c, Body scales; d, Coenenchymal scales.

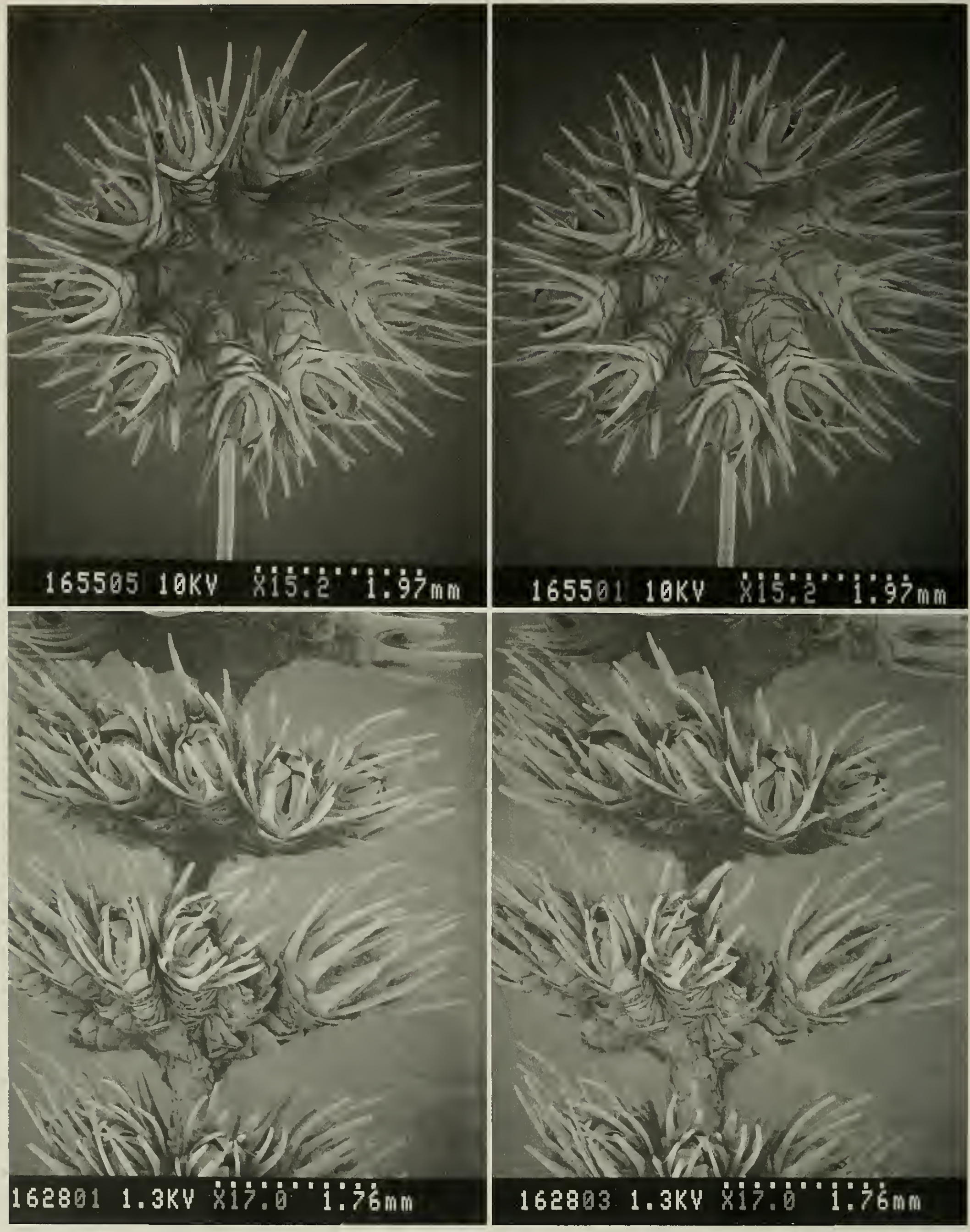


Fig. 11. *Callozostron diplodiadema,* new species, USNM 77386. Top, Complete whorl seen from above (SEM 1655); Bottom, Two whorls from the side (SEM 1628). Stereoscopic pairs.

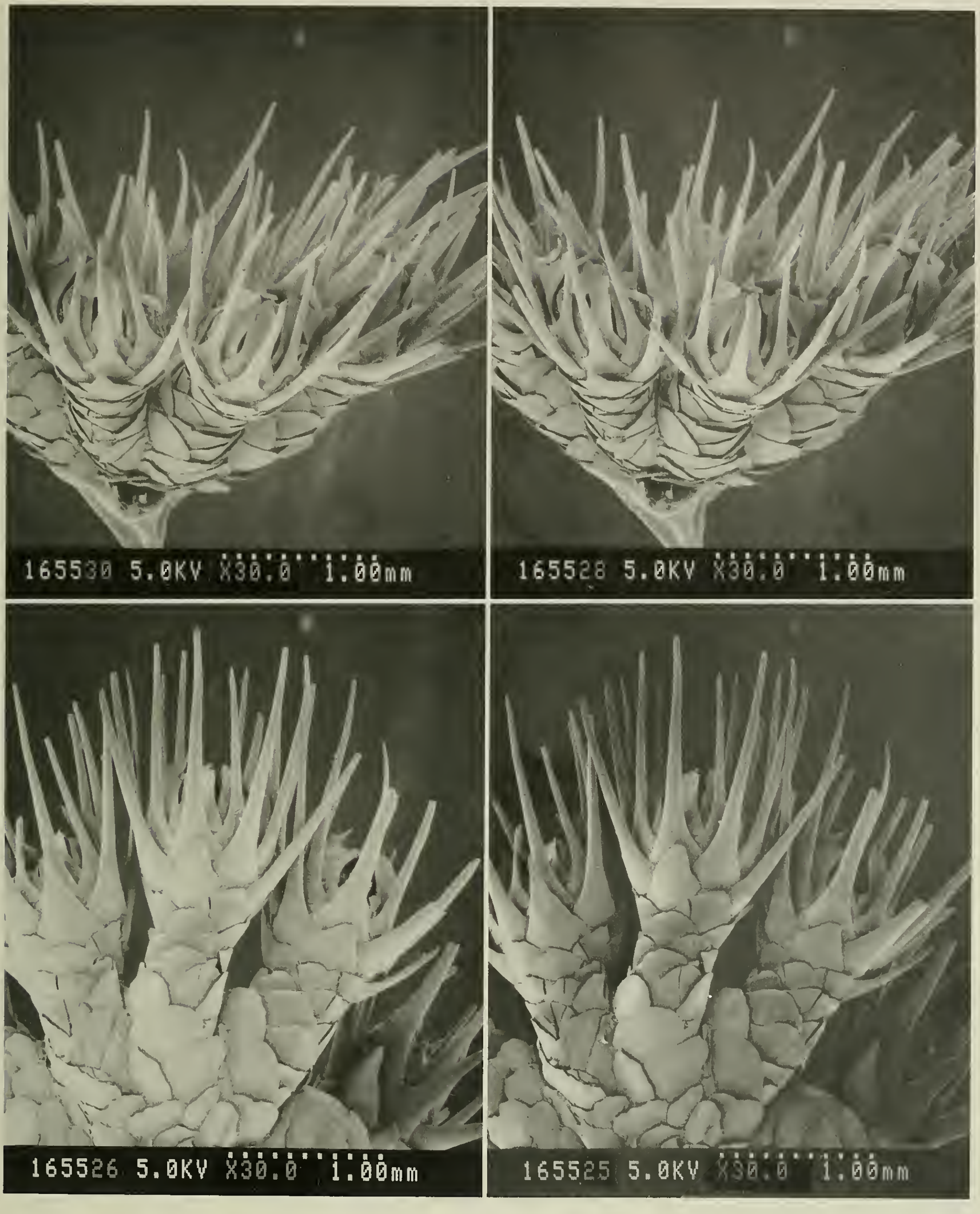


Fig. 12. *Callozostron diplodiadema,* new species, USNM 77386. Top, Part of whorl, side view; Bottom, Detail of polyps. Stereoscopic pairs (SEM 1655).

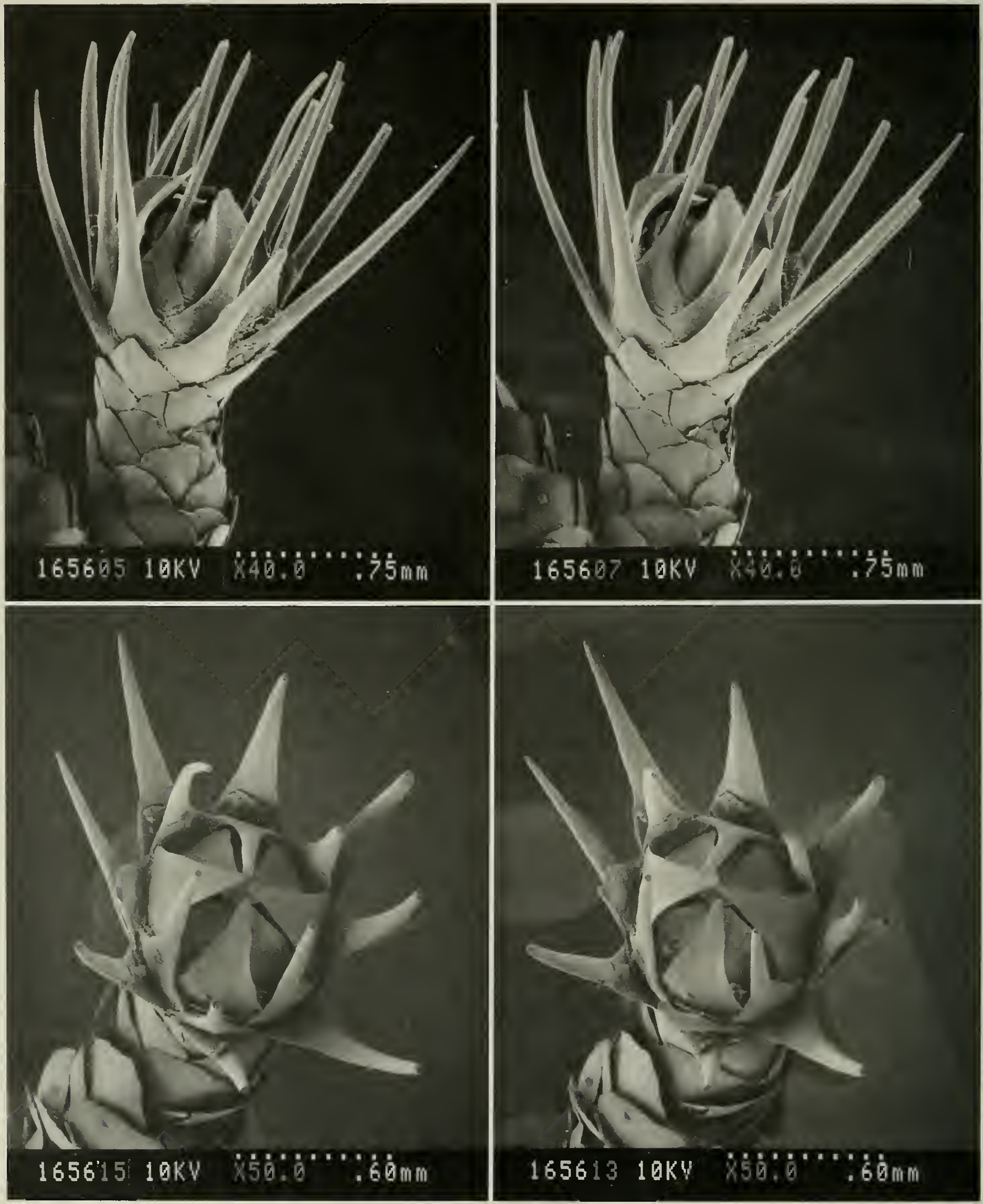


Fig. 13. *Callozostron diplodiadema,* new species, USNM 77386. Detail of polyp. Top, Side view; Bottom, Oral view. Stereoscopic pairs (SEM 1656).

Tasmania (Fig. 19, left) are somewhat more slender than those of either the type specimens examined or the colony from New Zealand and could be associated with the reproductive condition of the colony. The adaxial scales of this specimen preserved in alcohol seem not so closely fitted as in the two lots of dried specimens.

The specimens sent to Gray were "covered with a calcareous coat of a cream-yellow colour" (Gray, 1850:147). The illustration given by Thomson & Mackinnon (1911; pl. 61, fig. 1) gives a fair idea of the appearance of the whorls.

Primnoella laevis
(Thomson & Mackinnon, 1911)
Fig. 20

Caligorgia laevis Thomson & Mackinnon, 1911:689, pl. 65, fig. 1; pl. 68, fig. 7; pl. 80.—Kükenthal, 1919:377; 1924:275, fig. 155.

Callogorgia laevis.—Bayer, 1982:122 (in key only; removed from *Callogorgia* and referred to *Primnoella* in footnote, but new combination was not actually printed there).

Material examined.—Syntypes (Australian Museum, Sydney).

Description.—See Thomson & Mackinnon, 1911:689.

Distribution.—Coast of New South Wales.

Remarks.—While on a brief visit to the Australian Museum, I was able to examine Thomson & Mackinnon's original material through the kindness of Dr. Pat Hutchings. As can be seen from the photograph of a specimen reproduced by Thomson & Mackinnon (1911:pl. 80), the branching of the colony is spare and open rather than "luxuriant" as described by Thomson & Mackinnon. Even the rather crude drawing of a single polyp given by Thomson & Mackinnon (1911:pl. 55, fig. 1) is adequate to demonstrate that the species does not belong to "*Caligorgia*" (= *Callogorgia*). Although the polyps (Fig. 38) are arranged in whorls as usual in both *Callogorgia* and *Primnoella* and are directed obliquely upward and curved toward the coenenchyme, they do not face inward toward the axis as is usual in *Callogorgia,* and the body sclerites are not strongly sculptured externally as commonly is the case in *Callogorgia* (e.g., see Bayer 1982:figs. 2, 4).

Although *Primnoella divaricata* (Studer) and *P. divergens* Hickson are described as branched they are very sparsely so, whereas *P. laevis* is repeatedly branched in a dichotomous manner.

Convexella, new genus

Primnoella.—Studer [& Wright], 1887:51.—Madsen, 1944:39.—Bayer, 1956:F220 (part).—Broch, 1965:20 (part).—Bayer, 1981:936 (part; in key only).—Bayer & Stefani, 1989:455 (part; in key only).

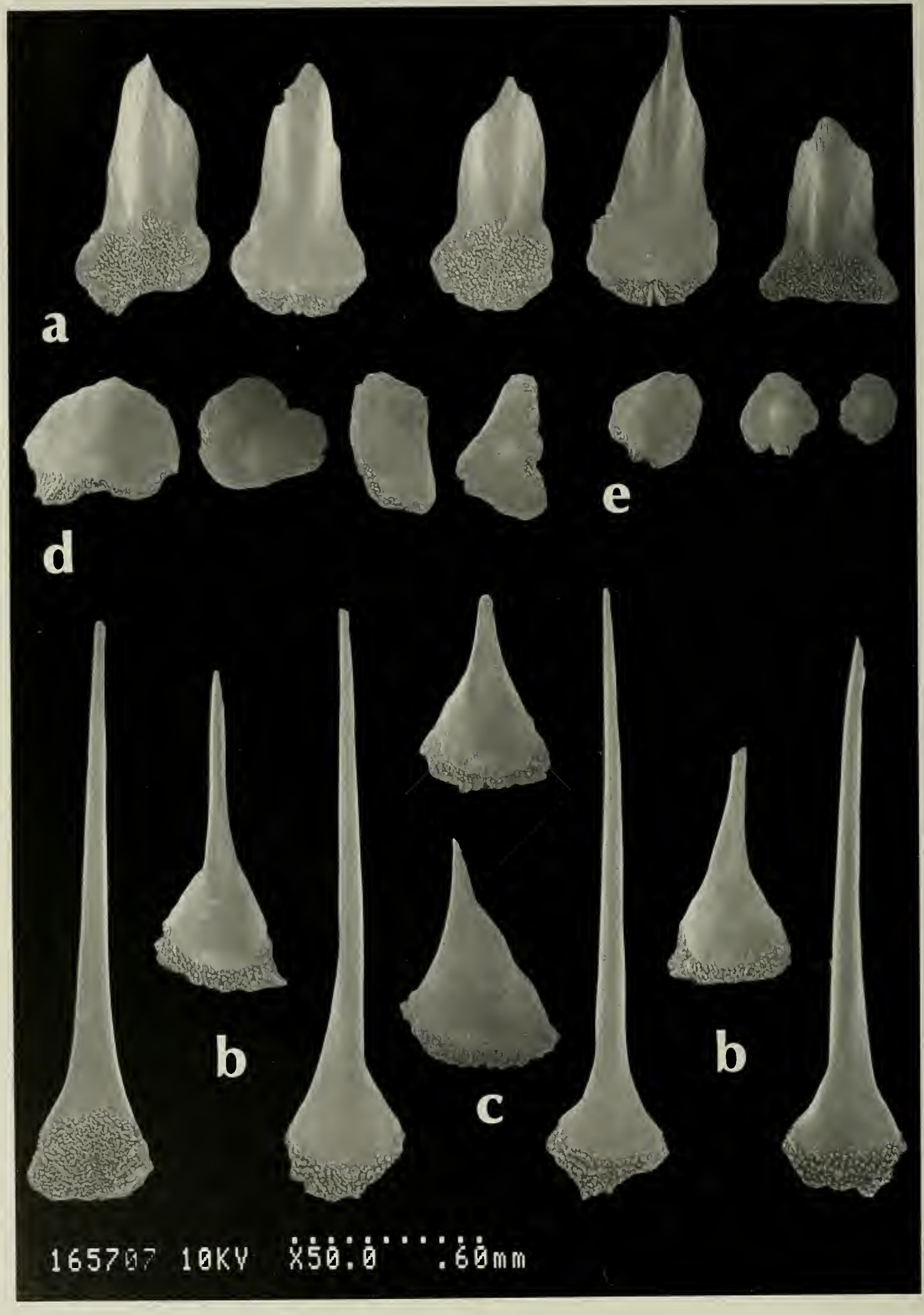
Primnoella Convexae.—Wright & Studer, 1889:83.—Versluys 1906:51.—Kükenthal, 1908:13; 1912:311; 1915:148; 1919:384; 1924:279.

Type species.—*Primnoella magelhaenica* Studer, 1879, here designated.

Diagnosis.—Flagelliform, unbranched or sparsely branched primnoids with polyps arranged in whorls, standing almost vertically or directed more or less obliquely upward, not appressed to axial cortex; marginal and sometimes submarginal scales folding over opercular scales, which are more or less hidden and not clearly differentiated from marginals; body of polyps cylindrical and weakly curved, not compressed, abaxial surface covered by four longitudinal rows of rounded or oval imbricating scales, adaxial and lateral surfaces covered by inner-lateral and adaxial scales of similar size, in rows that may be somewhat shorter than the abaxial and outer-lateral rows. Surface of coenenchyme covered with rounded, imbricating scales; walls of longitudinal stem canals with irregular, tuberculate sclerites.

Remarks.—The type species is now illustrated extensively to demonstrate its variability and to show its similarities to *Callozostron,* without prematurely speculating upon phylogenetic relationships.

Species.—Kükenthal (1924:280) referred seven species to the "Convexae" group of *Primnoella: flagellum* Studer, 1879; *vanhoeffeni* Kükenthal, 1909; *magelhaenica*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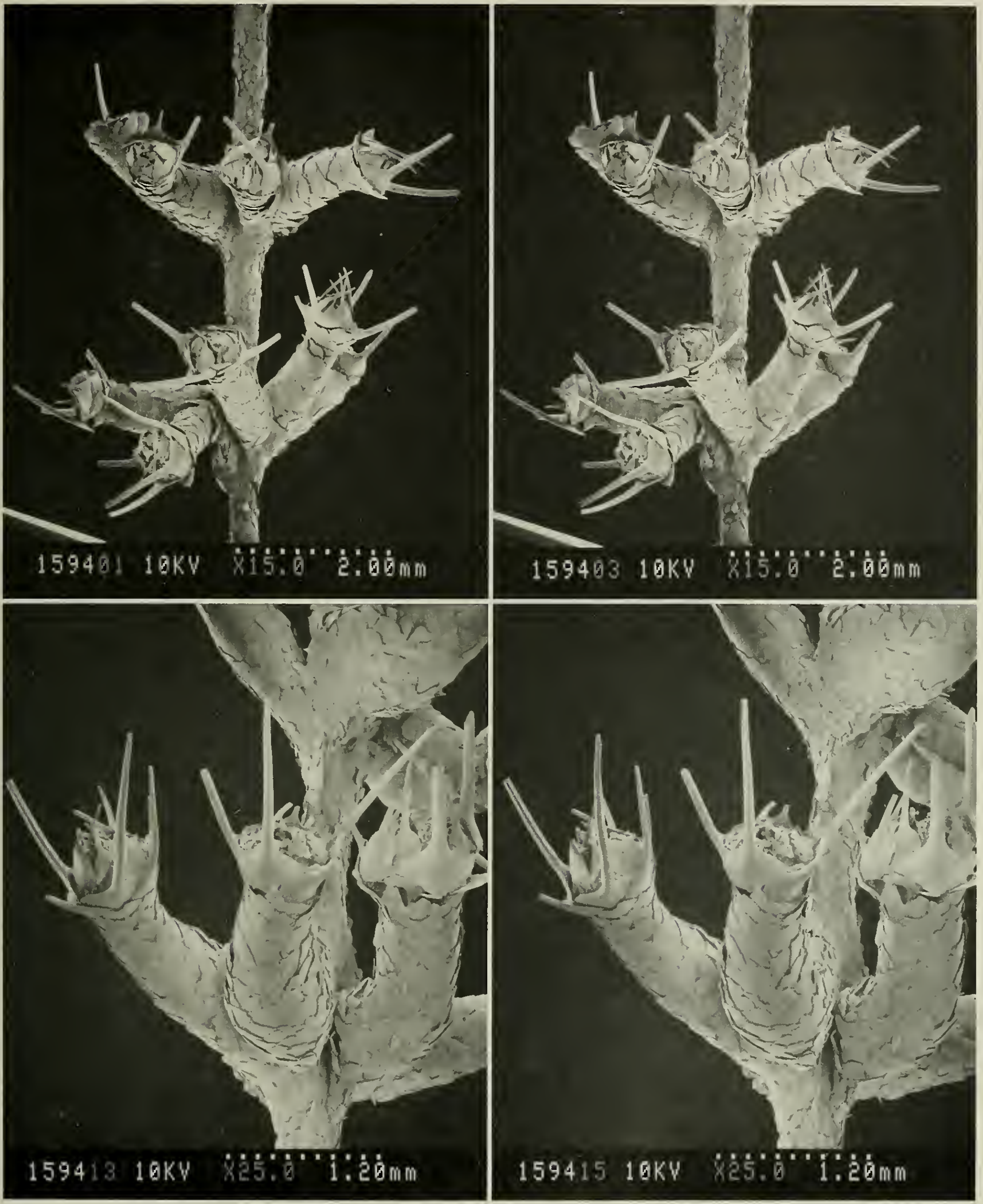

Fig. 15. *Callozostron acanthodes,* new species, USNM 94575. Top, Part of branch with two whorls of polyps; Bottom, Detail of whorl. Stereoscopic pairs (SEM 1594).

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Fig. 14. *Callozostron diplodiadema,* new species, USNM 77386. Sclerites (SEM 1657). a, Opercular scales; b, Marginal and submarginal scales; c, Body scales with acute apex; d, Body scales; e, Coenenchymal scales.

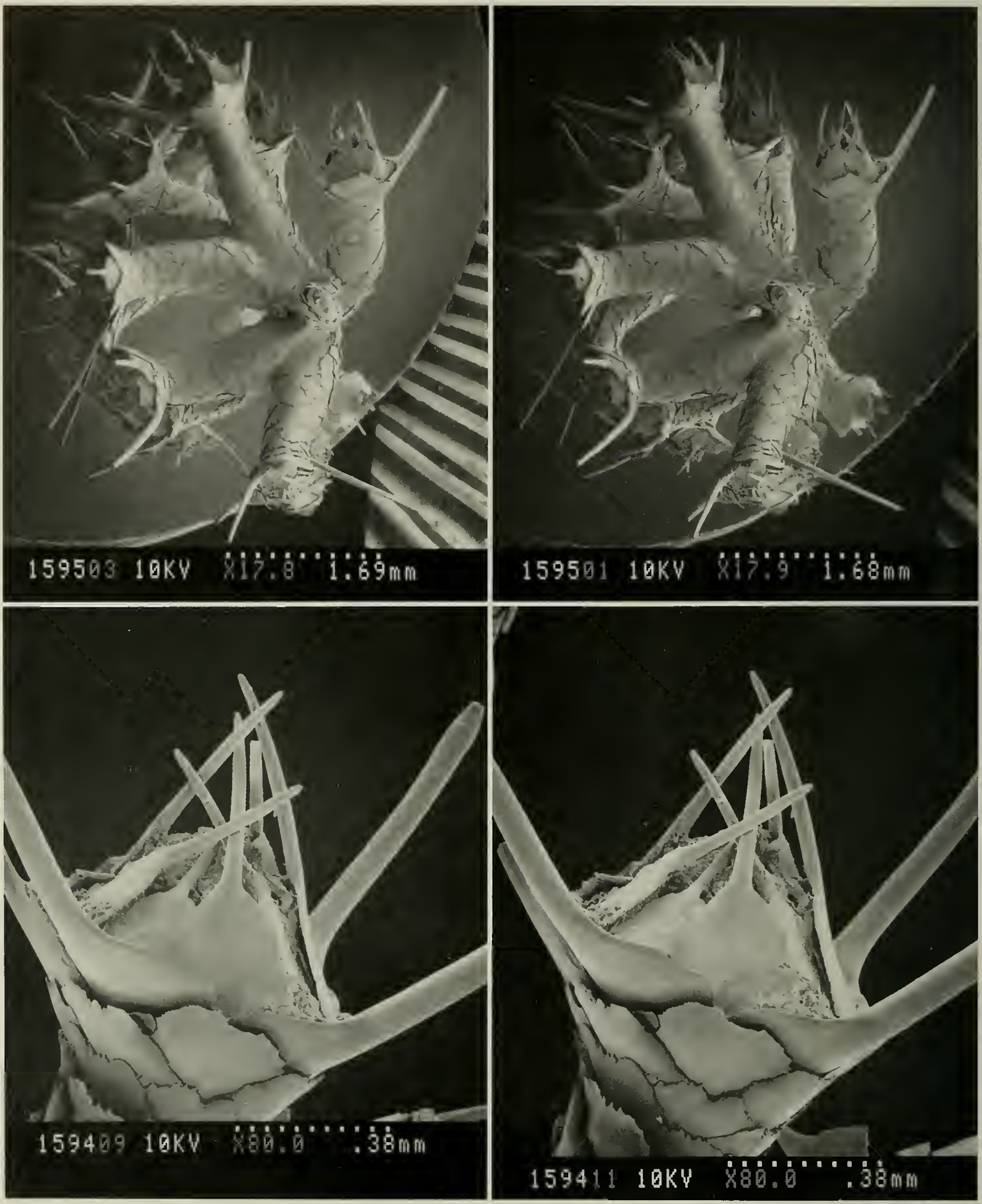


Fig. 16. *Callozostron acanthodes,* new species, USNM 94575. Top, Part of branch viewed from above, showing two pairs of basally united polyps (SEM 1595); Bottom, Distal end of polyp showing opercular scales in closed position (SEM 1594). Stereoscopic pairs.

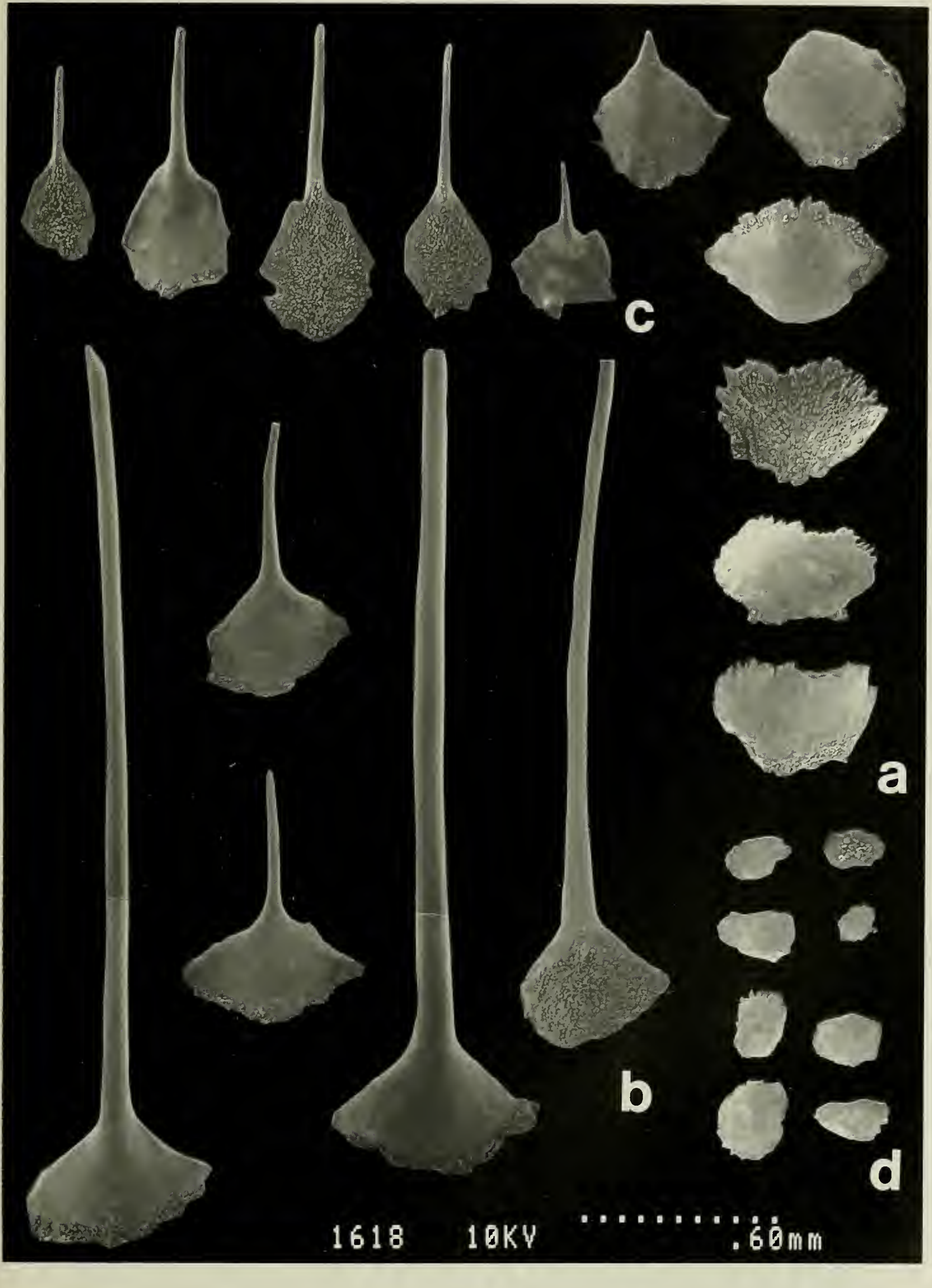


Fig. 17. *Callozostron acanthodes,* new species, USNM 94573. Sclerites (SEM 1618). A, Body scales; b, Marginal scales; c, Opercular scales; d, Coenenchymal scales.

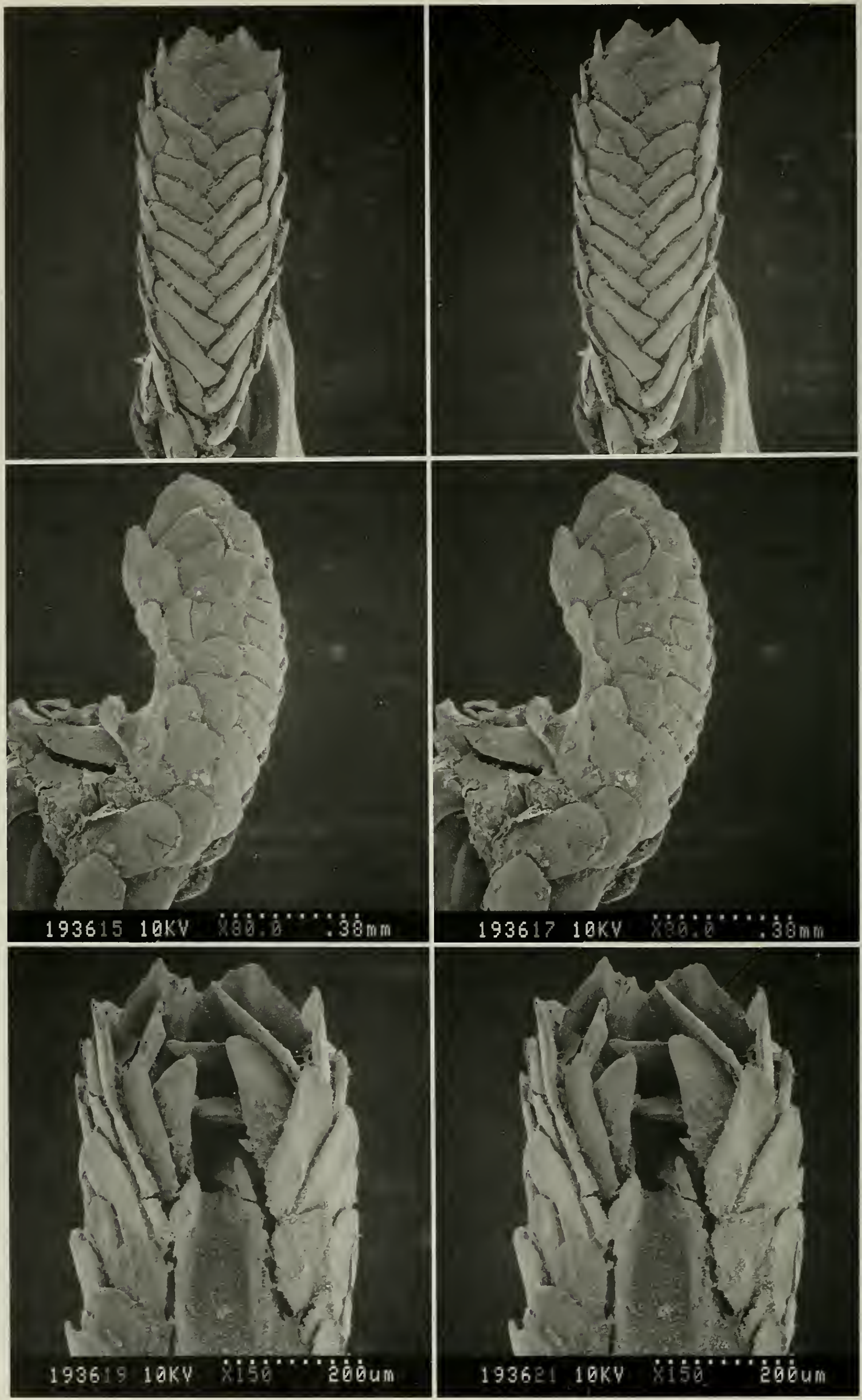


Fig. 18. *Primnoella australasiae* Gray, BM(NH) 1850.1.21.1/6/10. Isolated polyp in abaxial, lateral, and oral view. Stereoscopic pairs (SEM 1936).

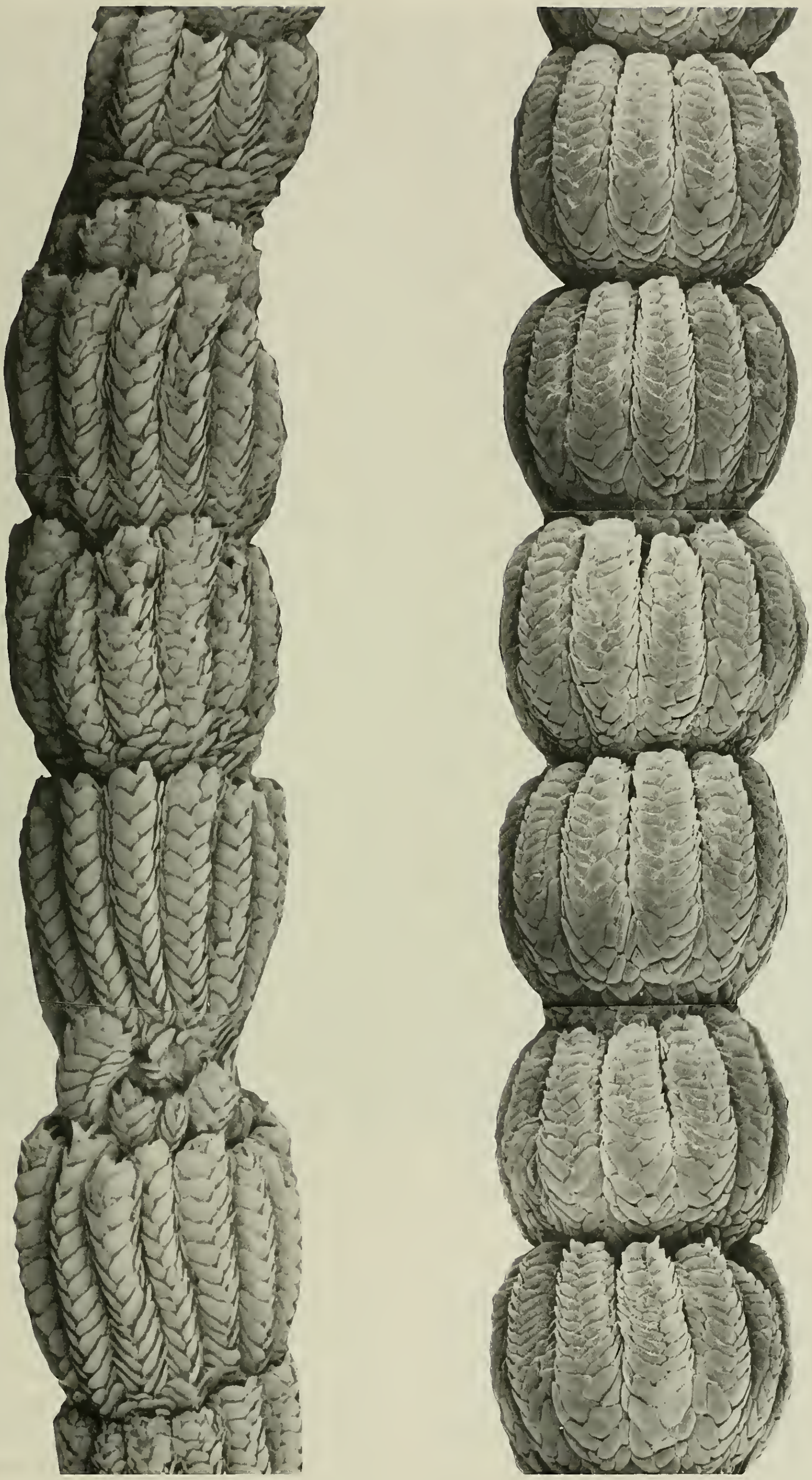


Fig. 19. *Primnoella australasiae* Gray. Left, from D'Entrecasteaux Channel, Tasmania, USNM 58926; Right, from Bluff Harbor, New Zealand, USNM 4505.

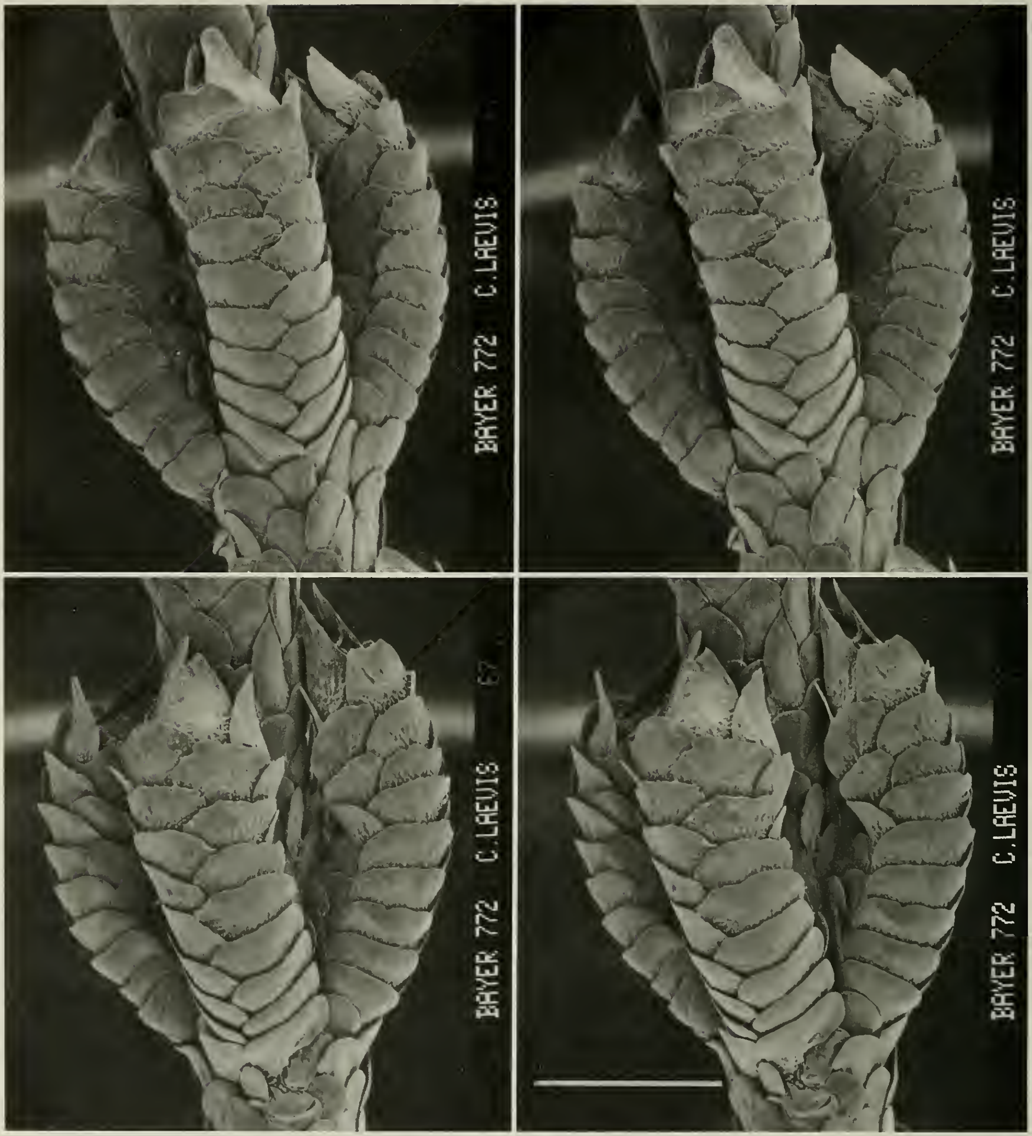


Fig. 20. *Primnoella laevis* (Thomson and Mackinnon), from east of Broken Bay, N.S.W., Australia. Two whorls from syntype, scale bar = 0.5 mm. Stereoscopic pairs (SEM 772).

Studer, 1879; *murrayi* Wright & Studer, 1889; *antarctica* Kükenthal, 1907; *distans* Studer, 1879; *divaricata* (Studer, 1879); and *divergens* Hickson, 1907.

Of these, *Primnoella flagellum* Studer, 1879, is here interpreted as a variant of *P. magelhaenica* Studer, 1879.

Kükenthal (1912:317) described *Primnoella vanhoeffeni* as similar to *P. magellanica* (sic), but his illustrations are not convincing.

Primnoella murrayi Wright & Studer (1889:84, pl. 18, figs. 3, 3a) is similar to *P. magelhaenica* but has a short apical spine or acute angle on the distal margin of the abaxial body scales, a character so variable in *P. magelhaenica* that the species can be considered synonymous.

Kükenthal (1919:387, 391) placed his *Primnoella antarctica* in the "Convexae" group of species because the polyps are not compressed, even though the adaxial side is mostly naked except for a few small scales below the mouth and near the base; it bears some resemblance to *Ophidiogorgia* but none at all to *Convexella magelhaenica.*

The polyps of *Primnoella distans* Studer, 1879, have only two visible rows of large abaxial scales (Wright & Studer 1889, pl. 18, fig. 1a), and very small, reduced adaxial scales, so must be referred to the "Compressae" group of species.

Based upon Studer's type, Versluys (1906:54) described *Primnoella divaricata* (Studer, 1879), as very similar to *P. australasiae* but with the adaxial side of the polyps completely covered by scales smaller than those of the abaxial rows; it conforms better with the "Compressae" group and therefore is here treated as a species of *Primnoella.*

About all that can be said about *Primnoella divergens,* given the inadequate description and figure originally provided (Hickson, 1907:10, pl. 1, figs. 8–10), is that it is not one of the "Compressae" group but may be a species of "Convexae."

As originally described and illustrated, both *Primnoella jungerseni* Madsen, 1944, and *P. krampi* Madsen, 1956, fall within the "Convexae" group of species, hence are here reassigned to *Convexella.* Although Madsen (1944:42) compared *P. jungerseni* with *P. distans* and *P. polita* Deichmann, 1936, in both of those species only two rows of abaxial scales are visible, making both referable to the "Compressae" group, hence *Primnoella* s.s.

Primnoella gracilis Molander, 1929, originally was compared with *P. flagellum* and, as described and illustrated (Molander 1929:63, figs. 17, 18; pl. 1, fig. 2), falls within the "Convexae" group on the basis of its well-developed adaxial scales. However, the marginal scales show no tendency to override the operculars, as is the case in both *Primnoella* and *Convexella,* so the species probably is excluded from both genera.

Gravier (1914:77) aligned his *Primnoella kuekenthali* with the "Convexae" group (1914:83), but his illustrations and lengthy description throw some doubt upon that assignment. The body scales are thick, scuptured externally by large ridges that may branch, and have strongly dentate margins, whereas the sclerites of *Primnoella* "Convexae" are thin and externally smooth. Gravier's statement that on the concave adaxial surface of the polyps "il y a une bande médiane qui reste à nu" suggests that *kuekenthali* may be referable to *Ophidiogorgia* Bayer, 1980. This conclusion is confirmed by specimens from Marguerite Bay (68°30′S, 68°30′W, USNM 56631), South Shetland Islands (62°17′30″S, 58°34′36″W, USNM 78398; 63°26′S, 62°10′W, USNM 77456; 62°16′42″S, 58°34′00″W, USNM 77361), Livingston Island (63°24′S, 62°14′W, USNM 82863), Anvers Island (64°46′28″S, 63°26′30″W, USNM 81544), Elephant Island (62°39′S, 56°10′W, USNM 82852), Adelaide Island (67°48′12″S, 68°54′06″W, USNM 77460), all from along the Antarctic Peninsula in the general vicinity of the type locality (64°50′S, 63°30′W), as well as from the South Orkney Islands (60°26′30″S, 45°53′18″W, USNM 77145), that agree in all essentials with Gravier's description of *Primnoella kuekenthali.* As in his material, the interval between whorls and the size of polyps within whorls is subject to considerable variation; in two specimens (USNM 56631, 77456), new whorls are intercalated between fully developed whorls just as illustrated by Gravier (1914:82, fig. 108). Gravier's drawing shows the body scales aligned longitudinally, unlike the case in *Ophidiogorgia paradoxa* Bayer but, in the specimens now available, this regular arrangement is disrupted in almost all fully developed polyps. It must be remembered that the then unique type specimen of *O. paradoxa* was deformed by the presence of some epizoan, possibly echinoderm, which may have disrupted the development of sclerites in the polyps of adjacent

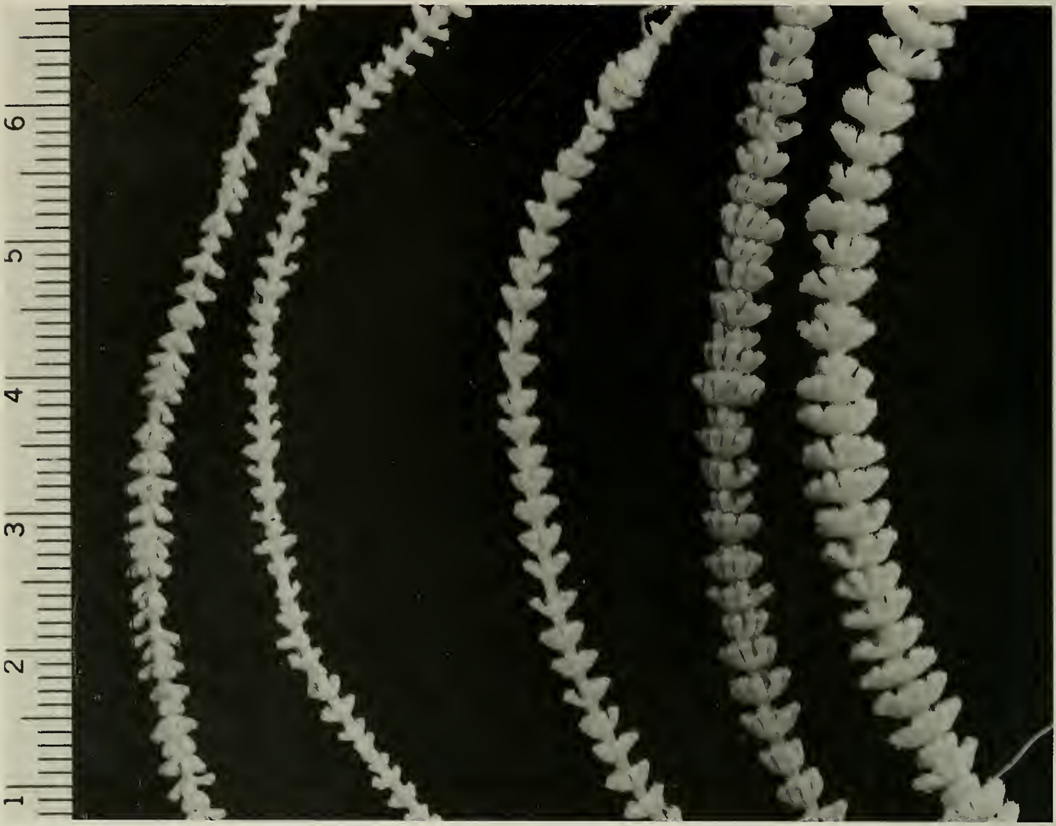


Fig. 21. *Convexella magelhaenica* (Studer), USNM 85300, from north of Cabo San Diego, Tierra del Fuego, 124–119 m, showing variation present among specimens from a single haul. See Figs. 27, 28.

whorls. Although Gravier described the distalmost scales of the polyps as an operculum, his drawing (1914:81, fig. 105) of one opercular scale is no more clearly differentiated from the body scales than are those of *O. paradoxa.* Accordingly, *Primnoella kuekenthali* Gravier, 1913, is here transferred to *Ophidiogorgia* as *O. kuekenthali,* new combination, pending detailed studies to clarify its relationship with *O. paradoxa.*

Distribution.—Except for *Convexella jungerseni* (Madsen), all species of *Convexella* are confined to the southern hemisphere.

Specimens from Balleny Islands (66°53′S, 163°19′E, USNM 77330) and the vicinity of Wilkes Station (66°15′24″S, 110°28′40″W, USNM 88775) clearly referable to *Ophidiogorgia* indicate that the genus and probably the species are of circum-Antarctic distribution.

Convexella magelhaenica (Studer, 1879), new combination
Figs. 21–38

Primnoella magelhaenica Studer, 1879:644, pl. 2, fig. 10a–c.—Kükenthal, 1919:389, pl. 40, figs. 50, 51; 1924:281 (references).—Broch, 1965:21, pl. 1, fig. 1.

Primnoella magellanica Wright & Studer, 1889:83, pl. 17, fig. 2; pl. 21, fig. 10. (incorrect subsequent spelling).—Thomson & Ritchie, 1906:855, pl. 1, fig. 3 (incorrect subsequent spelling).—Versluys, 1906:51 (unjustified emendation).

Primnoella flagellum Studer, 1879:645, pl. 2, fig. 11a–c.—Wright & Studer, 1889:

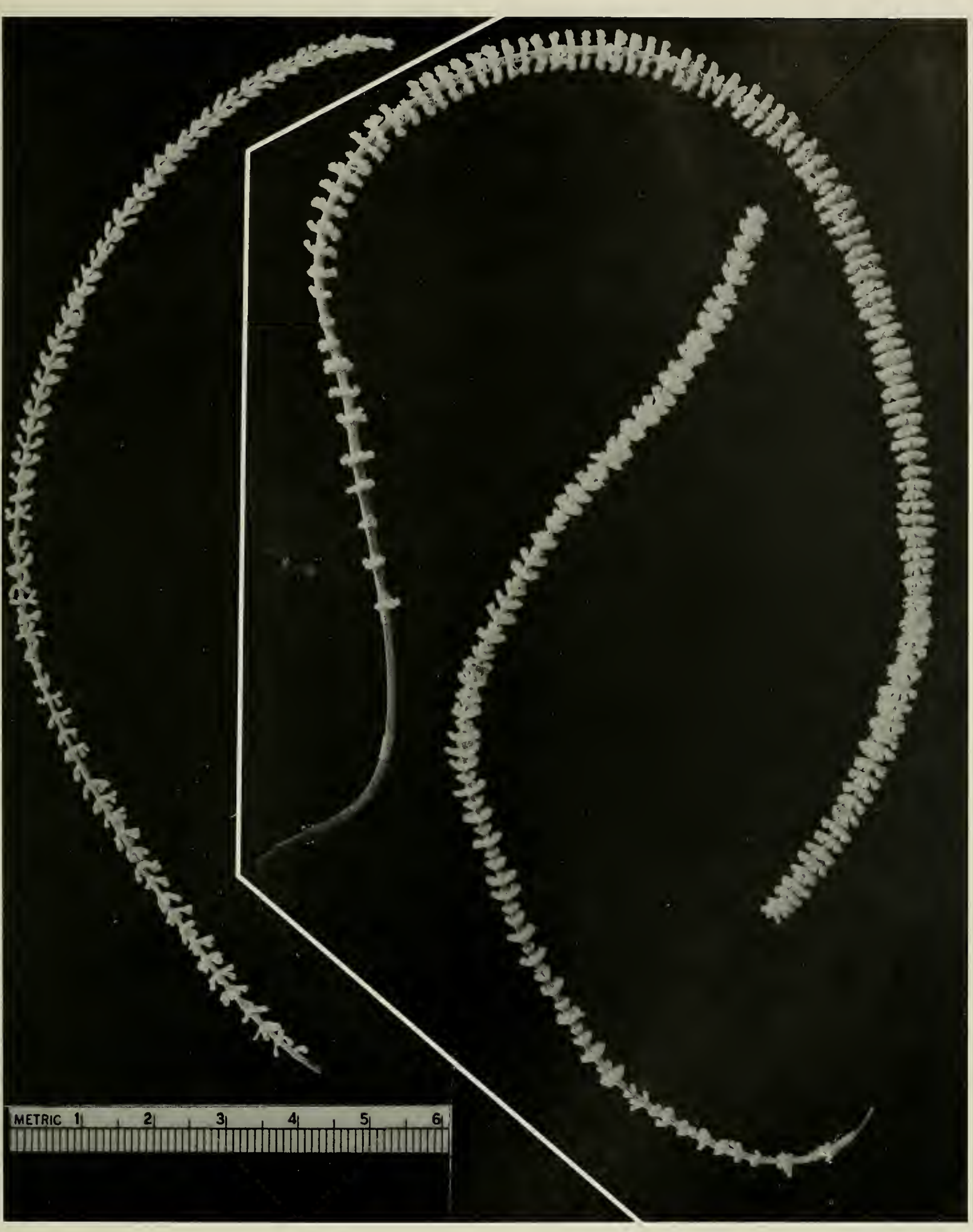


Fig. 22. *Convexella magelhaenica* (Studer). Left, Colony from off Isla Desolacion, Magellanes, Chile, 1500–1666 m, showing polyps directed distad on distal part, basad on basal part, USNM 82856 (see Fig. 35 for detail of polyps); Right, Two colonies from off Cabo San Sebastian, Tierra del Fuego, 86 m, USNM 85306, showing polyps standing vertically as in *Callozostron* (compare figs. 1, right, and 7, top; see Figs. 23, 24 for detail of whorls and polyps).

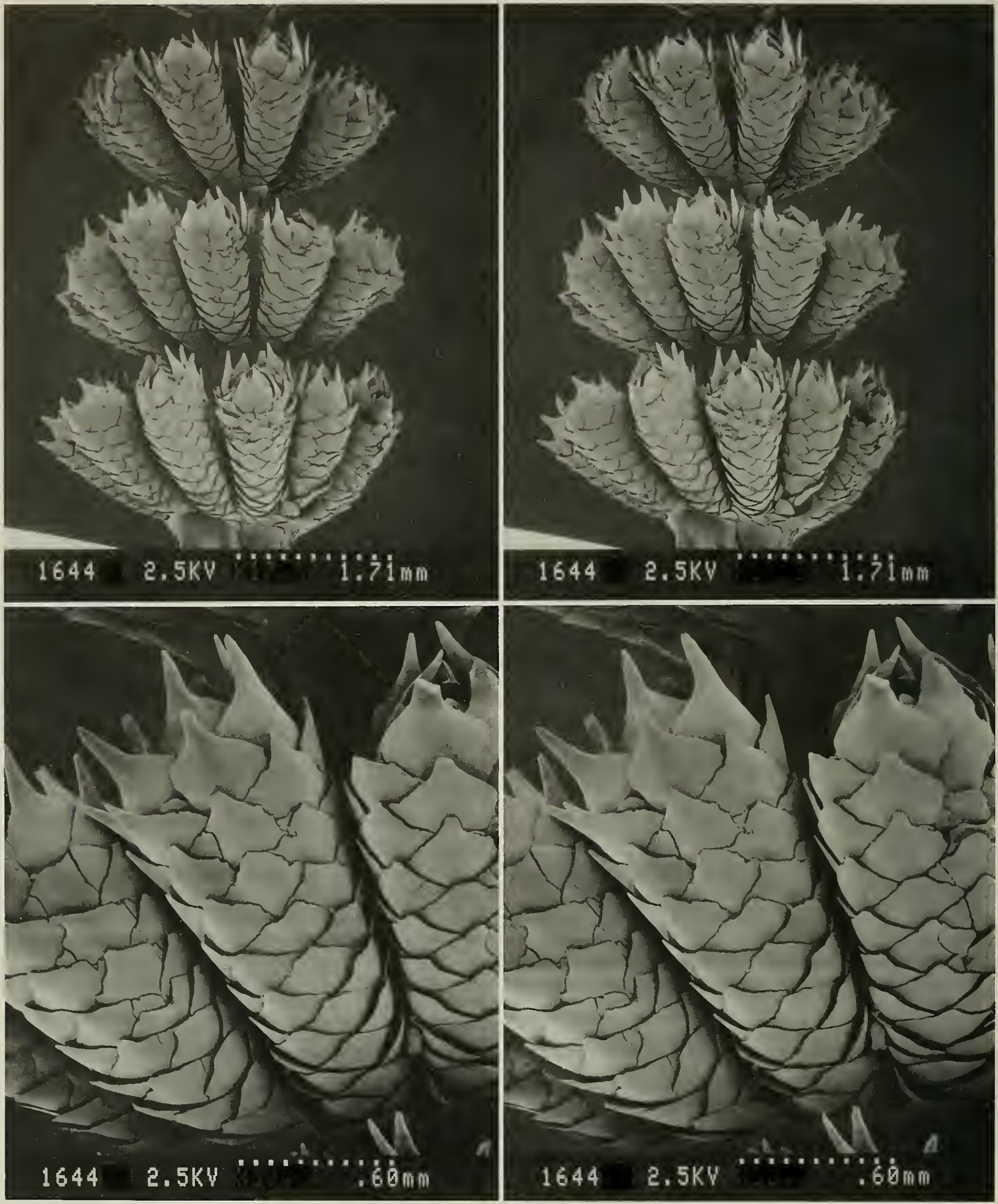


Fig. 23. *Convexella magelhaenica* (Studer), USNM 85306, from off Cabo San Sebastian, Tierra del Fuego, 86 m. Top, Three whorls; Bottom, Detail of polyps showing development of apical spines on distal body scales. Stereoscopic pairs (SEM 1644).

85, pl. 18, figs. 2, 2a; pl. 21, fig. 12.—Versluys, 1906:51.

?*Primnoella flagellum*.—Thomson & Mackinnon, 1911:688.

Material examined.—35 lots. See appendix.

Discussion.—Studer's (1879) original description and illustrations of *P. magel-*

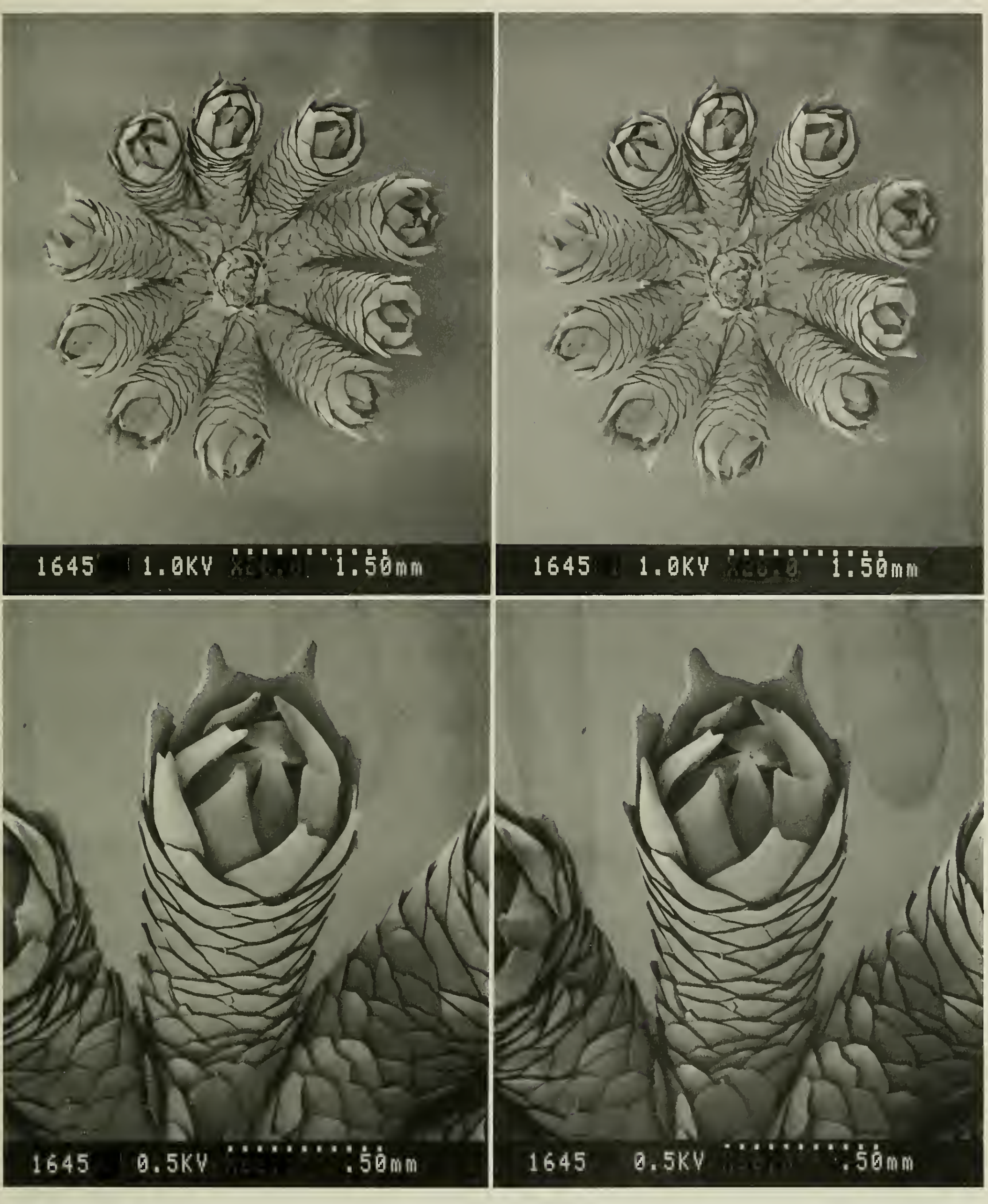


Fig. 24. *Convexella magelhaenica* (Studer), USNM 85306, from off Cabo San Sebastian, Tierra del Fuego, 86 m. Top, Whorl of polyps seen from above; Bottom, Oblique view of polyp showing circumoperculum. Stereoscopic pairs (SEM 1645).

haenica, collected at a depth of 42 fathoms (= 77 m) in the Straits of Magellan by the *Gazelle,* are not adequate to distinguish the species from others described subsequently. Wright & Studer (1889), Thomson & Ritchie (1906), Kükenthal (1919), and Broch (1965) have described and illustrated specimens purported to be *magelhaenica,* but in

Fig. 25. *Convexella magelhaenica* (Studer), USNM 89344, from between Tierra del Fuego and Falkland Islands, 128 m. Top, Part of slender colony with whorl of new polyps between fully developed whorls (SEM 1934); Bottom, Part of stouter colony showing new polyp between fully developed individuals within a whorl, as well as new whorl almost hidden by fully developed whorl (SEM 1931). Stereoscopic pairs.

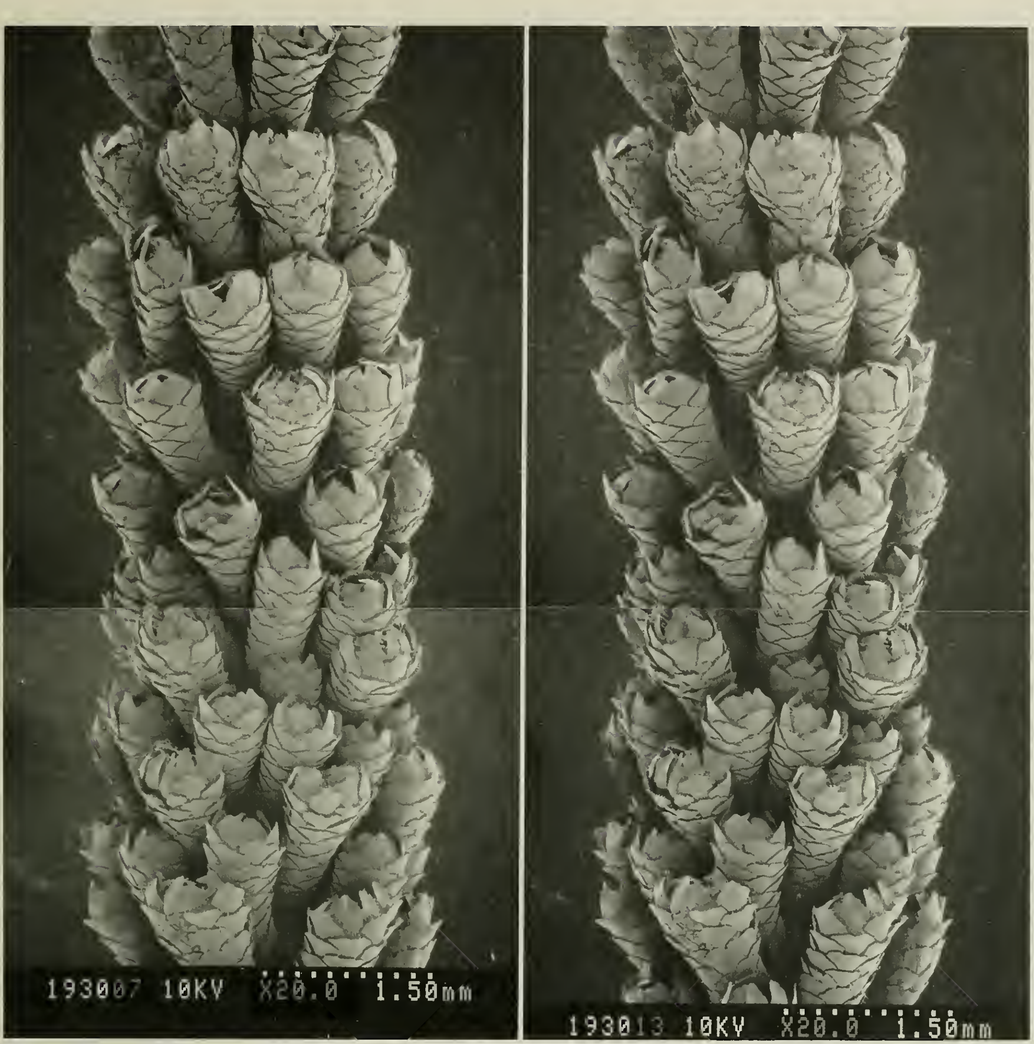


Fig. 26. *Convexella magelhaenica* (Studer), USNM 89344, from between Tierra del Fuego and Falkland Islands, 128 m. Part of stout colony with polyps exceptionally crowded. Stereoscopic pairs (SEM 1930).

no case was identification confirmed by comparison with the type specimen. It is reasonably certain that the specimens in the present collection are conspecific with Thomson & Ritchie's, Kükenthal's, and Broch's material. Wright & Studer's descriptions and illustrations of both *P. magellanica* (incorrect subsequent spelling of *magelhaenica*) and *P. flagellum* are consistent with the numerous specimens now on hand from the same general geographical area. It should be remembered, however, that if future study should prove Wright & Studer's specimen of "*magellanica*" to represent a species different from *P. magelhaenica,* it may take the available name *magellanica* dating from Versluys, 1906.

The present material, consisting of specimens of a wide range in size, from young colonies 2.5 cm tall with 7 whorls of polyps in 2's and 3's, to mature specimens more than 40 cm tall, with 7 whorls of 15 polyps each in 1 cm, comprises colonies agreeing with the characters heretofore described for *P. magelhaenica, P. flagellum,* and *P.* "*magellanica.*" Colonies of intermediate size

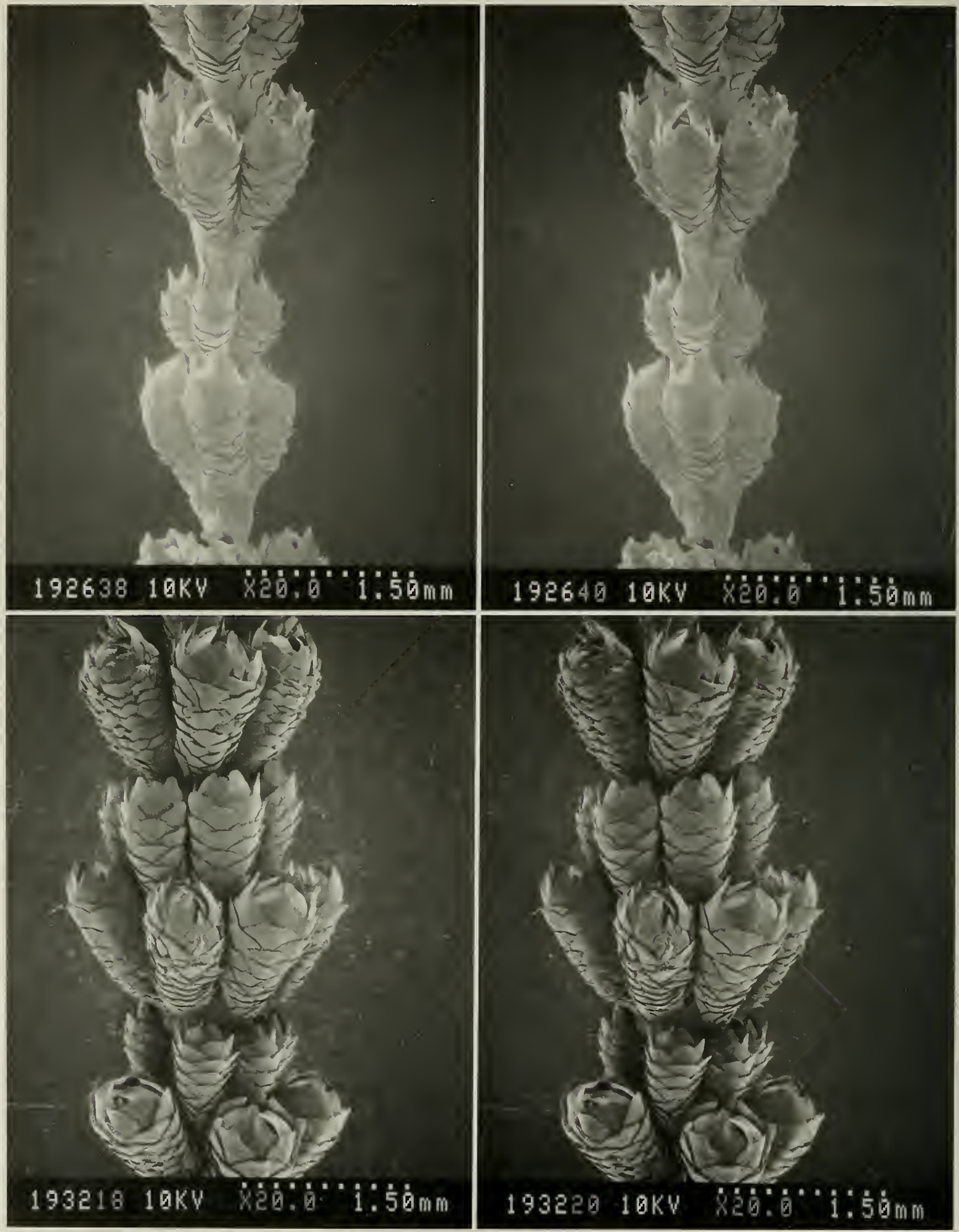


Fig. 27. *Convexella magelhaenica* (Studer). Top, USNM 85300, from north of Cabo San Diego, Tierra del Fuego, 124–119 m; part of slender colony with whorl of new polyps between two fully developed whorls (SEM 1926). Bottom, USNM 89344, from between Tierra del Fuego and Falkland Islands, 128 m; part of stouter colony with crowded whorls of different ages (SEM 1932). Stereoscopic pairs.

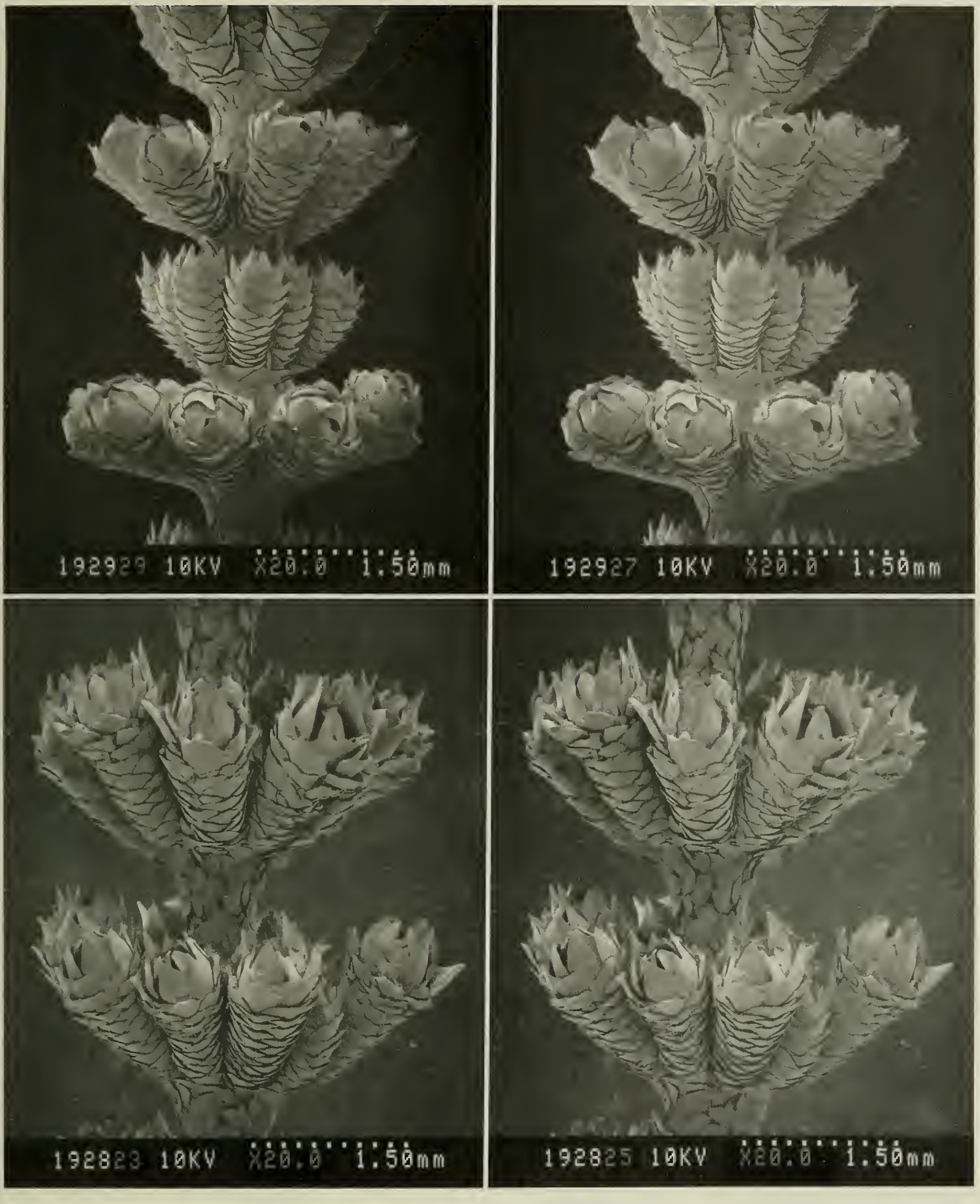


Fig. 28. *Convexella magelhaenica* (Studer), USNM 85300, from north of Cabo San Diego, Tierra del Fuego, 124–119 m. Top, Part of stout colony with whorl of upturned new polyps between two fully developed whorls of outwardly directed polyps (SEM 1929); Bottom, Part of stouter colony having polyps with exceptionally strong circumopercular spines (SEM 1928). Stereoscopic pairs.

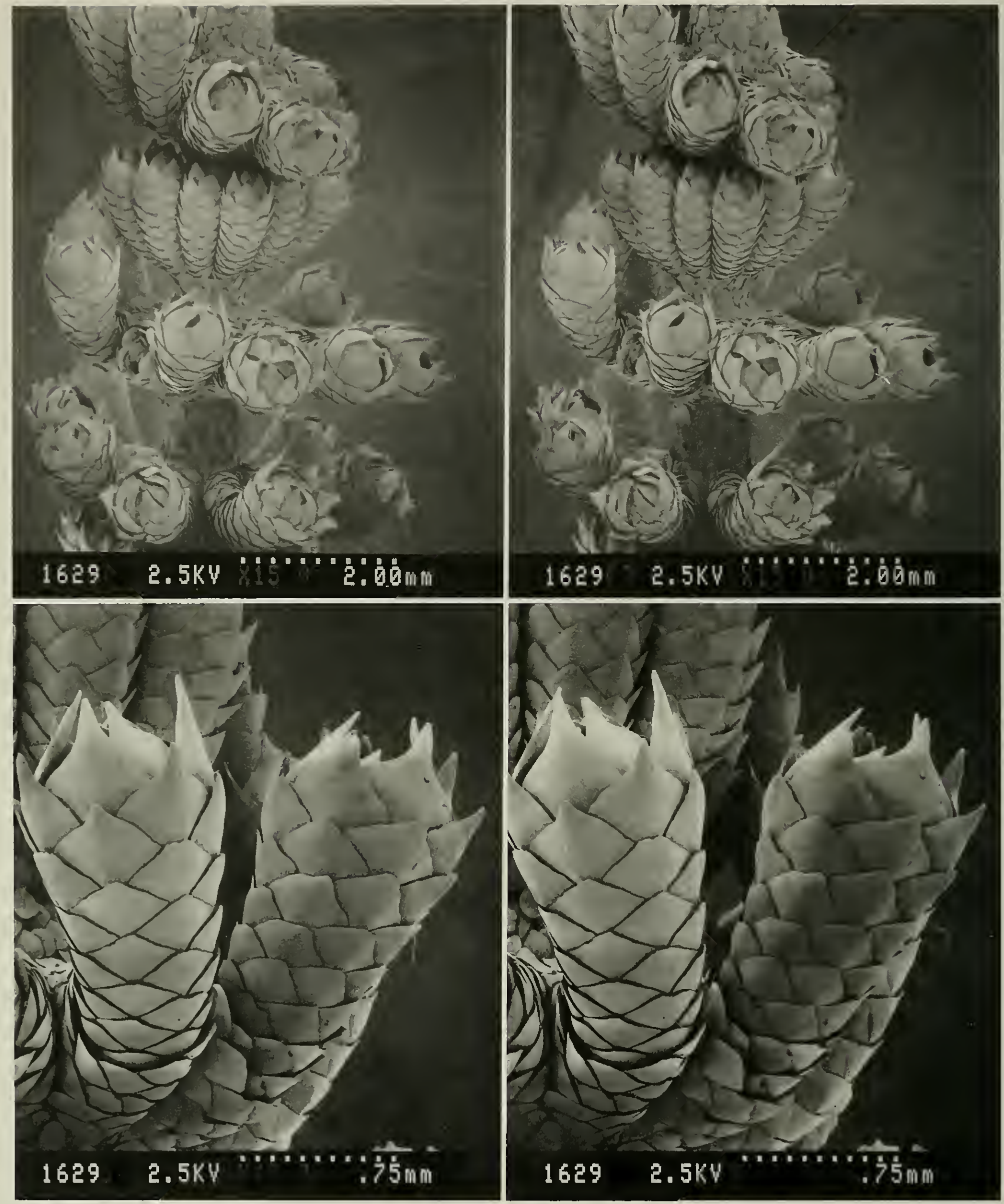


Fig. 29. *Convexella magelhaenica* (Studer), USNM 58441, from Strait of Le Maire, 229–265 m. Top, Part of branch showing young whorl with polyps turned strongly upward, situated between fully developed whorls with some polyps projecting almost vertically from axis; Bottom; Detail of two polyps. Stereoscopic pairs (SEM 1629).

may have from 3 to 7 whorls in 1 cm of axial length, varying from 3 to 8 or more polyps per whorl, the distalmost sometimes only 2.

Broch (1965:21) did not provide a formal decription of his specimens of *P. magelhaenica* from Burdwood Bank but commented that his "rather copious collection exhibits a comparatively broad variation" from "slender specimens" to "more coarse

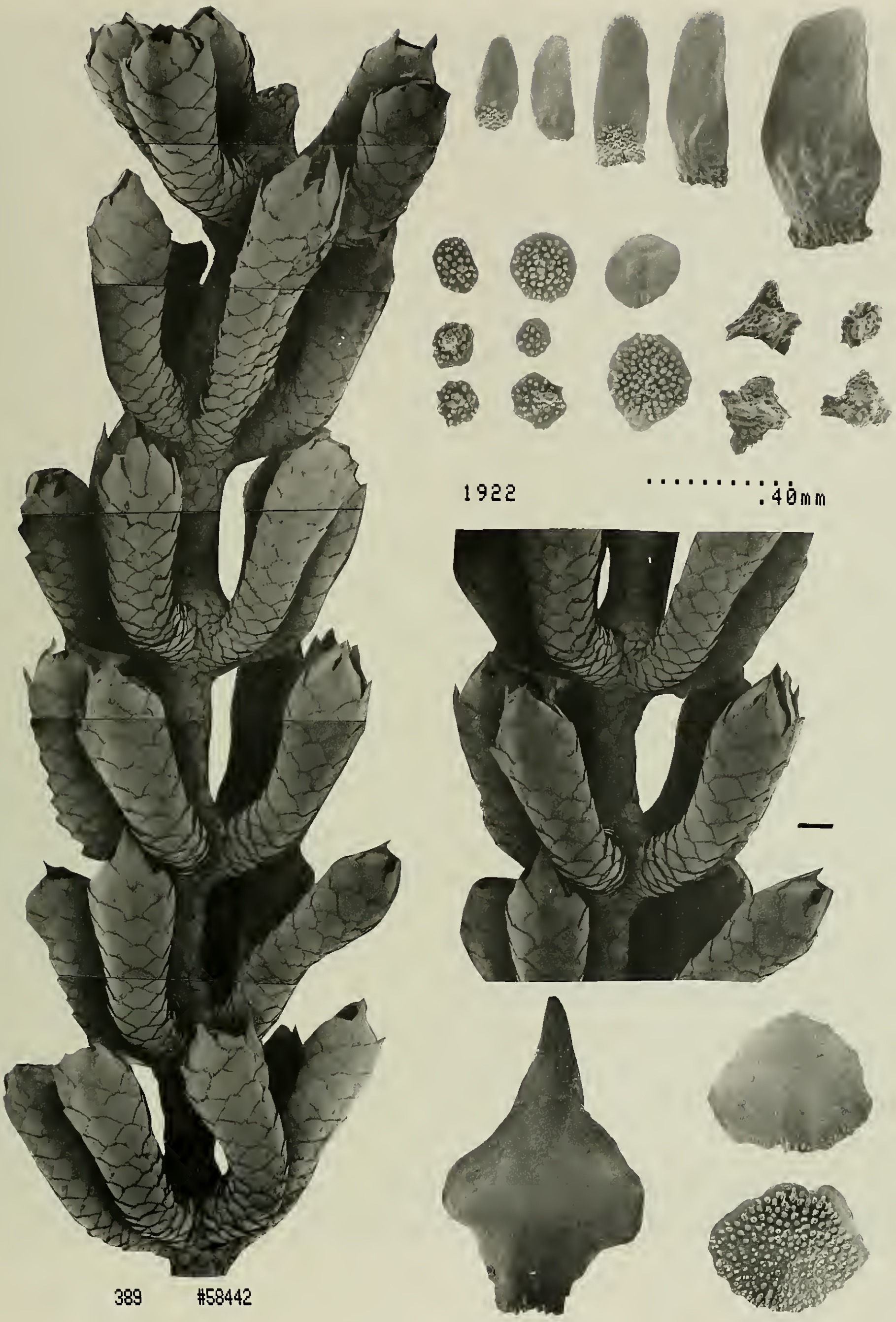


Fig. 30. *Convexella magelhaenica* (Studer), USNM 58442, from east of Cape Horn, 384–394 m. Part of stem with polyps bent upward but not appressed to stem; middle portion in stereoscopic view, scale bar = 1 mm (SEM 389). Isolated sclerites (SEM 1922): top row, operculars; second row, outer (left group) and inner (right group) coenenchymals; bottom row, circumopercular and body scales.

Fig. 31. *Convexella magelhaenica* (Studer), USNM 85288, from Sars Seamount in Drake Passage, 512–622 m. Top, Part of branch with whorls of polyps; Bottom, Polyp in side view, showing negligible development of marginal points on distal body scales. Stereoscopic pairs (SEM 1647).

colonies." His specimens were 12–18 cm long, a size not unusual in the material reported here. However, the longest specimen from *Eltanin* station 217 from off Cabo San Diego, Tierra del Fuego (USNM 78403), is a slender colony 48 cm long. The type specimen of *Primnoella magelhaenica* was 22 cm long, and that of *P. flagellum* 53 cm, so

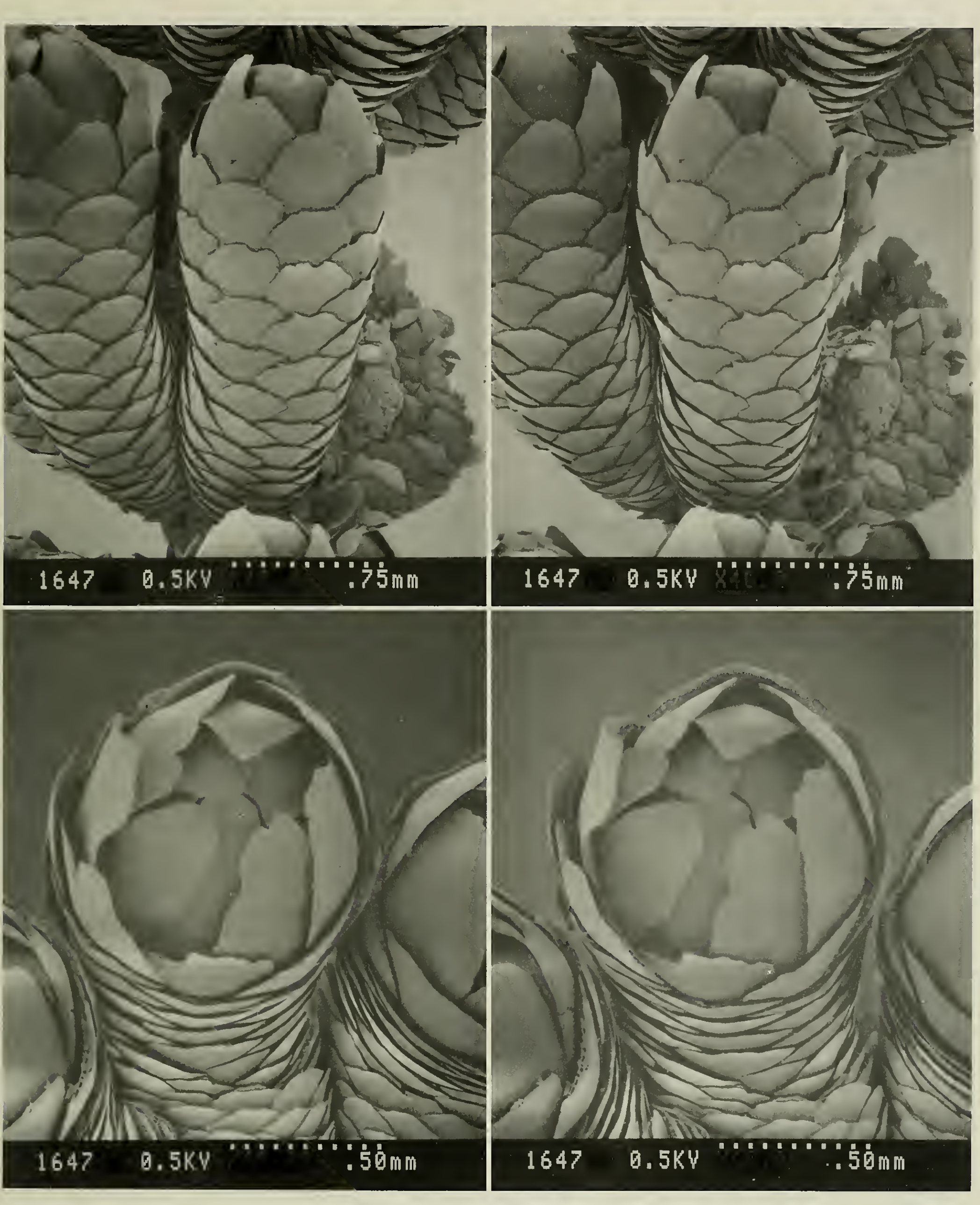


Fig. 32. *Convexella magelhaenica* (Studer), USNM 85288, from Sars Seamount in Drake Passage, 512–622 m. Top, Polyp in abaxial view; Bottom, Oral view of polyp with circumopercular scales closed over operculars. Stereoscopic pairs (SEM 1647).

it is probable that the former is a colony similar to the "more coarse colonies" mentioned Broch and abundantly represented in the present material, whereas *P. flagellum* is like Broch's "slender specimens." Both extremes are present in the lots from *Eltanin* stations 217 (USNM 78403), 369 (USNM 77371), 974 (USNM 85300), and 976 (USNM 89344), all from east of Tierra del Fuego.

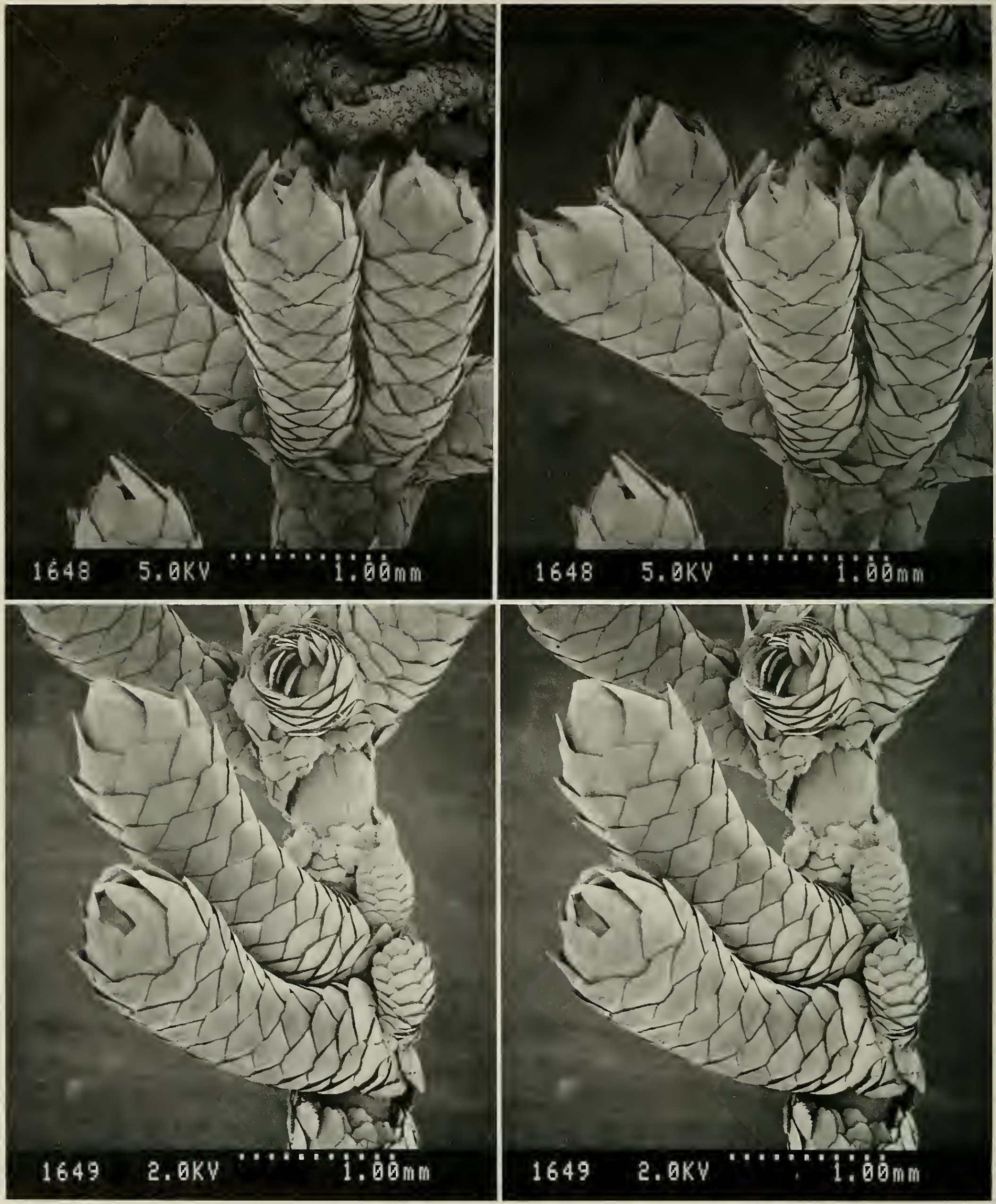


Fig. 33. *Convexella magelhaenica* (Studer), USNM 85298, from Strait of Le Maire, 641–596 m. Top, Detail of whorl showing polyps in abaxial and lateral views (SEM 1648); Bottom, Young polyps developing between adult polyps within two whorls from which some of the adult polyps have been removed. The young polyps have 7 scales in the abaxial rows compared to 13 in the adults, showing that the number of scales can be age dependent (SEM 1649). Stereoscopic pairs.

Broch (1965:20–22) commented on the production of new polyps and new whorls in *Primnoella* and reported some differences in this respect among *P. magelhaenica, P. scotiae,* and *P. vanhoeffeni.* He reported that new whorls arise in the middle and upper parts of the polyparium in *P. magelhaenica.* In the present material, development of new whorls is very variable. In some colonies, few new whorls are intercalated between fully developed whorls but, in others, new whorls may arise throughout the length of the colony, indicating different states of colonial growth at the time of collection. In a specimen from *Eltanin* station 976, two new whorls of different sizes may occur in the space between two fully developed whorls.

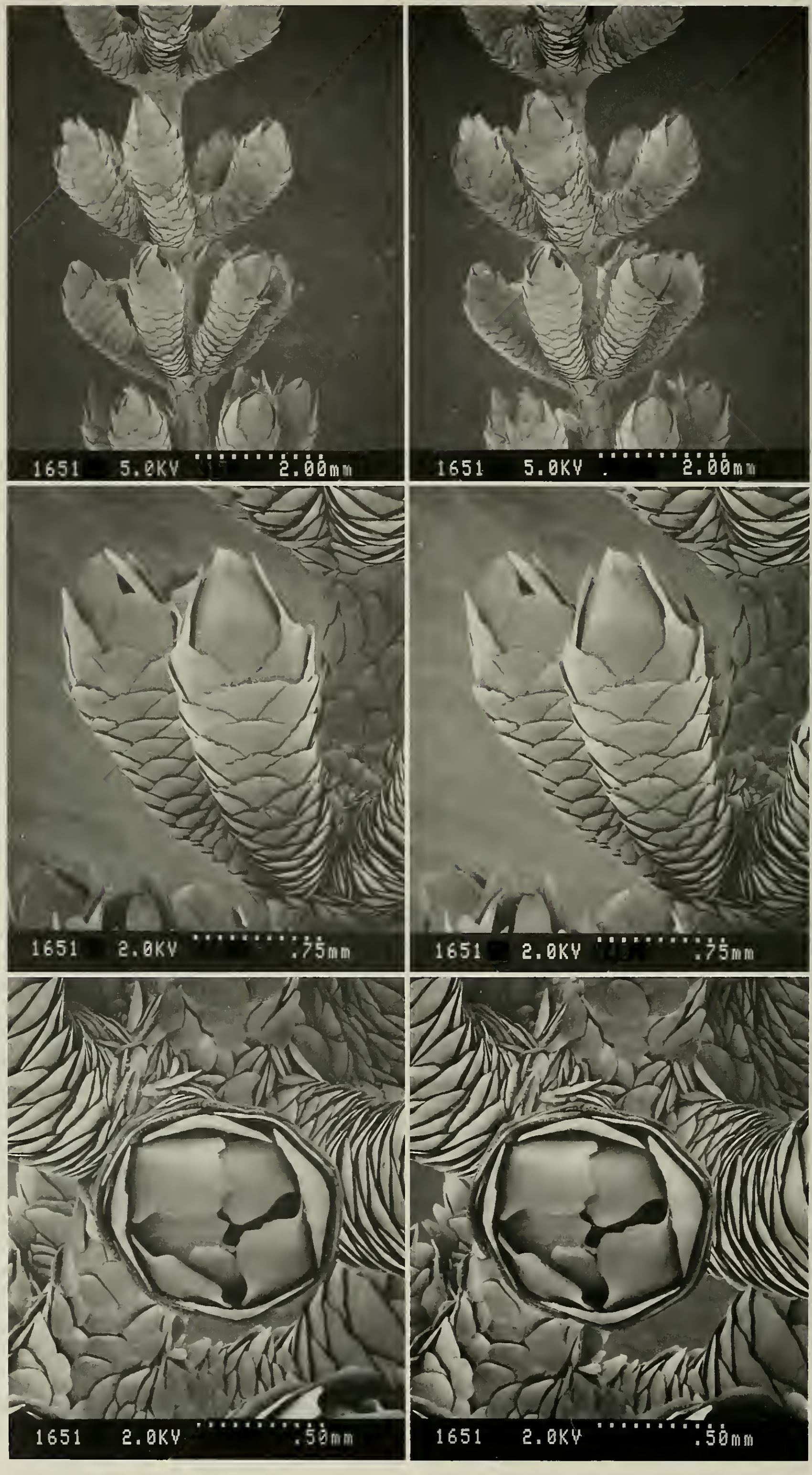
Studer (1879:645) reported that the body scales "stehen in 13–14 Querreihen um die Kelche," and Wright & Studer (1889:83) wrote that "ten to thirteen calyx scales may be counted" in the length of the calyx, but in neither case do the accompanying illustrations suggest so many. Studer (1879:645) said that in *P. flagellum* the body scales "stehen um die Kelche in acht Reihen," a number that occurs in the present material.

Colonies are sometimes attached to a stone or shell by a small, discoidal, calcified holdfast, but the supporting substrate is not often collected with the specimens. Most are broken off just above the holdfast, part of which may be present, suggesting that the usual substrate is rocky. However, the numerous slender colonies obtained at *Eltanin* station 976 show no sign of attachment. Although all specimens are more or less broken and the axis of most is partially decorticated, in no case can a growing tip at both ends be confirmed. Pogonophoran tubes among the gorgonian stems suggest that the bottom was muddy at this location, making it plausible to conclude that the very flexible colonies lie prone on the substrate in life, as is the case with some species of *Leptogorgia* (Bayer 1961:218–222, Grasshoff 1988:116).

The straight or slightly curved polyps vary in their stance from almost perpendicular to the axis, to directed strongly upward. In no case are they strongly bent inward with the operculum facing the axis. A specimen without holdfast (USNM 82856, Fig. 21, left) has the polyps along the distal half of the colony directed toward the apex, those along the proximal half toward the base. In any given colony, the number of body scales in the abaxial rows may vary from 7 or 8 in polyps near the middle of the colony, to as few as 5 in the polyps of the distalmost and basalmost few whorls; in colonies with the tallest polyps, the abaxial rows commonly consist of 10–11 scales below the circumoperculars, but as many as 14 is unusual. Young polyps have fewer abaxial scales than do fully developed individuals (Figs. 25, 27, 33).

Close observation of isolated polyps during maceration with Sodium hypochlorite shows that the scales of the distalmost circle of 8 body sclerites forming the circumoperculum are not distinctly differentiated functionally from the following 2 or 3 circles, all of which participate in protecting the mouth and withdrawn tentacles during contraction. The distalmost narrow, tongue-shaped sclerites (Fig. 30) that comprise the theoretical "operculum" can fold nearly flat over the mouth in contraction. These are not consistently 8 in number but vary from 6 to 9 or even 10 among polyps of the same whorl. In some cases these differ in size among themselves only slightly and are distinctly smaller than the circumopercular scales; in others the adaxials are very small and the abaxials are as large as, and indistinguishable from, the circumoperculars. These and intermediate conditions exist not only in a single colony, but even among the polyps of one whorl.

The arrangement of opercular and circumopercular sclerites resembles that described for *Thouarella hilgendorfi* by Kinoshita (1908:5, fig. 1). In both *Thouarella* and *Primnoella,* sclerites are so large that eight scales cannot fit around the circumference of the polyp in a single circle. In-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stead, each circle of eight scales surrounding the body is composed of two "transverse rows" of four scales that alternate with one another (Kinoshita 1908), so the "operculum" consists of transverse rows I and II, and the circumoperculum of rows III and IV. The scales seem to be arranged in spirals around the polyp as well as longitudinally, as is shown in Fig. 23.

The abundant material here reported strongly suggests that Studer's *Primnoella magelhaenica* and *P. flagellum* represent a single species, and that Wright & Studer's Kükenthal's, and Broch's records of "*magellanica*" and *magelhaenica* are the same thing. The present material comes from the remarkable bathymetric range from 75 to more than 1500 m. The general aspect of some colonies from the two bathymetric extremes is considerably different and would, in the absence of intermediates, easily be considered specifically distinct. However, morphological variation among specimens from the extremes of bathymetric range differs little from that present among specimens from a single shallow station, making discrimination of two or more species impossible on any objective basis so far detected.

To convey some idea of the similarities and differences among colonies of *P. magelhaenica* over its wide bathymetric range, scanning stereomicrographs have been made of a selection of specimens from the shallowest to the deepest available records, some of which are here presented to document the morphological diversity of this abundant gorgonian.

The shallowest record in the present collection is 73 m, obtained off the north entrance of the Strait of Lemaire, Tierra del Fuego (USNM 85308). Specimens from 86 m off Cabo San Sebastian (USNM 85306) are typical of shallow-water colonies (Figs. 23, 24). The polyps are directed obliquely upward but the whorls do not overlap in the contracted condition; scales of the three distalmost rings of body sclerites have a distinct, smooth apical spine, and the theoretical operculum is concealed during contraction by the uppermost rings of circumopercular scales.

Colonies trawled from 128 m between Tierra de Fuego and the Falkland Islands (USNM 89344) reveal a range of growth-form from slender, with well separated whorls of few polyps (Fig. 25, top) to unusually stout, with crowded, overlapping whorls of eight or more polyps (Fig. 26). Small, evidently young polyps may occur between fully developed individuals within a whorl (Fig. 25, bottom).

A haul made north of Cabo San Diego, Tierra del Fuego in 124–119 m yielded several colonies of diverse aspect (USNM 85300), from slender (Fig. 27, top) to rather stout (Fig. 28). New whorls are intercalated between fully developed ones (Figs. 27, top; 28, top), and the younger individuals may be more strongly inclined toward the axis than are the older (Fig. 28, top), which may stand almost vertically. In one colony the circumopercular scales are so strongly developed that it approaches *Callozostron* in appearance (Fig. 28, bottom).

Colonies from the Strait of Le Maire in 229–265 m (USNM 58441) demonstrate the insertion of new whorls of polyps between fully developed whorls of almost perpendicularly placed individuals (Fig. 29).

A colony from east of Cape Horn in 384–494 m (USNM 58442) has the tallest polyps observed in the present material (Fig.

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Fig. 34. *Convexella magelhaenica* (Studer), USNM 82865, from south of Isla de los Estados, Tierra del Fuego, 771–903 m. Top, Part of branch showing two whorls of polyps with points scarcely developed on distal body scales; Middle, Oblique view of polyps showing scant development of marginal points on body scales; Bottom, Oral view of polyp with circumopercular scales in closed position. Stereoscopic pairs (SEM 1651).

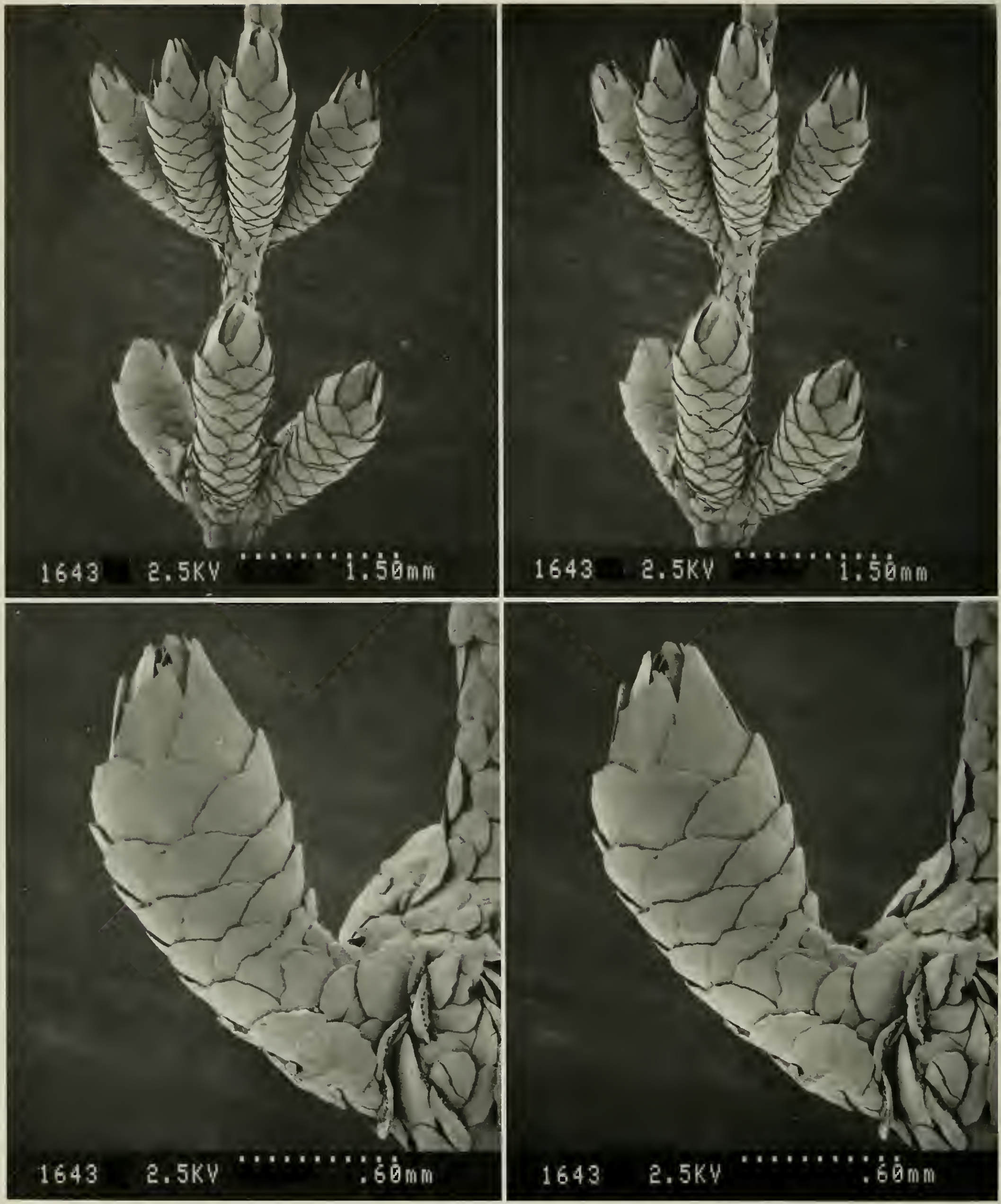

Fig. 35. *Convexella magelhaenica* (Studer), USNM 82856, from off Isla Desolacion, Magellanes, Chile, 1500–1666 m. Top, Part of stem with two whorls; Bottom, Polyp in side view, showing alternating tall and wide circumopercular scales and weak development of apical points. Stereoscopic pairs (SEM 1643).

30). They have 12–13 scales in the abaxial rows, and only the scales of the distalmost transverse row have a strong apical point.

The polyps of a colony from Sars Seamount in Drake Passage trawled in 512–622 m (USNM 85288) are strongly inclined upward and have as many as 13 or 14 scales in the abaxial rows; the the circumopercular

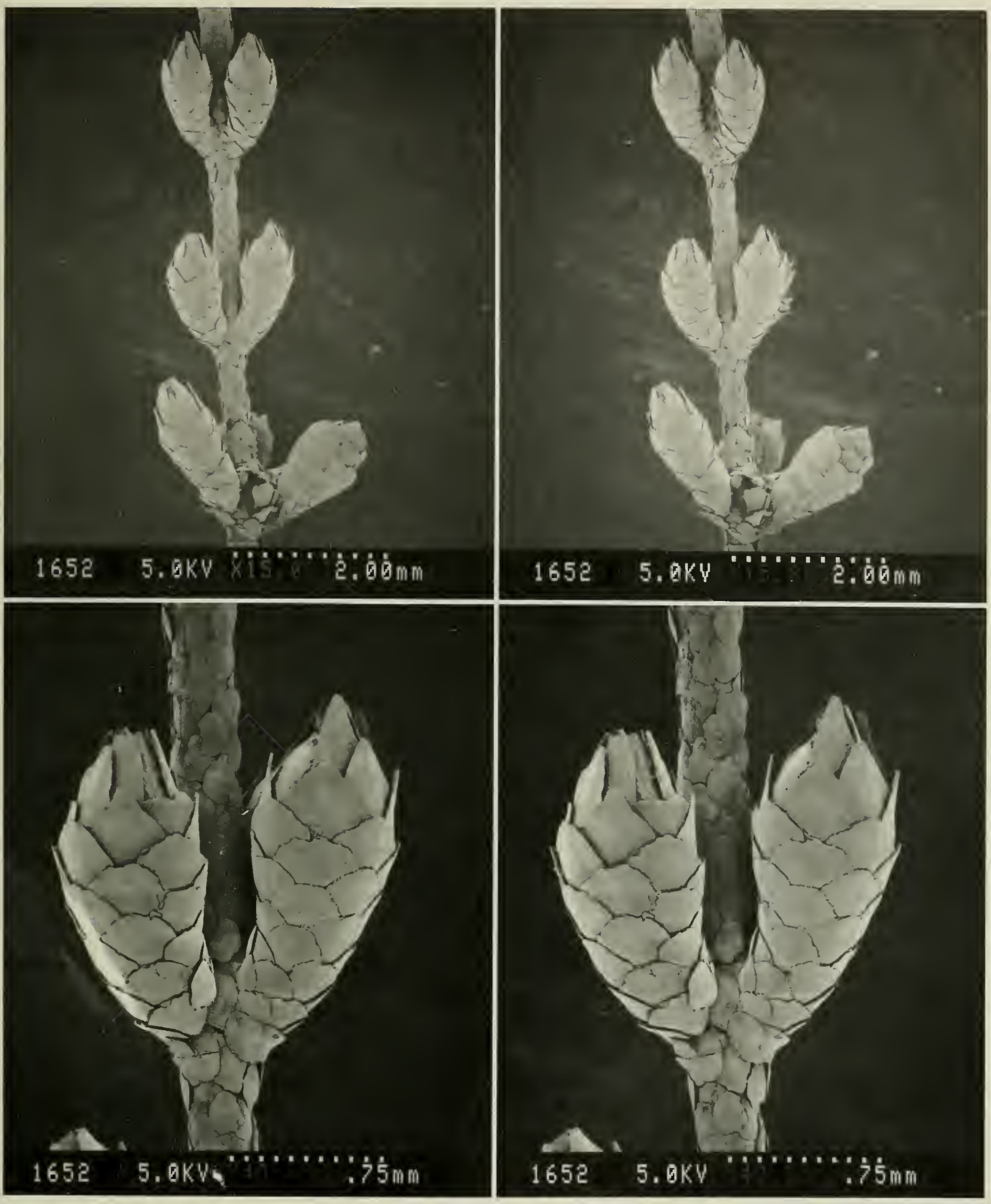

Fig. 36. *Convexella magelhaenica* (Studer), USNM 85302, from east edge of Burdwood Bank, 1647–2044 m. Top, Part of stem with three whorls; Bottom, Detail of polyps. Stereoscopic pairs (SEM 1652).

scales completely obscure the operculars, and have only a low, rather blunt apex (Figs. 31, 32).

A colony from 641–586 m in the Strait of Le Maire (USNM 85298) has polyps with 10–11 scales in the abaxial rows and circumopercular scales with weakly developed apical angle (Fig. 33). Young polyps developing between fully developed individuals have fewer abaxial scales, showing

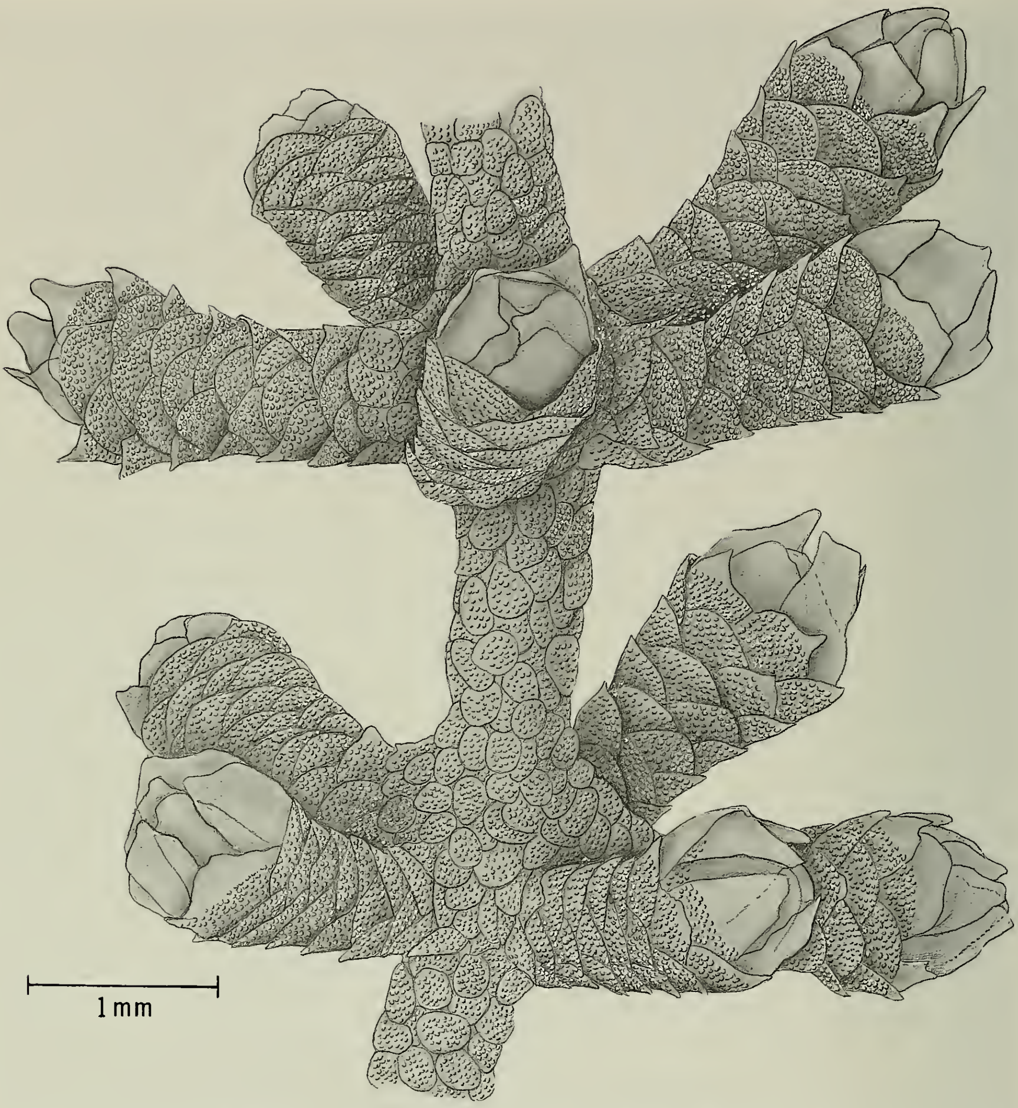

Fig. 37. *Convexella magelhaenica* Studer, USNM 59102, from east of Cape Horn, 384–494 m. Two whorls; camera lucida drawing by Constance Stolen McSweeny from alcoholic specimen, for contrast with SEM images. The tubercles on the inner surface of the scales are clearly visible through the glassy clear sclerites, which are opaque and externally smooth as depicted by SEM.

that the number of scales in the longitudinal rows increases with age.

In colonies from depths of 771–903 m south of Isla de los Estados, Tierra del Fuego (USNM 82865), the uppermost four scales of the circumoperculum are tall and triangular, alternating with the lower four scales which are broader and have a low apical point (Fig. 34).

Colonies from west of Isla Desolacion, Chile, in 1500–1666 m (USNM 82856) are slender, with well spaced whorls of 5 or 6 upwardly directed polyps (Fig. 35). Four tall, triangular circumopercular scales alternate with four broader scales with a low apical angle.

The tendency to be slender and more delicate continues in colonies from 1647–2044

Fig. 38. *Convexella magelhaenica* (Studer), USNM 59102, from east of Cape Horn, 384–494 m. SEM image for comparison with camera lucida drawing in Fig. 36. (SEM 1646.)

m on the eastern edge of Burdwood Bank (USNM 85302), which have well spaced whorls of 3 or 4 upwardly directed polyps (Fig. 35). The four lower circumopercular scales are shorter than the four upper scales, but are more like them than is the case in USNM 82856.

Remarks.—Because heavy reliance upon scanning electron microscopy for highly accurate representation of external morphology causes us to lose sight of the fact that primnoid sclerites are more or less translucent, a camera lucida drawing (Fig. 37) of one specimen is given for comparison with SEM representation (Fig. 38). The sclerites of *P. magelhaenica* are translucent, almost glassy clear when wet, so the tubercular sculpture of their inner surfaces is clearly visible with the light microscope but invisible with SEM.

In view of the morphological similarities of *Primnoella magelhaenica* with *Callozostron carlottae* Kükenthal and *C. diplodiadema* new species, it might be as reasonable either to regard *P. magelhaenica* as a weakly spinose *Callozostron,* or *C. carlottae* and *C. diplodiadema* as very spiny species of *Primnoella,* apart from the fact that irregularly tuberculate sclerites are abundantly present in the walls of the longitudinal stem canals in *P. magelhaenica* as they are in *P. australasiae,* but not in species of *Callozostron.*

Distribution.—West and east coasts of the southern extremity of South America, Straits of Magellan and Le Maire, Drake Passage, Tierra del Fuego, eastward to Falkland and South Orkney Islands, 73–1647 m (this collection). Burdwood Bank, 61 fathoms (Broch 1965). This species has not been found in any of its variants anywhere else around the Antarctic continent.

Acknowledgments

Dr. P. F. S. Cornelius of The Natural History Museum (London) made it possible for me to examine Gray's type specimens of *Primnoella australasiae,* and Dr. D. A. Ritz provided specimens recently collected in the type locality by A. J. Blackman. Dr. Pat Hutchings of the Australian Museum (Sydney) provided access to Thomson & Mackinnon's type material of *Caligorgia laevis.* Dr. Manfred Grasshoff of the Naturmuseum Senckenberg (Frankfurt) generously shared his broad knowledge of gorgonacean taxonomy during the preparation of this manuscript and provided many helpful criticisms. The numerous scanning electron micrographs that vastly enhance the value of this paper were made by Mr. Walter R. Brown, head of the SEM Laboratory, National Museum of Natural History. Plates illustrating the sclerites were assembled and mounted by Ms. Molly Ryan, staff illustrator, Department of Invertebrate Zoology, National Museum of Natural History. I here express my sincere thanks to all those who contributed their time and skills toward the preparation of this report.

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Appendix

Convexella magelhaenica (Studer)

Material examined (listed in sequence of USNM catalogue numbers).

58441: Strait of Le Maire: 54°56′S, 65°03′W, 229–265 m, *Eltanin* sta. 969, 10 Feb 1964. Two colonies with holdfast, one attached to bivalve shell. (SEM 1629.)

58442: East of Cape Horn: 56°06′S, 66°19′W, 384–494 m, *Eltanin* sta. 740, 18 Sep 1963. One colony. (SEM 389.)

59102: East of Cape Horn: 56°06′S, 66°19′W, 384–494 m, sta. 740, 18 Sep 1963. Four small colonies originally attached to pebbles and shell, now detached. (SEM 1646.)

59288: East of Cape Horn: 56°06′S, 066°19′W, 384–494 m, *Eltanin* sta. 740, 18 Sep 1963. One colony.

77371: Tierra del Fuego, east northeast of Cabo San Diego: 54°04′S, 63°35′W, 247–293 m, *Eltanin* sta. 369, 12 Dec 1962. 25 colonies, more or less damaged, and 3 denuded axes.

77394: East edge of Burdwood Bank: 54°43′S, 55°30′W, 1647–2044 m, *Eltanin* sta. 1592, 14 Mar 1966. 16 colonies, 8 attached to stones, 5 with part of holdfast, 3 lacking holdfast. (SEM 1652, 1653, 1924.)

78399: Tierra del Fuego, off north entrance to Strait of Le Maire: 54°29′S, 64°00′W, 104 m, R/V *Hero* sta. 863, 22 Oct 1971. Five colonies, one badly damaged.

78403: Tierra del Fuego, east northeast of Cabo San Diego: 54°22′S, 64°42′W, 106–110 m, *Eltanin* sta. 217, 23 Sep 1962. Five colonies lacking holdfast.

78656: Tierra del Fuego, north of Isla de los Estados: 54°50′S, 63°59′W, 0205–0208 m, R/V *Hero* sta. 880, 28 Oct 1971. One colony lacking holdfast.

78657: Tierra del Fuego, north of Isla de los Estados: 54°34′S, 64°40′W, 84–85 m, R/V *Hero* sta. 903, 6 Nov 1971. One colony lacking holdfast.

78661: Chile, west of Isla Desolacion, Magellanes: 52°52′S, 75°18′W, 119–329 m, *Eltanin* sta. 288 Cruise 21*, 6 Dec 1965. Four colonies lacking holdfast, and three fragments.

82847: Between Tierra del Fuego and Falkland Islands: 52°45′S, 66°34′W, 92 m, *Eltanin* sta. 337, 2 Dec 1962. Two damaged colonies.

82856: Chile, west of Isla Desolacion, Magellanes: 53°13′S, 75°41′W, 1500–1666 m, *Eltanin* sta. 283 Cruise 21*, 5 Dec 1965. Three colonies, two somewhat damaged. (SEM 1643, 1923.)

82865: Tierra del Fuego, south of Isla de los Estados: 54°55′S, 64°00′W, 0771–0903 m, R/V *Hero* sta. 875, 27 Oct 1971. Three colonies, smallest with holdfast, and three denuded axes attached to shells. (SEM 1651.)

82866: Tierra del Fuego, off Isla de los Estados: 54°46.9′S, 64°04′W, depth not recorded, R/V *Hero* sta. 881, 29 Oct 1971. Two damaged colonies.

82867: Tierra del Fuego, north of Isla de los Estados: 54°34′S, 64°30′W, 73–75 m, R/V *Hero* sta. 907, 7 Nov 1971. Two incomplete colonies.

85288: Sars Seamount, Drake Passage: 59°49′S, 68°52′W, 512–622 m, *Eltanin* sta. 254, 10 Oct 1962. One colony lacking holdfast, and pieces of denuded axis (SEM 1647).

85290: South of Falkland Islands, vicinity of Beauchene Is.: 53°08′S, 59°23′W, 567–578 m, *Eltanin* sta. 340, 3 Dec 1962. Two colonies, one attached to pebble.

85298: Strait of Le Maire: 54°59′S, 64°53′W, 641–586 m, *Eltanin* sta. 970, 11 Feb 1964. Four small colonies, somewhat damaged. (SEM 1648–1650.)

85300: Tierra del Fuego, north of Cabo San Diego: 53°32′S, 64°57′W, 124–119 m, *Eltanin* sta. 974, 12 Feb 1964. 22 more or less damaged colonies. (SEM 1926–1929.)

85302: East edge of Burdwood Bank: 54°43′S, 55°30′W, 1647–2044 m, *Eltanin* sta. 1592, 14 Mar 1966. Two small colonies, attached to stones with alcyoniids. (SEM 1652.)

85306: Tierra del Fuego, off Cabo San Sebastian: 53°06′S, 67°04′W, 86 m, R/V *Hero* sta. 450, 5 Mar 1970. Nine colonies, one attached to stone, one to pebble, others lacking holdfast. (SEM 1644, 1645, 1658–1660, 1921.)

85308: Tierra del Fuego, off north entrance to Strait of Le Maire: 54°34′S, 64°10′W, 73 m, R/V *Hero* sta. 856, 20 Oct 1971. Five colonies, 2 with holdfast.

85312: Tierra del Fuego, south of Isla de los Estados: 54°55.6′S, 64°21.8′W, 303–358 m, R/V *Hero* sta. 893, 2 Nov 1971. Two colonies lacking holdfast.

88359: Tierra del Fuego, east of Cabo San Sebastian: 53°15′S, 66°51′W, 79–80 m, *Eltanin* sta. 222, 27 Sep 1962. One colony lacking holdfast.

88362: South of Falkland Islands, vicinity of Beauchene Is.: 53°05′S, 59°31′W, 512–586 m, *Eltanin* sta. 339, 3 Dec 1962. Five colonies, three attached to pebbles.

88747: East of Cape Horn: 56°06′S, 66°19′W, 384–494 m, *Eltanin* sta. 740, 18 Sep 1963. Two colonies, one lacking holdfast, one attached to pebble.

88756: Tierra del Fuego, off north entrance to Strait

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* Eltanin station numbers 181–297 (Cruise 5, 1962) were duplicated in Cruise 21 (1965).

of Le Maire: 54°34′S, 64°20′W, 91 m, R/V *Hero* sta. 853, 20 Oct 1971. One colony lacking holdfast.

88757: Tierra del Fuego, off north entrance to Strait of Le Maire: 54°29′S, 64°10′W, depth not recorded, R/V *Hero* sta. 855, 20 Oct 1971. One colony.

88758: Tierra del Fuego, off north entrance to Strait of Le Maire: 54°33′S, 64°00′W, 84 m, R/V *Hero* sta. 870, 24 Oct 1971. Two colonies lacking holdfast.

88759: Tierra del Fuego, north of Isla de los Estados: 54°39′S, 63°50′W, 135–137 m, R/V *Hero* sta. 874, 26 Oct 1971. Three colonies, two lacking holdfast.

88760: Tierra del Fuego, off north entrance to Strait of Le Maire: 54°29′S, 63°50′W, 112 m, R/V *Hero* sta. 876, 27 Oct 1971. One colony lacking holdfast.

88763: Tierra del Fuego, Strait of Le Maire: 54°59.9′S, 64°50′W, 438–548 m, R/V *Hero* sta. 895, 3 Nov 1971. One colony lacking holdfast.

89344: Between Tierra del Fuego and Falkland Islands: 52°35′S, 65°08′W, 128 m, *Eltanin* sta. 976, 13 Feb 1964. Forty more or less complete colonies lacking holdfast. (SEM 1930–1934.)

89345: Between Tierra del Fuego and Falkland Islands: 52°35′S, 65°08′W, 128 m, *Eltanin* sta. 976, 13 Feb 1964. About 40 more or less completely denuded pieces of axis.

The 123rd Annual Meeting of the Biological Society of Washington will be held on Tuesday, 7 May, 1996, at 12:00 noon in the Waldo Schmitt Room, National Museum of Natural History, Washington, D.C.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Applications published in the *Bulletin of Zoological Nomenclature*

The following Applications were published on 28 September 1995 in Vol. 52, Part 3 of the *Bulletin of Zoological Nomenclature.* Comment or advice on any of these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary (I.C.Z.N.), % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Case No.

2947 *Patella longicosta* Lamarck, 1819 (Mollusca, Gastropoda): proposed conservation of the specific name.

2909 *Glomeris* Latreille, 1802 (Diplopoda): proposed conservation; *Armadillo vulgaris* Latreille, 1804 (Crustacea, Isopoda): proposed conservation of the specific name; and *Armadillo* Latreille, 1802 (Crustacea, Isopoda): application for a ruiing on its status.

2894 *Monstrilla* Dana, 1849 and *Thaumaleus* Krøyer, 1849 (Crustacea, Copepoda): proposed conservation.

2967 *Chaetodacus latifrons* Hendel, 1915 (currently *Bactrocera latifrons*; Insecta, Diptera): proposed precedence of the specific name over that of *Dacus parvulus* Hendel, 1912.

2933 *Eudistoma* Caullery, 1909 (Tunicata): proposed precedence over *Paessleria* Michaelsen, 1907.

2966 *Cyclodomorphus praealtus* (Reptilia, Squamata): a proposal that availability of the specific name be taken from the intended description by Shea, 1995.

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 28 September 1995 in Vol. 52, Part 3 of the *Bulletin of Zoological Nomenclature.* Copies of these Opinions can be obtained free of charge from the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Opinion No.

1815. *Chromadora* Bastian, 1865 and *Euchromadora* de Man, 1886 (Nematoda): conserved by the designation of *C. nudicapitata* Bastian, 1865 as the type species of *Chromadora.*

1816. *Lithobius piceus* L. Koch, 1862 (Chilopoda): specific name conserved.

1817. *Clavella* Oken, 1815 and *Pennella* Oken, 1815 (Crustacea, Copepoda): conserved, and *Pennella diodontis* Oken, 1815: specific name conserved.

1818. *Rhopalosiphum monardae* Davis, 1911 (currently *Hyalomyzus monardae*; Insecta, Homoptera): specific name conserved.

1819. *Bhatia* Distant, 1908 (Insecta, Homoptera): *Eutettix olivaceus* Melichar, 1903 confirmed as the type species.

1820. A.A.H. Lichtenstein's (1796, 1797) *Catalogus musei zoologici . . . Sectio Tertia Continens Insecta* and D.H. Schneider's (1800) *Verzeichniss einer Parthei Insekten . . .* : suppressed, with conservation of some Lichtenstein (1796) names (Insecta and Arachnida).

1821. *Cliola (Hybopsis) topeka* Gilbert, 1884 (currently *Notropis topeka*; Osteichthyes, Cypriniformes): specific name conserved.

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CONTENTS

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Three new species of precious coral (Anthozoa: Gorgonacea, genus *Corallium*) from Pacific waters

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Abstract.—Two new species of *Corallium* from New Caledonia with the consolidated axial skeleton having smooth pits with beaded margins accommodating the autozooids are described, *Corallium thrinax* with double-club sclerites, *C. nix* without. A third new species, *C. kishinouyei,* lacking smooth, well-defined axial pits and lacking double-club sclerites, is described from Cross Sea Mount south of Hawaii. Preliminary observations of axis formation are reported.

Program BIOCAL conducted in 1985 by ORSTOM aboard R/V *Jean Charcot* in the vicinity of New Caledonia obtained two species of the genus *Corallium* that cannot be assigned to any species heretofore described. Investigations of seamounts south of the Hawaiian Islands in 1993 by the Woods Hole Oceanographic Institution using the research submersible *Pisces V* obtained another undescribed species. These are now placed on record.

Suborder Scleraxonia Studer, 1887
Family Coralliidae Lamouroux, 1812
Genus *Corallium* Cuvier, 1798

Synonymy.—See Bayer, 1956:70; 1964: 466.

Type species.—*Madrepora rubra* Linnaeus, by subsequent monotypy, Lamarck, 1801.

Diagnosis.—Dimorphic Gorgonacea with continuous, solid, calcareous supporting axis without hollow core. Coenenchymal sclerites including 6-, 7-, and 8-radiate capstans sometimes asymmetrically modified as "opera-glass forms" or "double clubs," spindles, rods, and crosses.

Remarks.—Following the conclusion by Lacaze-Duthiers (1864) that the calcareous skeleton of *Corallium rubrum* is composed of sclerites cemented inseparably to form a continuous, unsegmented axis, the genus *Corallium* has been classified in the suborder Scleraxonia, in which the supporting axis unquestionably is composed of more or less completely fused sclerites as is the case in such families as the Paragorgiidae, Briareidae, and Melithaeidae. However, thin sections of the axis of *Corallium* examined under the light microscope do not show convincing evidence of spicular structure in spite of the statements to the contrary by various authors up to the present time (Müller 1910, Kükenthal 1924, Hyman 1940, Bayer 1956, Weinberg 1976).

It has now been demonstrated that in *Corallium rubrum* formation of the axis at the apex of branches begins as an agglutination of sclerites that become immersed in "rectilinear" calcite, which later comprises the predominant structural component (Grillo et al. 1993). This finding supports the inclusion of *Corallium* (family Coralliidae) in the gorgonacean suborder Scleraxonia.

However, Lawniczak (1987) concluded that in *C. johnsoni* Gray the axis is composed entirely of fibrocrystalline calcium carbonate, without inclusion of sclerites. As it is illogical to assign species otherwise closely similar in morphological (dimorphic polyps) and skeletal (sclerites of virtually identical size and form) characters to different orders (and, necessarily, different families) on the basis of a percieved difference in skeleton formation observed in a limited sample of a rare and poorly known species, the family Coralliidae is retained in the Scleraxonia pending a wider investigation of axis formation in as many species of *Corallium* as can be obtained for study.

The description of *Corallium thrinax,* new species, was originally composed in French by Jeffrey Stefani, translated into English and edited by F. M. Bayer, so the species correctly bears joint authorship. The descriptions of *C. nix* and *C. kishinouyei* were prepared solely by the present author.

Corallium thrinax Bayer & Stefani, new species
Figs. 1–6

Material examined.—New Caledonia, 23°06.50′S, 167°53.74′E, BIOCAL 1985, R/V *Jean Charcot* station DW-50, 240 m, 31-VIII-85. Sixteen colonies with holdfast, and some fragments: Holotype and 16 paratypes (NMNH Paris); 8 paratypes, USNM 96511 (SEM 1328–1331, 2416, 2466).

Diagnosis.—*Corallium* branched dichotomously and laterally with tendency to remain in one plane, small, usually with no more than three or four bifurcations and a few short lateral twigs; autozooids forming low verrucae concentrated on one side of the branches; axis with distinct pits bordered by prominent beaded rim located beneath autozooids. Predominant sclerites are 6-radiate capstans and double clubs ("opera glasses") with smooth, globose heads. Colonies white, sclerites colorless.

Description.—The colonies are small, sparingly branched dichotomously, often with a few short lateral twigs (Fig. 1). They range from 3.7 to 6 cm in height, and between 3 and 6 cm in width. The holdfast is a narrow basal expansion of the trunk. For the most part branching is in one plane, but in some colonies a branch may stand at nearly 90° from the plane of the principal fan. There are no anastomoses. In most cases there is a short main trunk, oval in cross section, about 0.6 cm × 1.2 cm in diameter, which bifuractes to produce principal branches approximately round in section, which in turn bifurcate as many as two or three times; a few short, blunt lateral twigs sometimes arise from one or more of the internodes between bifurcations. In some cases, principal branches 2–4 mm in diameter arise directly from the holdfast.

The surface of the axis is longitudinally grooved (Fig. 2) and covered with minute tubercles ornamented with thorny projections (Fig. 3 bottom). At the position of each autozooid, the axis has a distinct rounded pit 0.75 mm wide and 1.05 mm long (Fig. 3 top) bordered by a beaded rim that in some cases is interrupted by a narrow gap for passage of a coelenteric canal (Fig. 2 bottom).

Examination of the apex of the axis of a twig tip by SEM shows tubercles some resembling axial processes, others resembling the tubercles of sclerites (Fig. 4). Clearly recognizable sclerites partially embedded in axial calcite were not found on the single sample examined. This might be expected if that twig tip had ceased upward growth at time of collection. Owing to the destructive nature of such preparations, no further samples have been made for the present purposes of taxonomic description.

Autozooids form low, inconspicuous verrucae distributed predominantly on one face (the "front") of the colony, with only an occasional stray on the back surface (Fig. 1). They are indistinct unless artificially stained with crystal violet. The tentacles are retracted flush with the coenenchyme, their bases forming an 8-lobed margin of the verrucal orifice. The autozooids are seated in distinct, rounded axial pits with a beaded rim (Figs. 2, 3). Siphonozooids are scarce and distributed randomly in the coenenchyme, so inconspicuous that they can be distinguished only by staining with crystal violet.

Fig. 1. *Corallium thrinax,* new species. a, Holotype colony; b, part of colony with zoanthid symbionts; c, Colony with autozooids stained with crystal violet, front surface; d, Colony with autozooids stained with crystal violet, back surface; paratype colony USNM 96511.

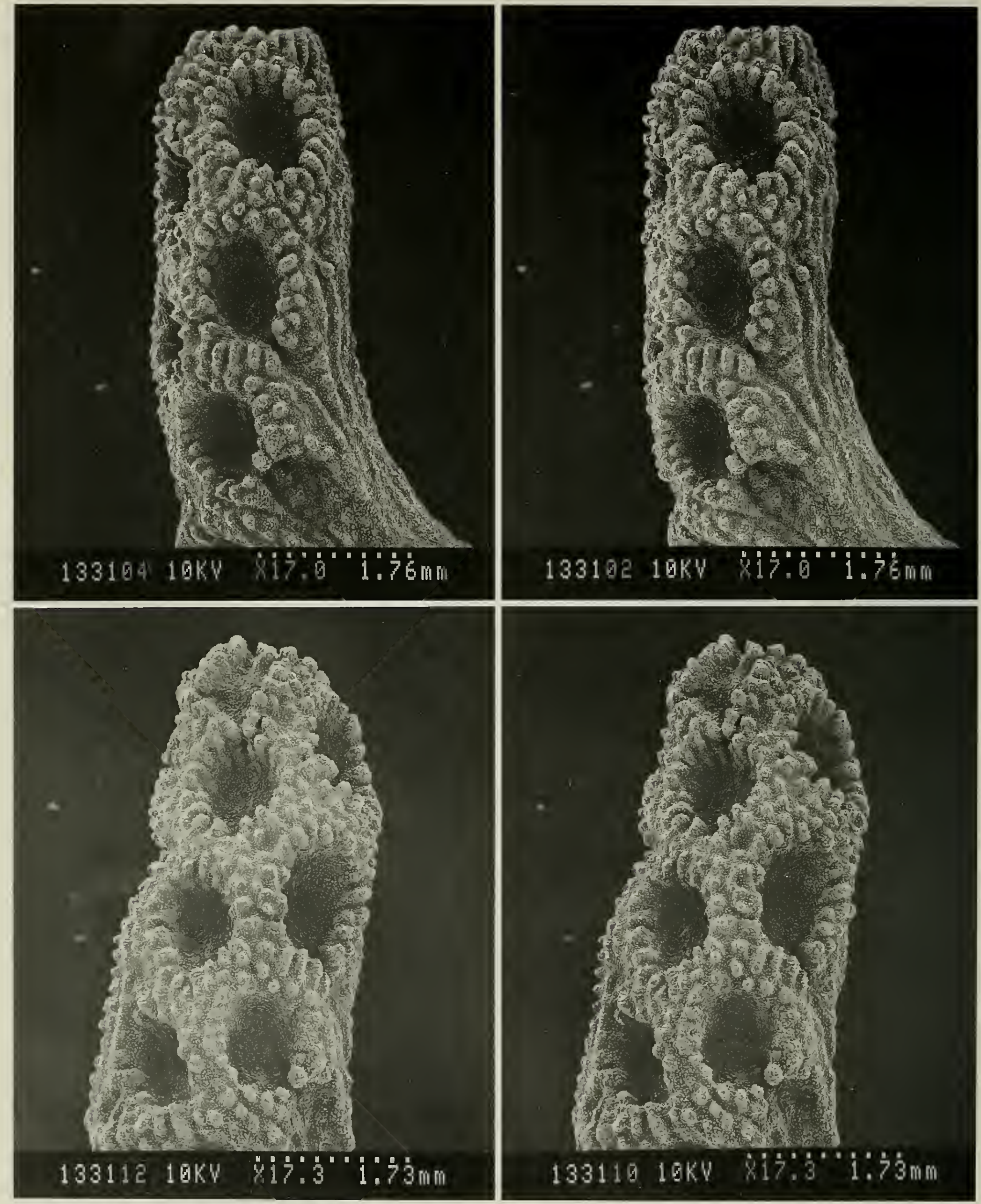

Fig. 2. *Corallium thrinax,* new species. Apex of axis in front and lateral views SEM 1331, stereo pairs.

The coenenchyme is so thin that the axial sculpture is exposed in areas subject to abrasion (Fig. 6 top). The longitudinal axial striations are clearly indicated through the coenenchyme, most clearly toward branch tips where the autozooids are closer together.

Sclerites (Fig. 5) of the coenenchyme include numerous 6-radiates up to 0.04 mm in length, many of which are modified as

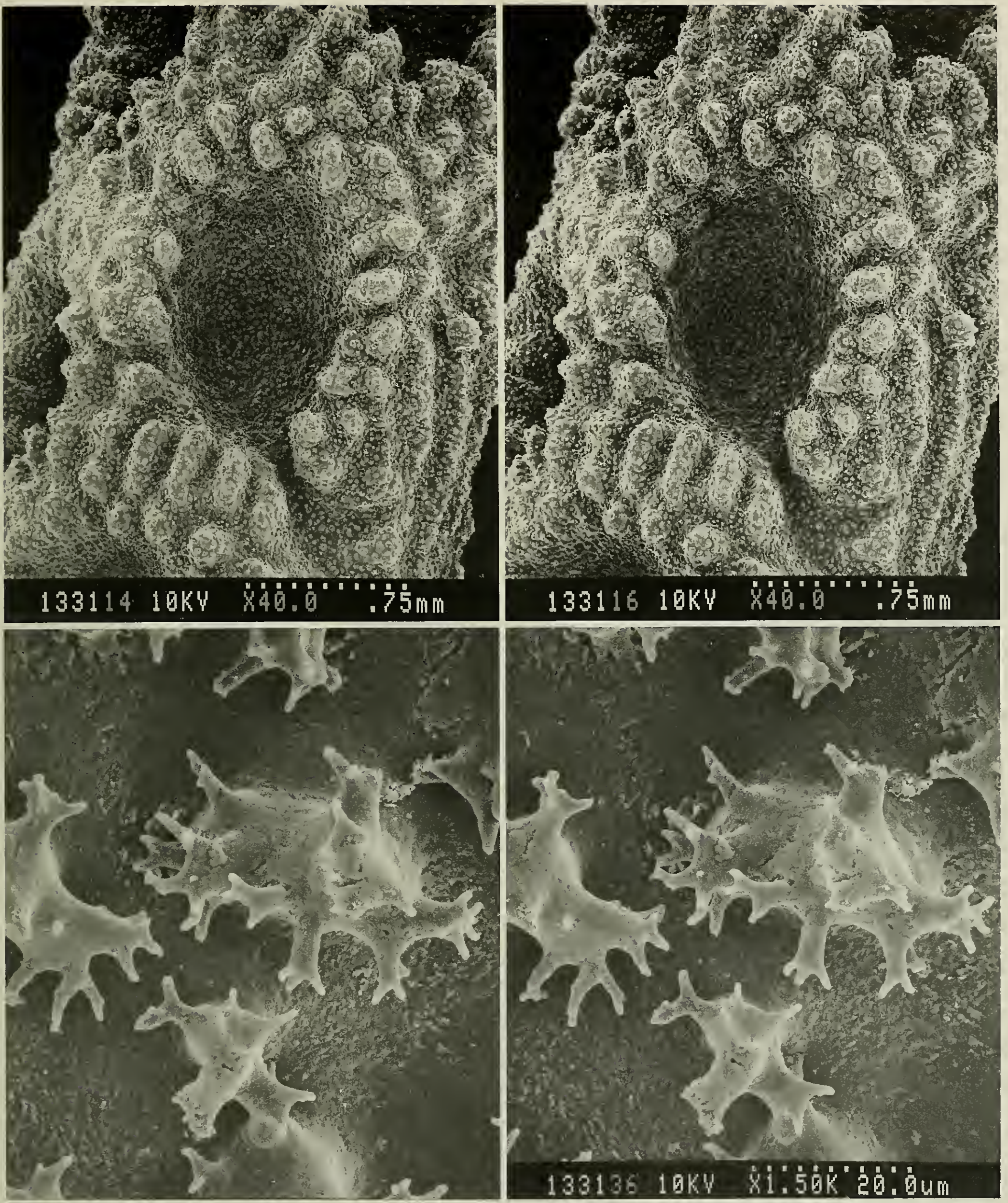

Fig. 3. *Corallium thrinax,* new species. Top, Axial pit at location of autozooid; Bottom, Axial protuberances. SEM 1331, stereo pairs.

globose double clubs by asymmetrical hypertrophy of two of the rays to form a pair of smooth, spheroidal processes. At the surface of the coenenchyme these lie crowded, with the spheroidal processes directed outward (Fig. 6 bottom). Sclerites intermediate between double clubs and 6-radiates with the hypertrophied rays more or less strongly modified are not uncommon. Irregular forms occur but are extremely rare. No crosses or 8-radiates were observed, and only a single small 7-radiate was found in

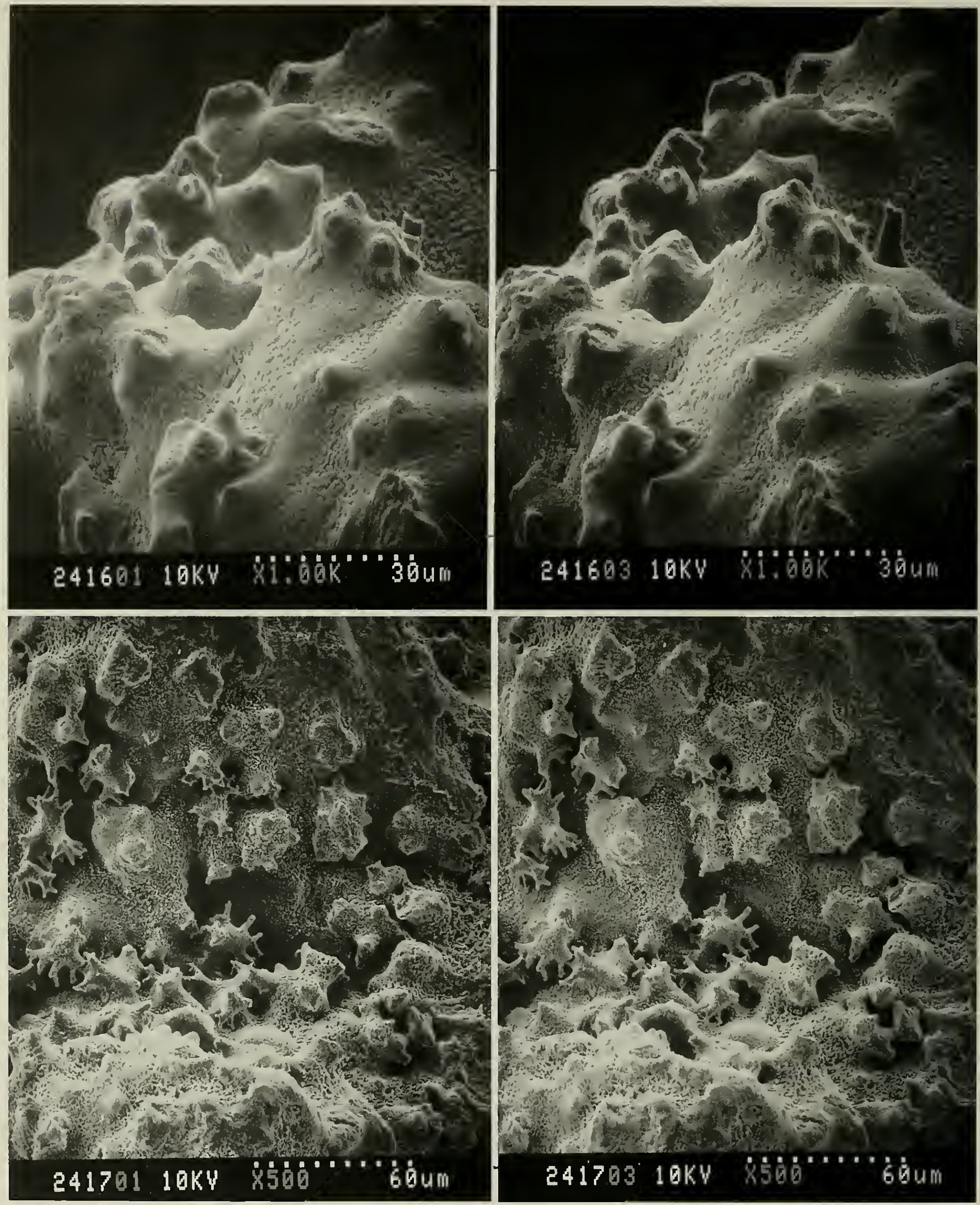

Fig. 4. *Corallium thrinax,* new species. Top, Apex of axis showing axial protuberances and tubercles similar to those of sclerites. SEM 2416, stereo pair; Bottom, Surface of axis near apex showing axial protuberances and tubercles similar to those of sclerites. SEM 2417, stereo pair.

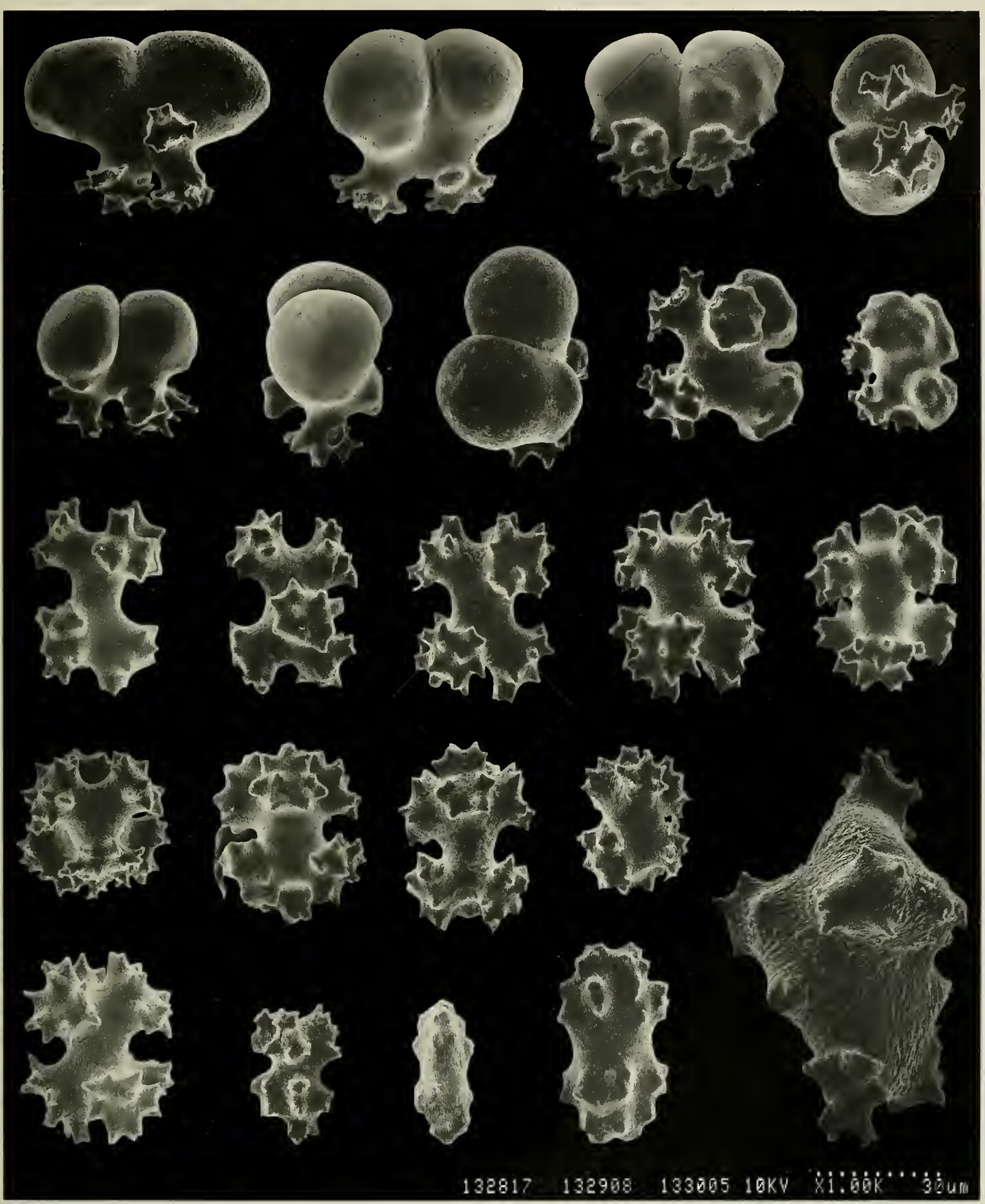

Fig. 5. *Corallium thrinax,* new species. Sclerites. SEM 1328–1330.

3 preparations for SEM. Small rods and 6-radiates are present in the tentacles, the distal ones decreasing in size to about 0.03 mm.

Colonies preserved in ethanol are white; the axis is white and the sclerites are colorless.

Comparisons.—The colonial form of *Corallium thrinax* is immediately distinguished from that of any other species of

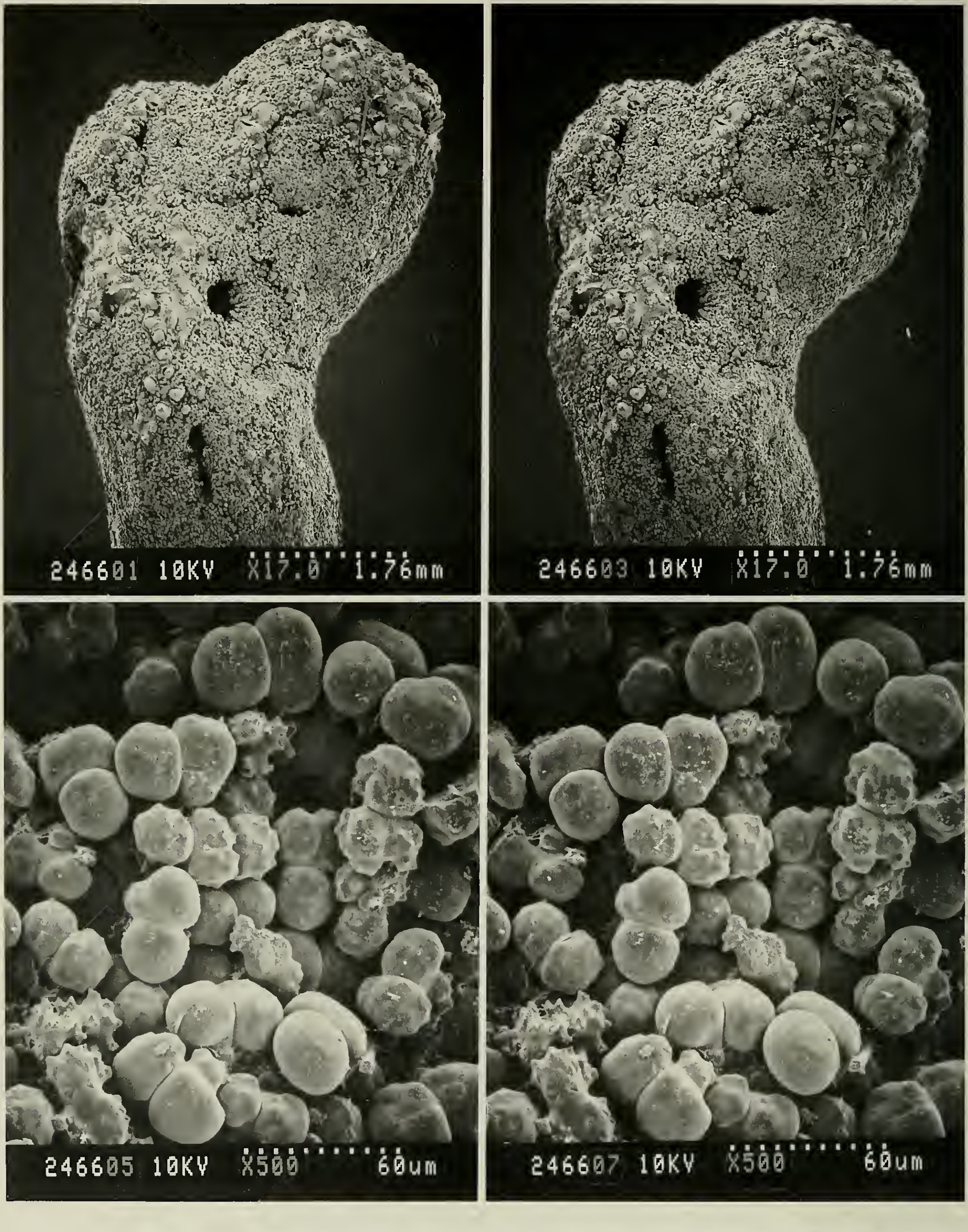

Fig. 6. *Corallium thrinax,* new species. Top, Tip of terminal twig; Bottom, Surface of coenenchyme showing predominance of double-club forms. SEM 2466, stero pairs.

Corallium known heretofore. Other nominal species having autozooids seated in axial pits with beaded rims are: *C. stylasteroides* Ridley, 1882, from Mauritius; *C. salomonense* Thomson & Mackinnon, 1910, from Salomon in the Indian Ocean; and *C. tortuosum* Bayer, 1956, from Hawaii, which was reduced, perhaps prematurely, to a subspecies of *salomonense* (Bayer, 1993); *C. inutile* Kishinouye, 1903, from Japan; and *C. nix* new species, described herein.

The axis of *Corallium japonicum* Kishinouye also is marked by small pits beneath the autozooids (Kishinouye 1905:22), as is that of *C. elatius* Ridley (Kishinouye, 1905: 24) and *C. rubrum* (Linnaeus) (Grillo, Goldberg & Allemand, 1993:121, fig. 1c), but in those species (and probably others as well) the pits are not bordered by a distinct, beaded margin. Among those with beaded pits, *C. stylasteroides, C. salomonense* and *C. tortuosum* lack double clubs among the sclerites. *C. inutile* has double clubs of somewhat different outline and only 6-radiates but no 7- and 8-radiates, and differs further in its colonial form, pale pink axis and reddish cortex. *C. borneense,* which is salmon pink with red calices and quite differently branched, has double clubs of similar size and shape, but its autozooids form distinctly hemispherical verrucae and are not seated in rimmed pits in the axial skeleton.

Etymology.—*thrinax* from Greek θριναξ, a three-pronged fork, in allusion to the forked braching of the colonies. Noun in apposition.

Symbionts.—A few of the specimens are host to a balanoid barnacle that is partially overgrown by coral skeleton, and the branch tips of a few are overgrown with what appears to be a fasciculate hydroid. Near the base of some colonies there are symbiotic zoanthideans (Fig. 1b), but these are not invariably present as seems to be the case in both *C inutile* and *C. tortuosum.*

Corallium nix, new species
Figs. 7–10

Material examined.—New Caledonia, 23°06.50′S, 167°53.74′E, BIOCAL 1985, R/V *Jean Charcot* station DW-50, 240 m, 31-VIII-85. One branch apparently part of a larger colony, holotype, Muséum National d'Histoire Naturelle, Paris.

Diagnosis.—*Corallium* irregularly branched; autozooids on all sides of the branches, seated in distinct pits in the axis, bordered by prominent beaded rim. Predominant sclerites are short 8-radiate capstans and 6- and 7-radiates some of which are weakly asymmetrical but in the form of double clubs; crosses extremely rare. Colonies white, sclerites colorless.

Description.—As the only specimen appears to be no more than a branch of a larger colony, it is not possible to provide a description of the general aspect of the complete colony. The single branch (Fig. 7) is sinuously curved, thick, approximately round in cross section, and 6.2 mm in greatest diameter at the base. Its shape suggests that branching probably proceeds roughly in one plane, as often is the case in species of *Corallium.* It produces short terminal branchlets mostly from two sides in roughly the plane of curvature, but a few small ones arise from the "front" of the branch.

The surface of the axis is longitudinally grooved (Fig. 8), as usual covered with minute axial protuberances ornamented with thorny projections (Fig. 9). The axis has a distinct rounded pit 0.75 mm wide and 1.05 mm long at the position of each autozooid, bordered by a beaded rim that commonly is interrupted where a coelenteric canal passes through to connect with the gastrovascular cavity of the autozooid (Fig. 8). Owing to the limitations of material available for study, an intact terminal twig was not prepared for examination by SEM to avoid damage to the unique type specimen. As expected, no clearly recognizable sclerites partially embedded in the subapical rectilinear calcite were observed.

Autozooids are distributed on all sides of the branch and terminal branchlets (Fig. 10). They retract flush within the rim of the axial pits, the bases of the infolded tentacles forming an 8-lobed margin of the closed verrucal apertures. Their distribution is most clearly revealed by staining with crystal violet, which stains the structures within the gastric cavities more darkly than the surrounding coenenchyme so that they con-

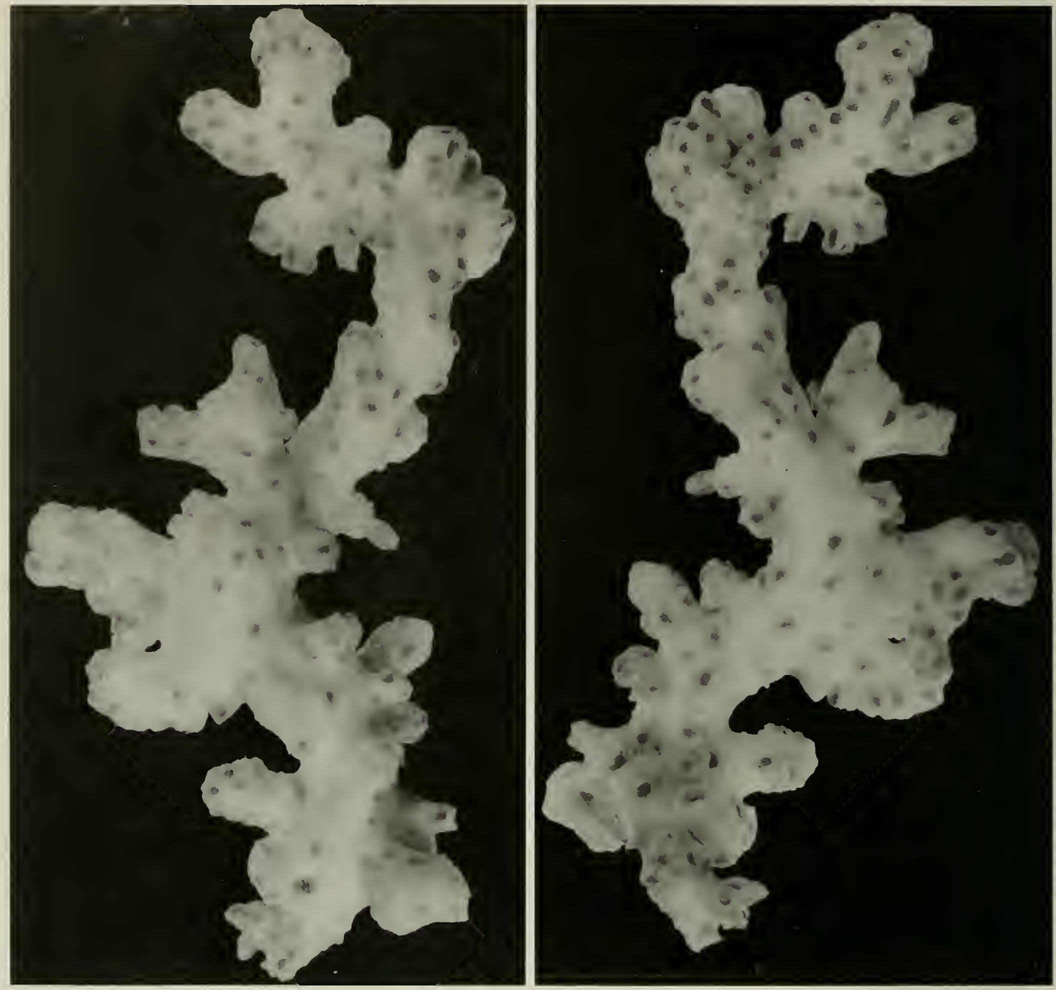

Fig. 7. *Corallium nix*, new species. Holotype branch with autozooids stained with crystal violet showing general distribution on front and back surfaces. Height overall, 5.75 cm.

trast sharply with the paler cortex as the highly soluble stain dissipates (Fig. 7).

The siphonozooids do not form distinct small verrucae and therefore are very difficult to detect, but commonly one is located in the tapered groove extending from the autozooid, and scattered individuals can be seen in the coenenchyme between and around the autozooids.

The coenenchyme is very thin, generally smooth but inconspicuously papillate in areas protected from abrasion, suggesting that elsewhere the minute papillae may either have been rubbed off during collection, or have contracted completely as the result of contact with other objects in the trawl. Inconspicuous sinuous longitudinal grooves indicate the location of the principal coenenchymal canals.

The predominant sclerites (Fig. 10) are short 8-radiate capstans reaching lengths of 0.06–0.07 mm, none of which are elongated as belted spindles, and very short, wide 6- and 7-radiates 0.04–0.06 mm long, which may be weakly asymmetrical but not clearly modified as double clubs ("opera glasses"); the shortest approach the tuberculate spheroid form. Crosses are absent or so

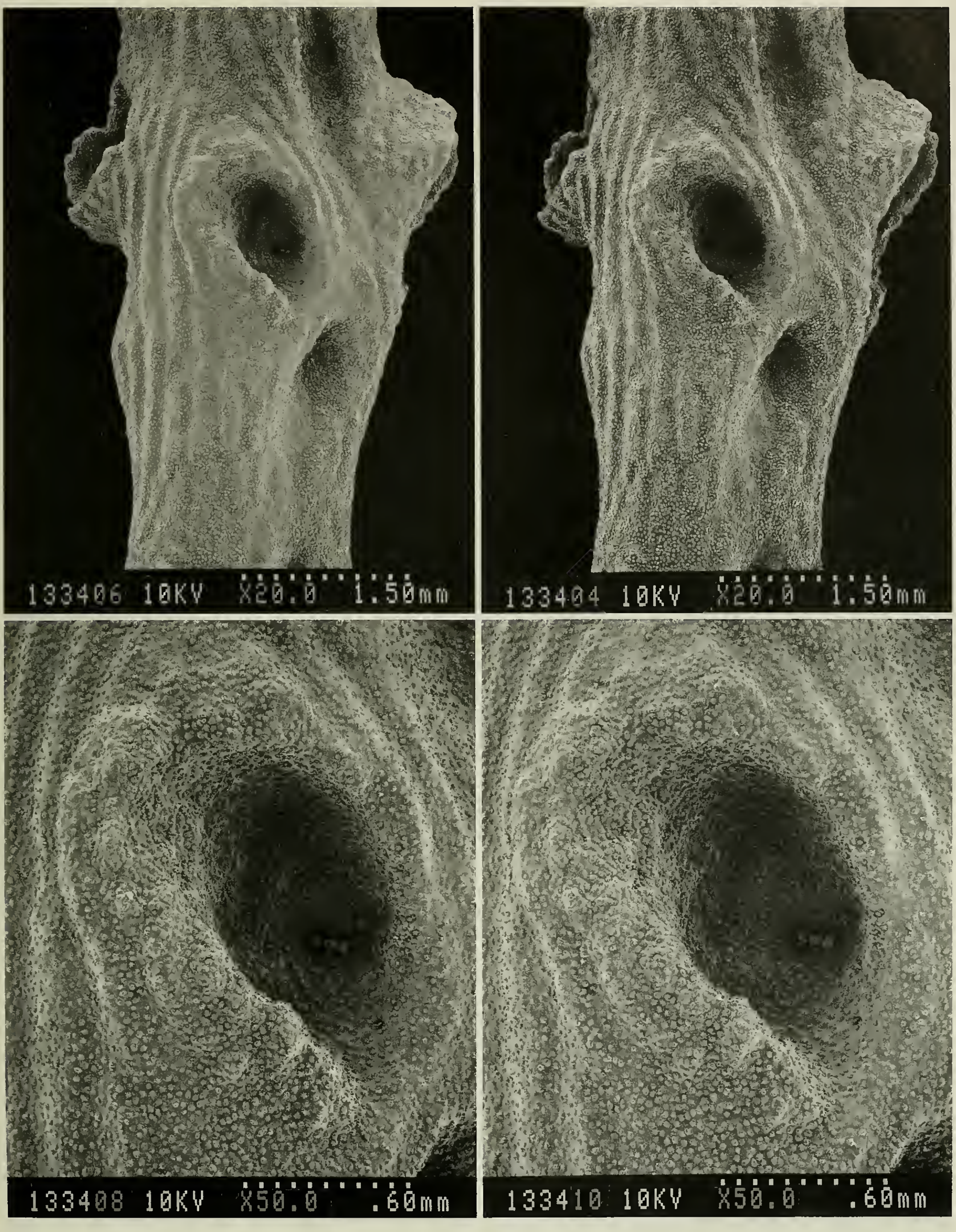

Fig. 8. *Corallium nix,* new species. Top, Part of branch with autozooid pits; Bottom, Detail of autozooid pit. SEM 1334, stereo pairs.

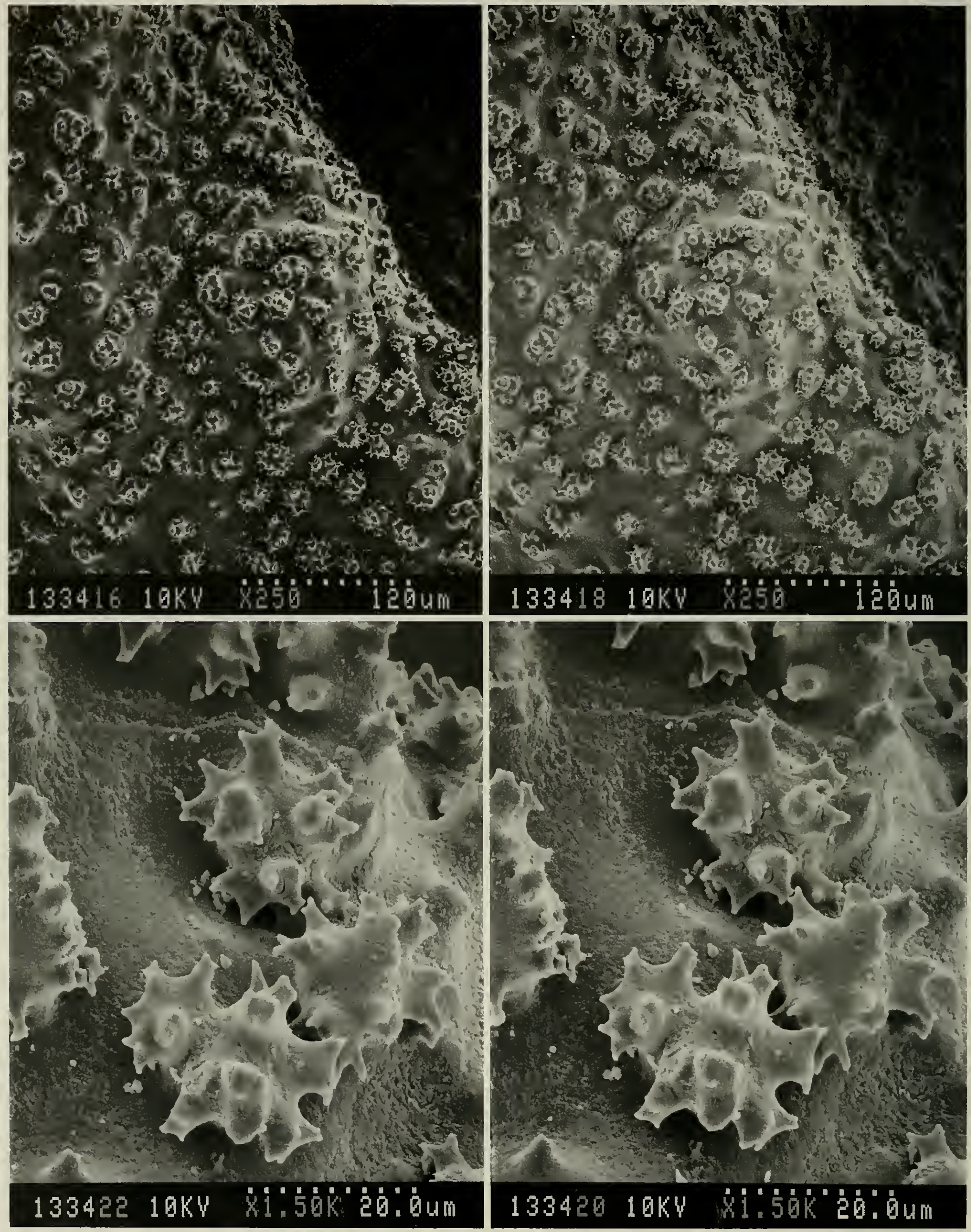

Fig. 9. *Corallium nix,* new species. Top, Surface of axis with axial protuberances; Bottom, Detail of axial protuberances. SEM 1334, stereo pairs.

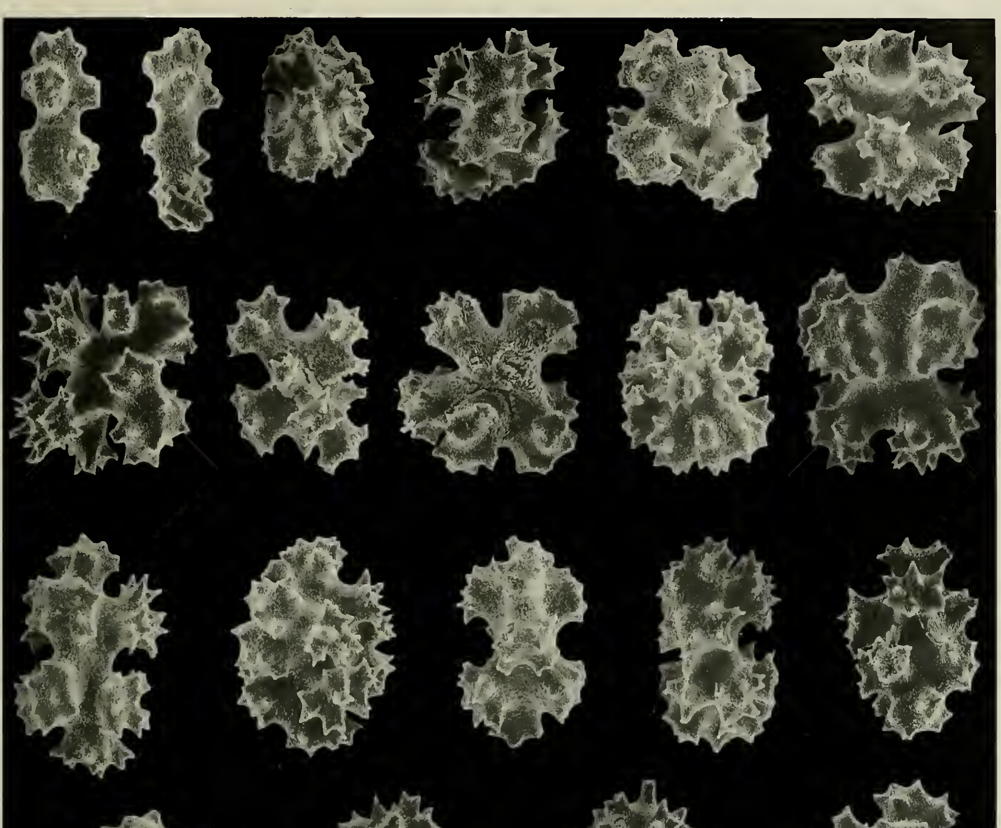

Fig. 10. *Corallium nix,* new species. Sclerites. SEM 1333.

vanishingly rare as to escape notice in preparations made both for SEM and light microscopy. The tentacles contain blunt rods derived from octoradiates, as shown by numerous intermediate forms.

Skeleton and coenenchyme white, sclerites colorless, translucent.

Etymology.—Latin *nix, nivis* f., snow, in allusion to the white corallum. Noun in apposition.

Comparisons.—The distinct axial pits with beaded margins in which the autozooids of *Corallium nix* are recessed are similar to those of *Corallium stylasteroides* Ridley, *C. salomonense* (Thomson & Mackinnon), and *C. thrinax* Bayer & Stefani. However, the sclerites of *C. stylasteroides* are smaller and not so sharply sculptured, and those of *C. salomonense* are both larger and more acutely sculptured. *C. thrinax* differs conspicuously in its small, dichotomously branched uniplanar growth form and its strongly asymmetrical double-club sclerites.

Corallium kishinouyei, new species
Figs. 11–19

Material examined.—Cross Seamount: 18°46.6′N, 158°14.8′W, 1145m. *Pisces V* dive PV235, coll. Scott France and Ewann Agenbroad, station CR105, 18 Aug 1993. Sample 1: One incomplete colony 11.5 cm tall with 2 detached branches, holotype USNM 94462 (SEM 2381, 2382, 2423). Sample 4: One incomplete colony consisting of one branch 12 cm tall and 4 smaller branches from the same colony, the largest 11 cm tall, USNM 94463, paratype (SEM 2285, 2455).

Diagnosis.—*Corallium* sparsely branched, roughly in one plane; autozooids biserial and weakly directed toward one face of the colony, a few on front of branches, not seated in distinct deep pits in the axis; axis longitudinally grooved. Predominant sclerites are short 8-radiate capstans and short, stubby 6- and 7-radiates not modified as double clubs; crosses extremely rare. Colonies white in ethanol, sclerites colorless.

Description.—Colonies sparingly branched in one plane, openly dichotomous or lateral (Fig. 11), the smaller terminal branchlets more or less clavate (Fig. 12). The stoutest main branch is nearly round, 7.2 mm in diameter; the terminal branchlets are about 4 mm in diameter, with a tendency to flattening in the plane of branching. Autozooids are situated biserially and directed slightly toward one face of the colony (the "front"), with occasional individuals also on the front face roughly between bilateral pairs, becoming more generally scattered on the stoutest branches. They retract to form low, moundlike verrucae about 3 mm in diameter and at most 1 mm in height, the orifices with marginal lobes not necessarily as many as 8 but depending upon the degree of contraction. Numerous small, bluntly conical papillae less than 0.5 mm in diameter, each with an apical pore, cover the surface of the coenenchyme around and between the autozooids, are interpreted as siphonozooids but not confirmed by histological examination.

The predominant coenenchymal sclerites (Fig. 13) are 8-radiate capstans from about 0.05 mm up to 0.13 mm in length; 6-radiates are present also, and 7-radiates are uncommon; crosses are present, as are a few irregular forms. The tentacles contain slender, bluntly pointed rods up to about 0.09 mm in length, derived from the predominant 8-radiate form.

The mature axis is longitudinally striated but there are no deep, smooth pits beneath the autozooids. Depressions in the axis accommodating the autozooids are confined to apical regions, where they are irregular and do not have smooth bottoms and prominent beaded margins (Figs. 18, 19 top). As usual, the surface is ornamented with small, thorny protuberances (Fig. 16, bottom) suggesting the sculpture of the sclerites, but these are not indicative of sclerites embedded in the axial calcite. Locally, some of the axial protuberances are very prominent

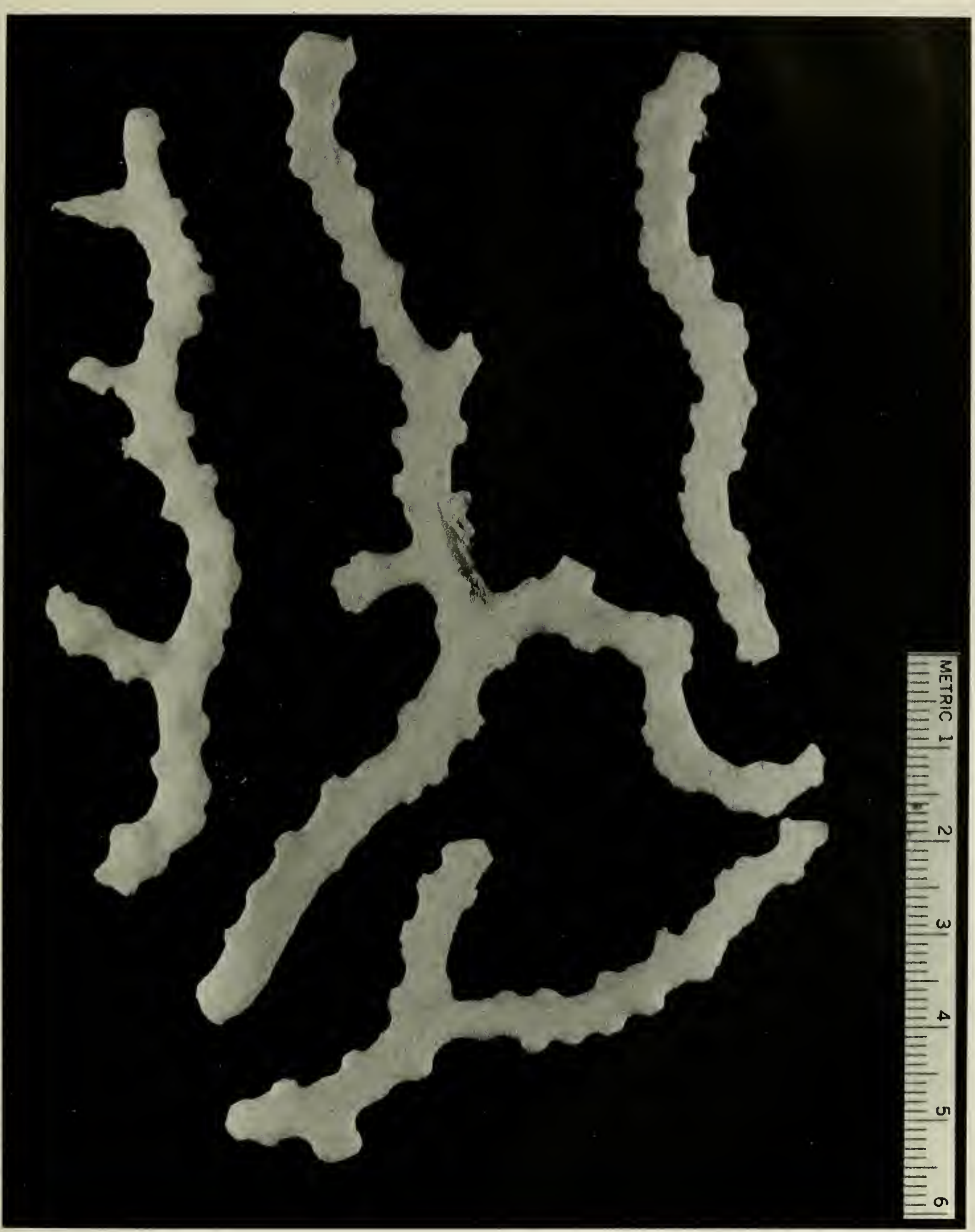

Fig. 11. *Corallium kishinouyei,* new species. Branches of holotype colony.

(Fig. 17, bottom) and resemble certain sclerites of other scleraxonians that do not occur in *Corallium* (e.g., the medullar sclerites of *Paragorgia*).

Owing to the limitations of the specimens available for study, only three apical samples from the axis from terminal twigs were prepared for examination by SEM,

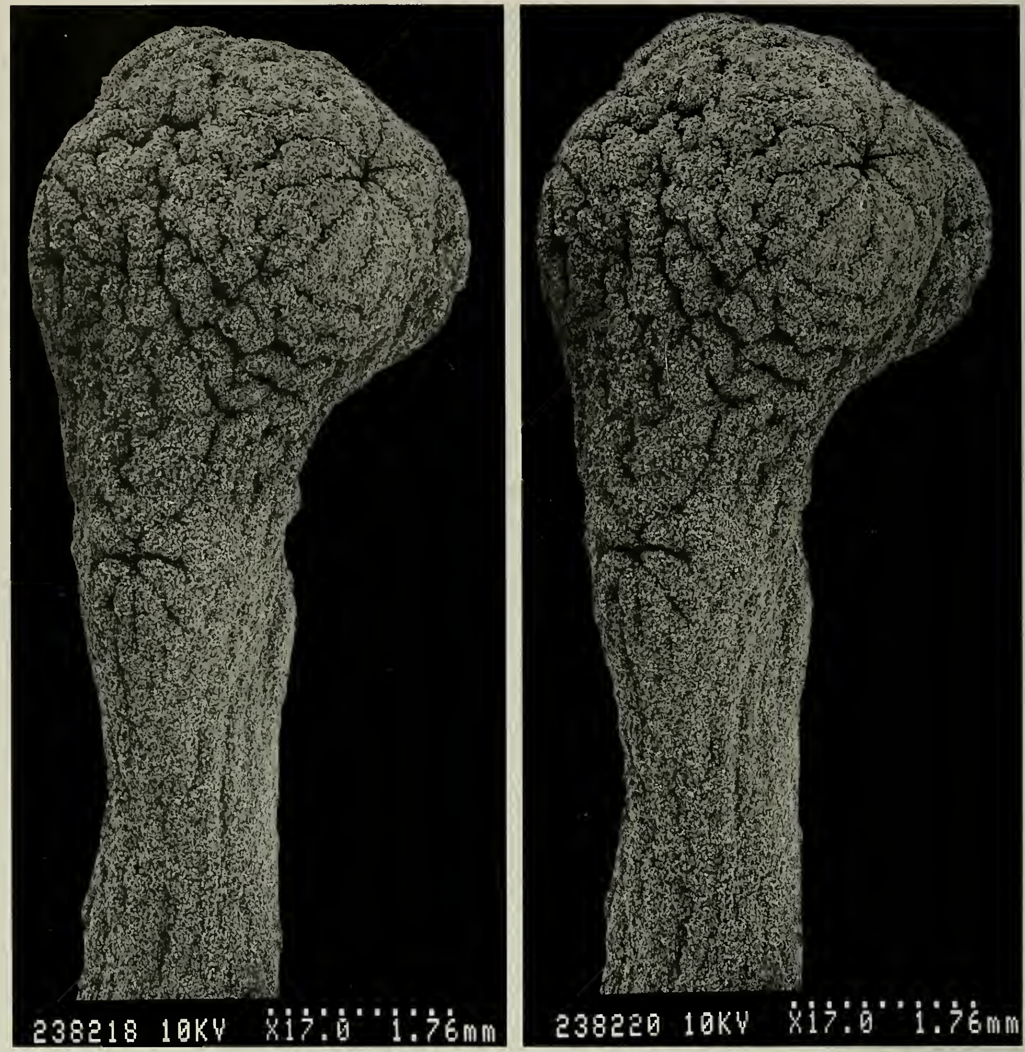

Fig. 12. *Corallium kishinouyei,* new species. Tip of terminal twig with coenenchyme intact. SEM 2382, stereo pair.

one from USNM 94463 (Figs. 18, 19) and two from USNM 94462 (Figs. 14–16). Of the latter, the distal tip of the axis is in one case flattened and blade-like, the two flat faces each with two narrow ridges (Fig. 14, bottom) that probably accommodated the major longitudinal coenenchymal canals; in the other sample it is tapered, bluntly pointed, flattened but without the prominent longitudinal ridges (Fig. 15). The one axis tip examined from USNM 94463 is tapered, bluntly pointed, roughly prismatic, flattened on the "back" side, with irregular longitudinal ridges and intervening rows of irregular pits (Figs. 18, 19 top), the larger of which doubtless were situated beneath autozooids; the smaller pits are too small and too close together to underlie autozooids.

In all cases, the apex of the axis is composed largely of sclerites bound together by intervening non-spicular calcite (Figs. 16 top, 17 top, 19 bottom). This agrees with the conclusion of Grillo et al. (1993:127)

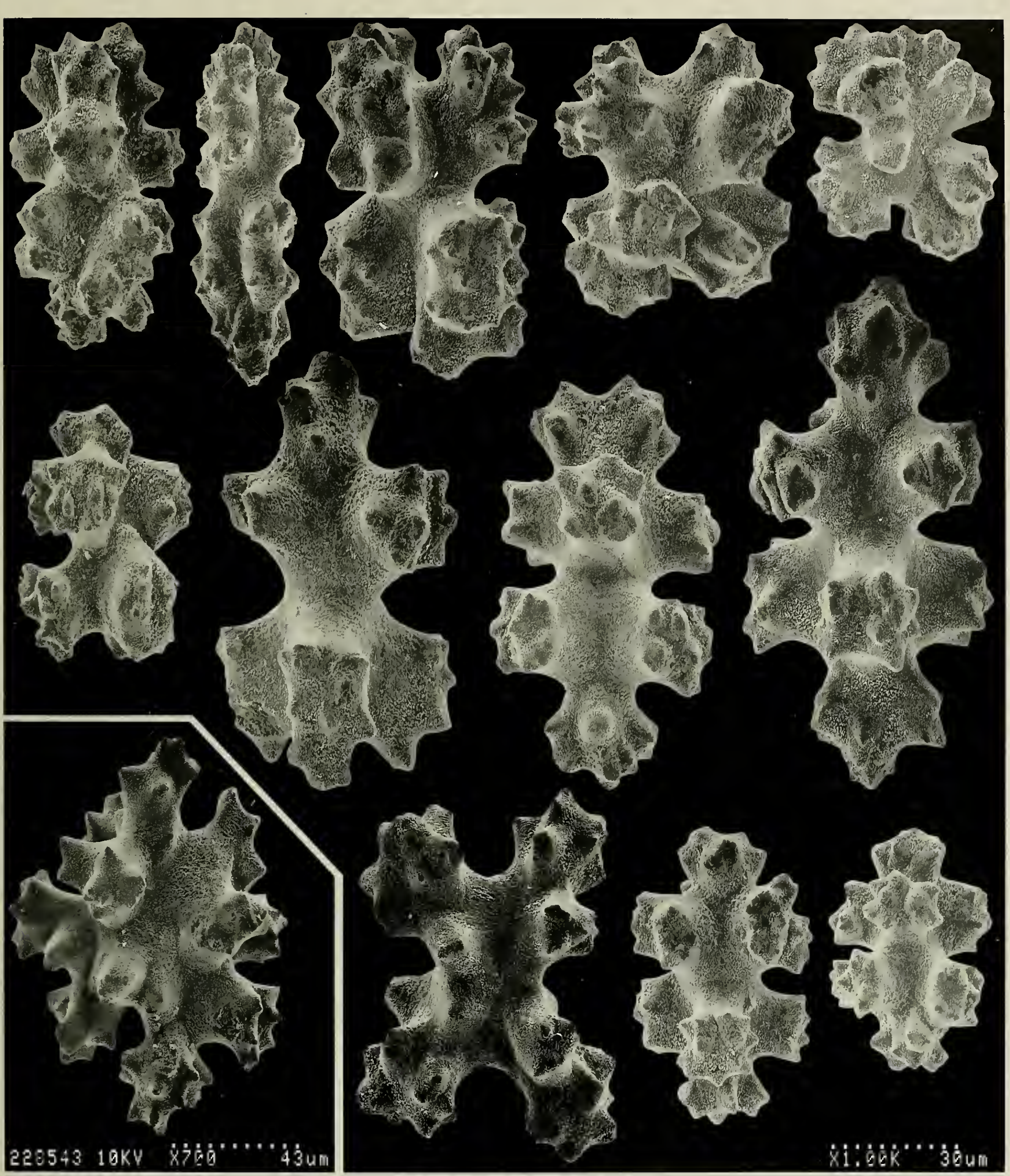

Fig. 13. *Corallium kishinouyei*, new species. Sclerites. SEM 2285.

that in *C. rubrum* "sclerites are incorporated to form the core of the nascent skeleton," subsequently becoming overlain by non-spicular calcite as the girth of the axis increases.

The color of the colonies in ethanol initially was distinctly yellowish white but the yellowish tint soon faded in alcohol; the sclerites are colorless. Those of the larger branches are predominantly opaque white, those of the terminal branches glass-clear, but there is no perceptible difference in

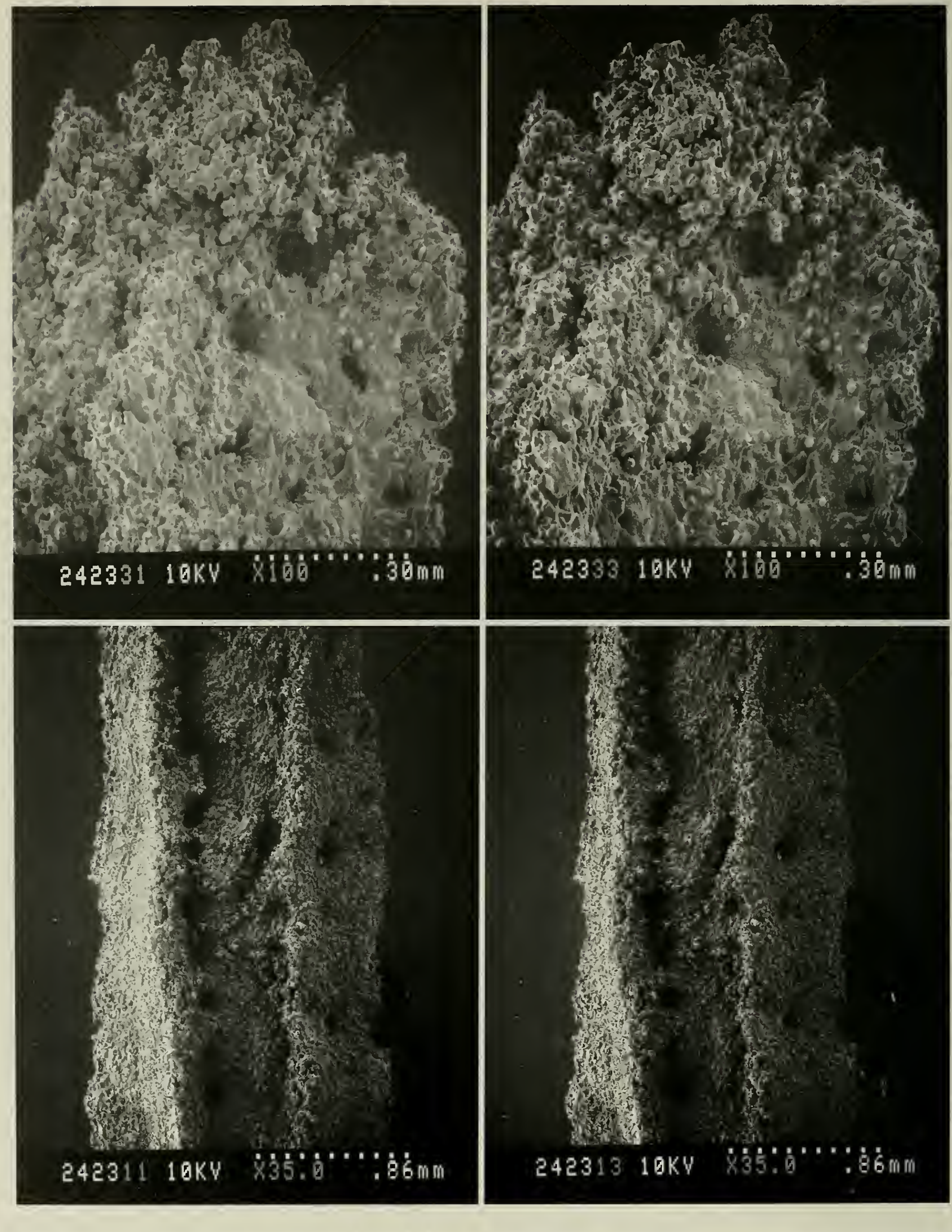

Fig. 14. *Corallium kishinouyei,* new species, axis of USNM 94462, preparation 1. Top, Apex; Bottom, Distal portion just below apex. SEM 2423, stereo pairs.

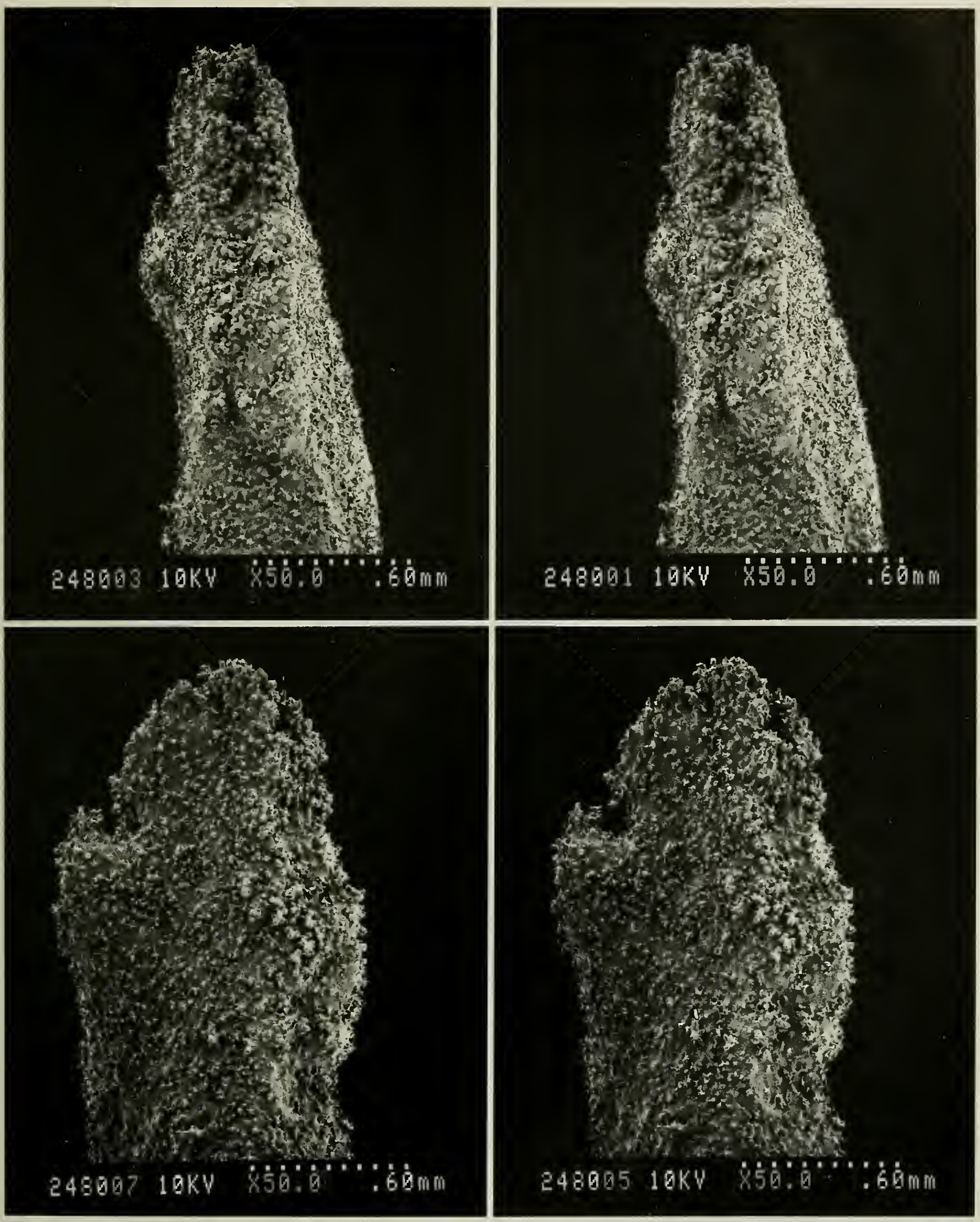

Fig. 15. *Corallium kishinouyei,* new species, axis of USNM 94462, preparation 2. Top, Apex from side; Bottom, Apex from front. SEM 2480, stereo pairs.

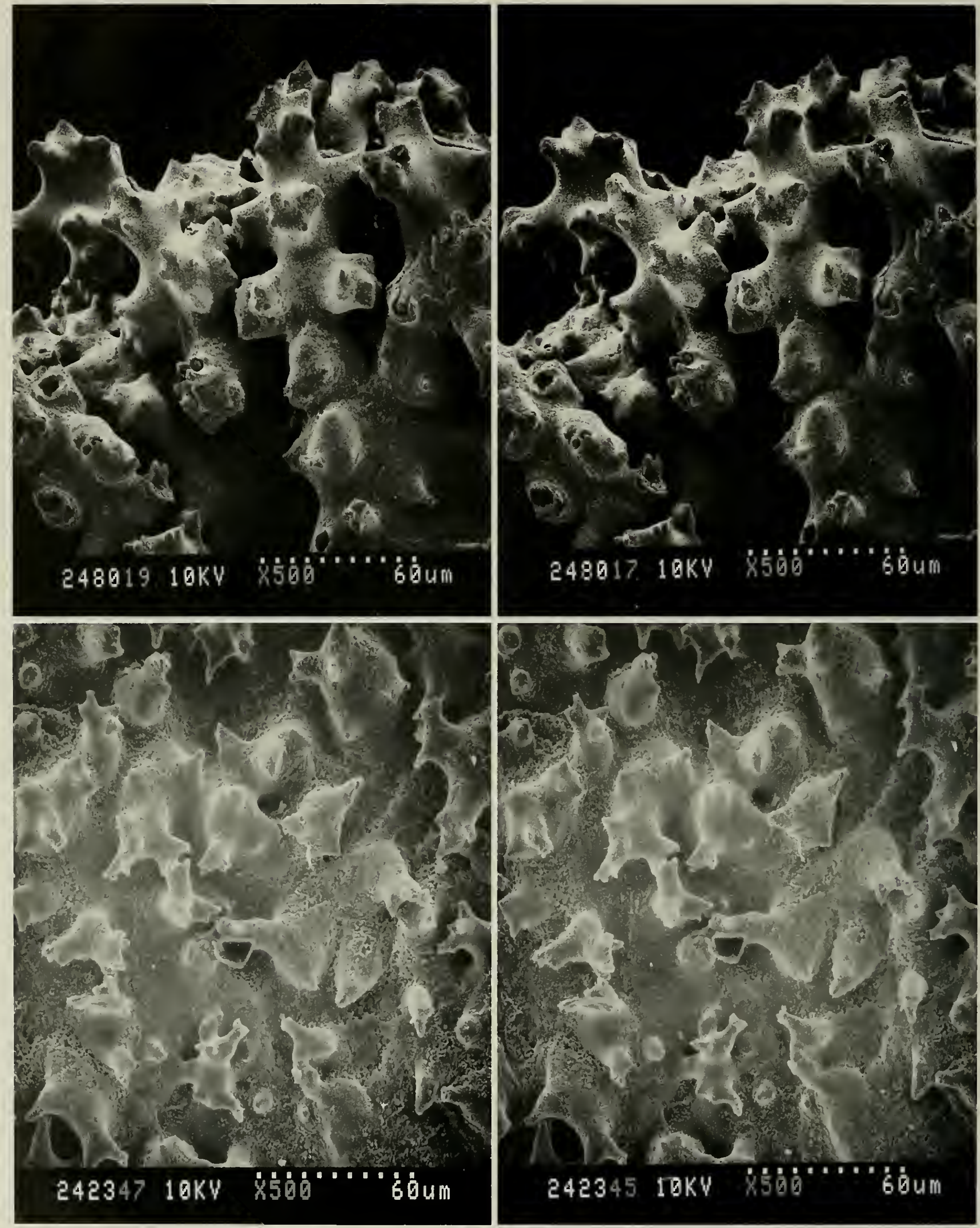

Fig. 16. *Corallium kishinouyei,* new species, axis of USNM 94462, preparation 1. Top, Sclerites embedded in non-spicular calcite at apex, SEM 2480; Bottom, Axial protuberances, SEM 2423. Stereo pairs.

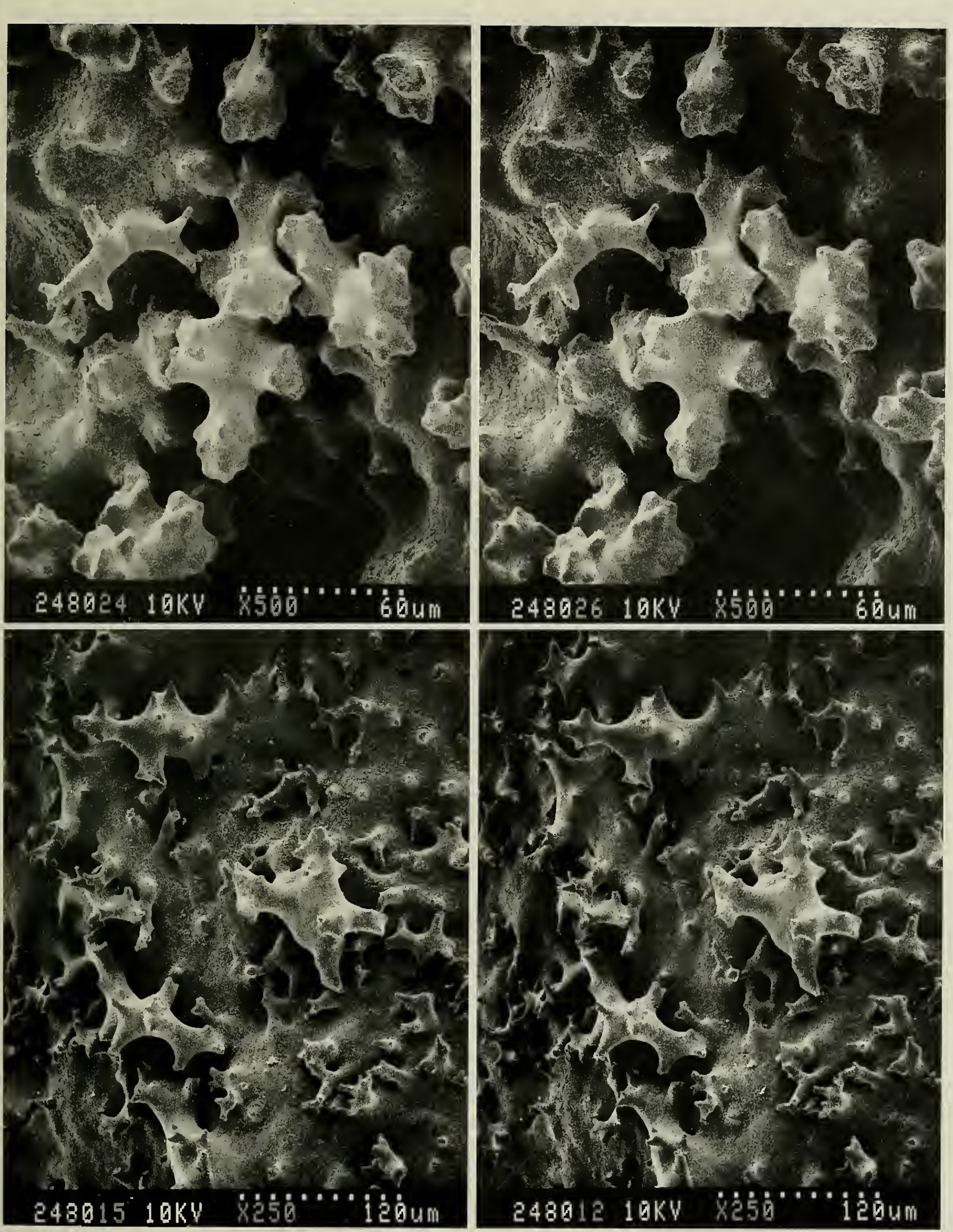

Fig. 17. *Corallium kishinouyei,* new species, axis of USNM 94462, preparation 1. Top, Surface of axis near apex, showing embedded sclerites and axial protuberance; Bottom, Surface of axis with typical axial protuberances and unusually large spiny projections. SEM 2480, stereo pairs.

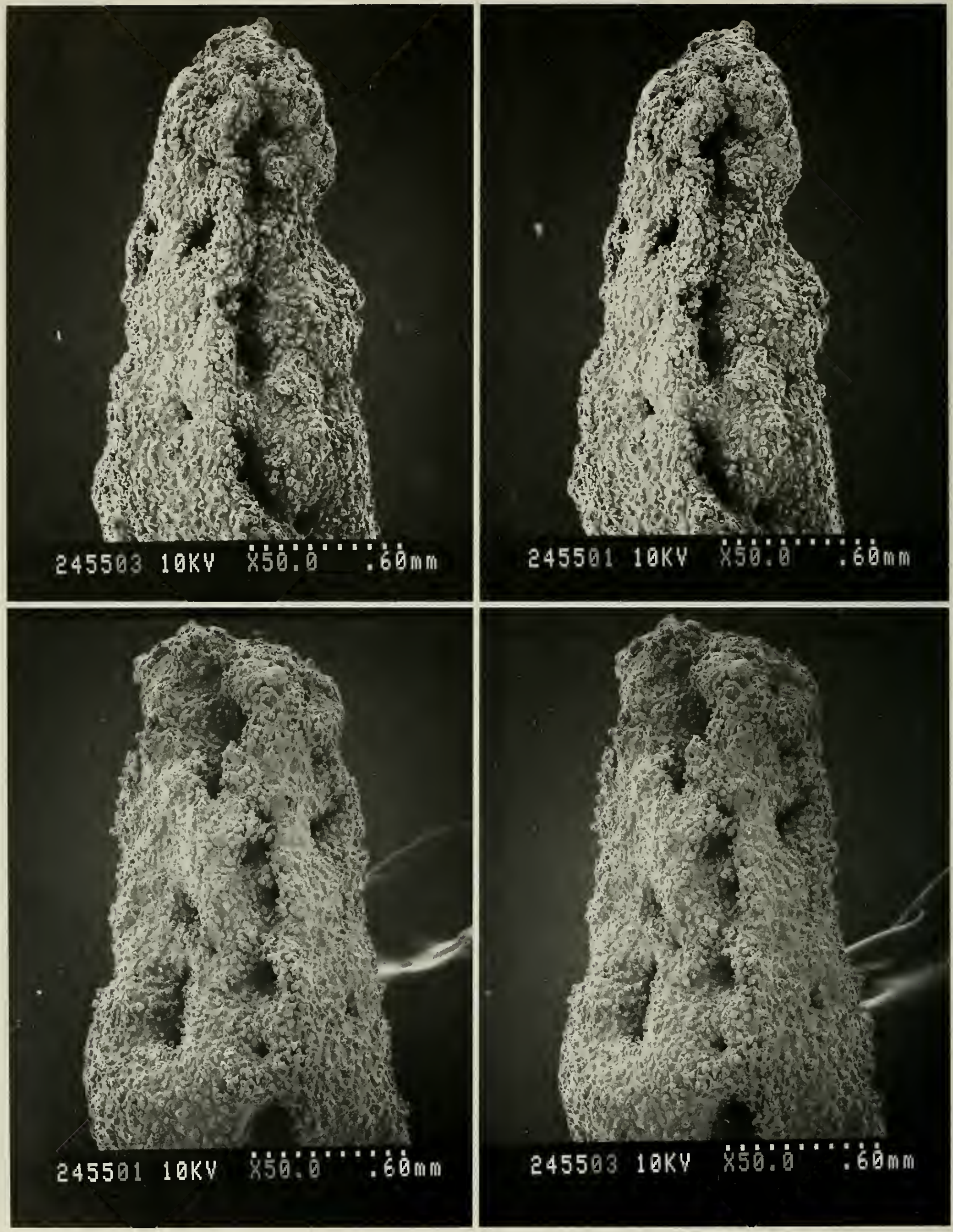

Fig. 18. *Corallium kishinouyei,* new species, axis of USNM 94463. Top, Apex of axis, side view; Bottom, Apex of axis, front view. SEM 2455, stereo pairs.

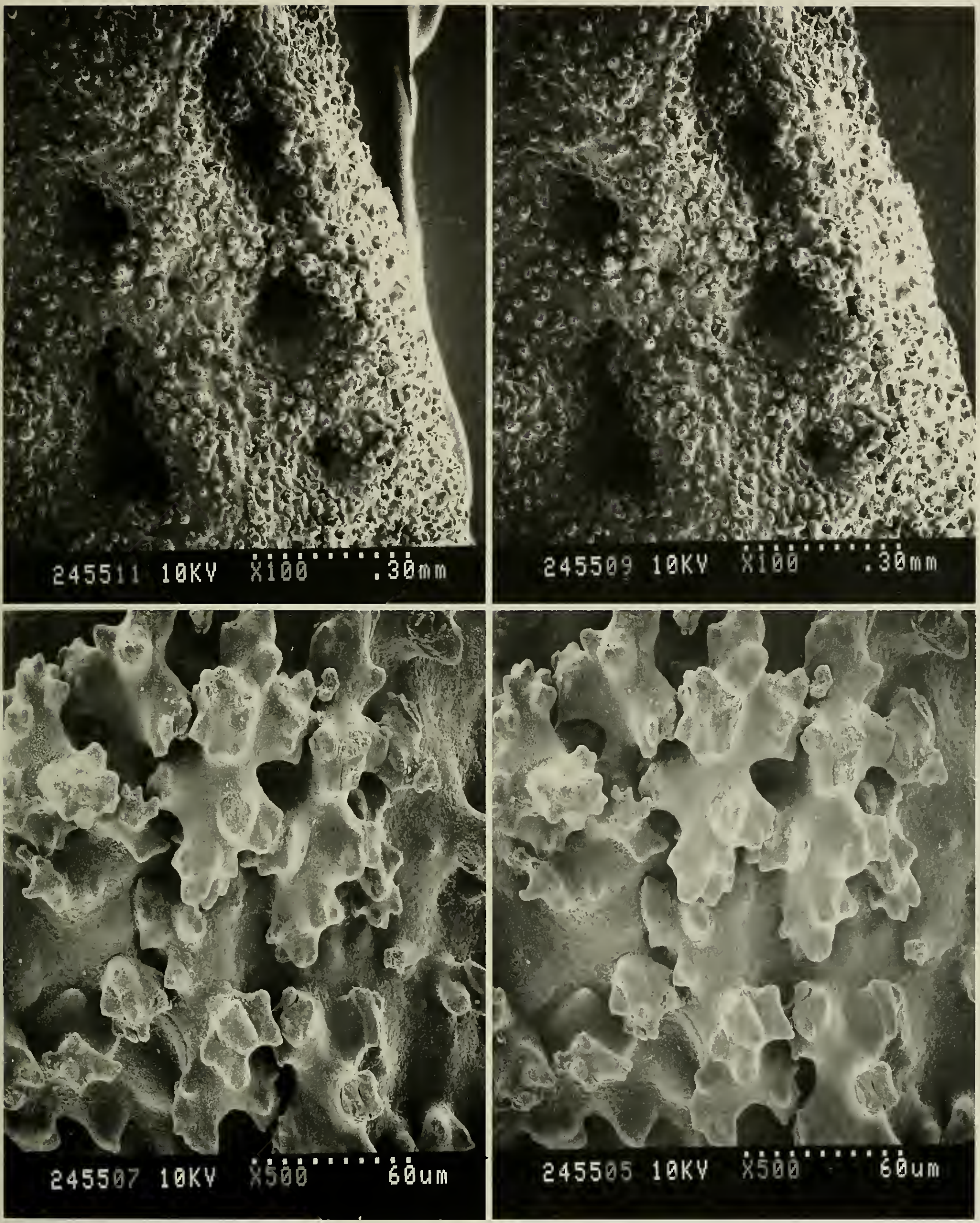

Fig. 19. *Corallium kishinouyei,* new species, axis of USNM 94463. Top, surface showing pits without beaded rim; Bottom, Surface near apex, showing embedded sclerites. SEM 2455, stereo pairs.

crystal structure that might account for this difference in opacity.

Etymology.—Named in honor of Kamakichi Kishinouye, pioneer Japanese investigator of precious corals.

Comparisons.—The openly branched, uniplanar colonial form of *Corallium kishinoueyi* is unlike any other species described so far, and the sclerites reach a larger size than in any species heretofore known.

Acknowledgments

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Reconsiderations of the species status of some South American Planarians (Platyhelminthes: Tricladida: Paludicola)

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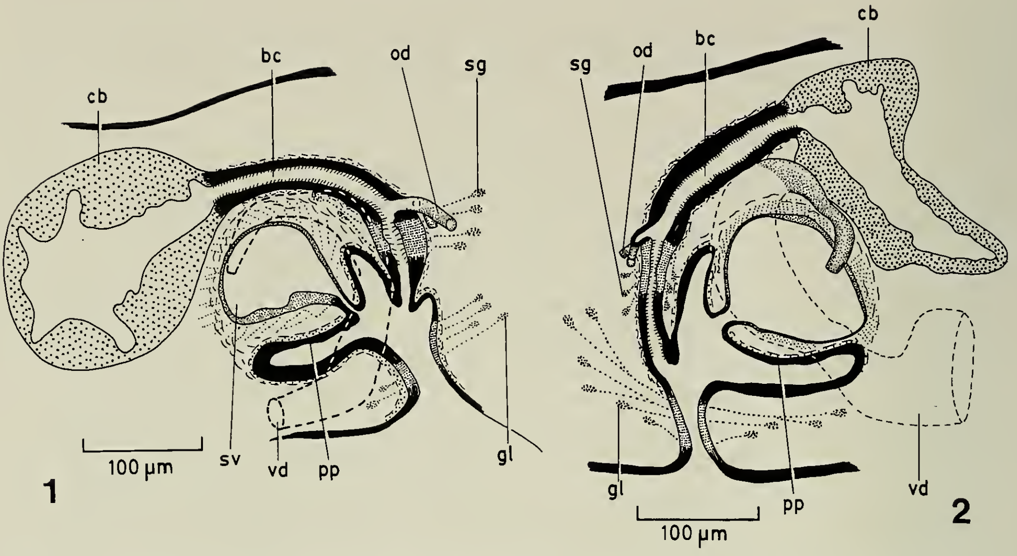
Abstract.—Reexamination of the type material of *Girardia veneranda* (Martins, 1970) revealed that this nominal species is very similar to *G. chilla* (Marcus, 1954). Therefore, *G. veneranda* is determined to be a junior synonym of *G. chilla.* For the first time a morphological description is provided of specimens collected in 1970 near Buenos Aires and identified as *G. anceps* (Kenk, 1930). The features of these *G. anceps* specimens conform in many details with Böhmig's (1902) redescription of this species. The material examined is compared also with more recent descriptions, from other localities, of *G. anceps* and with taxonomically related species.

Adequate assessment of the world's biodiversity depends on up to date knowledge on the diversity of species, their characteristics, and their distribution. The literature often features species descriptions and identifications that are poorly documented or cannot stand scrutiny. In each of these circumstances published results need to be checked on available, original material. This paper analyzes and discusses the species status of several South American planarians from the genus *Girardia* Ball, 1974. Planarians exemplify the situation that species are frequently characterized by a unique combination of diagnostic features instead of showing apomorphic characters (see Sluys 1991 for a review on species concepts). The variability that is encountered in these softbodied animals has made species recognition in *Girardia* often very complex and difficult.

De Vries & Sluys (1991) analyzed the phylogenetic relationships between the various genera and subgenera within the Dugesiidae Ball, 1974. They showed that the subgenera *Dugesia* Girard, 1850, *Schmidtea* Ball, 1974, and *Girardia* Ball, 1974, are separate phylogenetic groups and that *Dugesia* is not closely related to the other two subgenera. Therefore, they proposed to raise each of these subgenera to the rank of genus. The postulated apomorphies for the genus *Girardia* are a pigmented pharynx and a high triangular head shape with pointed auricles, being features that characterize many paludicolans from North America, Central and South America, and the Caribbean.

The present paper for the first time provides morphological evidence supporting the suggestions of Ball (1974) and Kenk (1974) that *G. veneranda* (Martins, 1970) from the State of São Paulo might be identical with *G. chilla* (Marcus, 1954) from southern Chile.

In 1970 Durán-Troise & De Lustig published the chromosome portrait of *Girardia anceps* (Kenk, 1930) from Buenos Aires, Argentina. Unfortunately, these authors did not provide a taxonomic description supporting the identification of their material. Apart from the fact that the identification of Durán-Troise & De Lustig needs proper documentation, examination of their material is also interesting in the light of Moretto's (1991) remark that *G. anceps* does



Figs. 1–2. *Girardia chilla.* 1, MZUSP 5829–5830. Sagittal reconstruction of the copulatory apparatus. bc: bursal canal; cb: copulatory bursa; gl: gland; od: oviduct; pp: penis papilla; sg: shell gland; sv: seminal vesicle; vd: vas deferens; 2, MZUSP 5819–5822. Sagittal reconstruction of the copulatory apparatus. bc: bursal canal; cb: copulatory bursa; gl: gland; od: oviduct; pp: penis papilla; sg: shell gland; vd: vas deferens.

not occur near Buenos Aires. Recently, Puccinelli & Deri (1991) also described the chromosomes of *G. anceps* from Buenos Aires, unfortunately without an anatomical description of their specimens or mentioning the deposition of voucher specimens.

Taxonomic Section

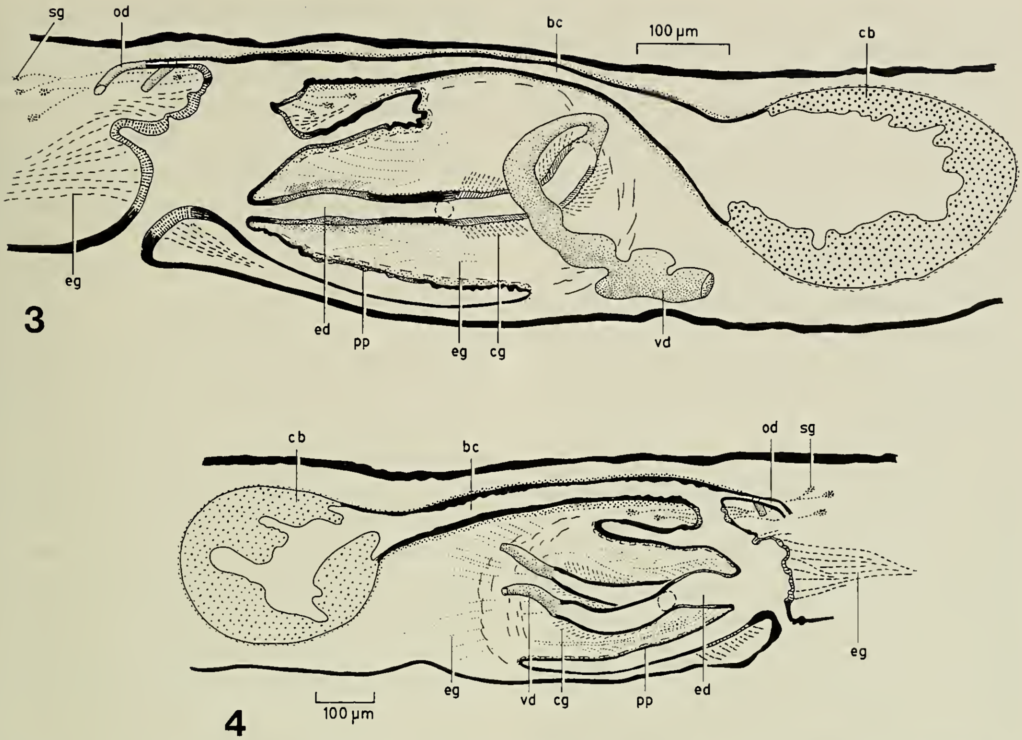
Girardia veneranda (Martins, 1970)
Figs. 1, 2

Material examined.—Although the major part of the material studied by Martins (1970) was examined, the present re-description is based mainly on the following preparations [housed in the Museu de Zoologia, Universidade de São Paulo, Seção Helmintologia (MZUSP)]: 5813–5816 (sagittal sections on 4 slides; slide no. 5813 missing), 5817–5818 (sagittal sections on 2 slides), 5819–5822 (sagittal sections on 4 slides), 5823–5825 (transverse sections on 3 slides), 5826–5828 (sagittal sections on 3 slides), 5829–5830 (sagittal sections on 2 slides), 5831–5834 (horizontal and transverse sections on 4 slides).

Description.—In the sectioned material no pigmentation appears to be present underneath the pharynx epithelium. The mouth opening is at about one-third of the distance between the hind wall of the pharyngeal pocket and the root of the pharynx.

The testes are principally situated dorsally, but large testes in the posterior end of the body may occupy the entire dorso-ventral space; the follicles extend from directly posterior to the ovaries to almost the posterior body end. The paired ovaries lie at a short distance behind the brain.

The vasa deferentia, which form well developed false seminal vesicles, recurve at about the level of the gonopore and open separately into the antero-lateral portions of the intrapenial seminal vesicle. This spherical or irregularly shaped seminal vesicle occupies most of the penis bulb and papilla. The wall of the vesicle is lined with a nucleate epithelium that is pierced by numerous openings of highly abundant cyanophilous glands, which lie within the penis bulb as well as directly outside of the bulb.



Figs. 3–4. *Girardia anceps.* 3, ZMA V. Pl. 871.5. Sagittal reconstruction of the copulatory apparatus. bc: bursal canal; cb: copulatory bursa; cg: cyanophilic glands; ed: ejaculatory duct; eg: erythrophilic glands; od: oviduct; pp: penis papilla; sg: shell gland; vd: vas deferens; 4, ZMA V. Pl. 871.1. Sagittal reconstruction of the copulatory apparatus. bc: bursal canal; cb: copulatory bursa; cg: cyanophilic glands; ed: ejaculatory duct; eg: erythrophilic glands; od: oviduct; pp: penis papilla; sg: shell gland; vd: vas deferens.

The secretion is also abundantly present in the seminal vesicle.

The penis papilla is a stubby cone, covered with a nucleate epithelium which is underlain with a layer of circular and longitudinal muscle, successively.

The copulatory bursa is situated directly anterior to the penis bulb. From the bursa, the bursal canal curves smoothly towards the postero-dorsal portion of the atrium; the canal is lined with cuboidal cells bearing long cilia. The canal is surrounded by a layer of intermingled circular and longitudinal muscle. The two oviducts fuse to form a very short common oviduct that immediately communicates with the bursal canal. Ventral to the opening of the common oviduct the bursal canal receives the erythrophilous secretion of shell glands. Another set of eosinophilous glands discharges their secretion into the gonopore.

Girardia anceps (Kenk, 1930) = *Planaria dubia* Borelli, 1895

Figs. 3, 4

Material examined.—The material examined consists of the material collected and described by Durán-Troise & De Lustig (1970) but identified by Prof. Benazzi. This material consists of the following series of slides, now housed in the Zoological Museum, Amsterdam (ZMA): V. Pl. 871.1: sagittal sections of one animal on 3 slides; V. Pl. 871.2: sagittal sections on 2 slides; V. Pl. 871.3: sagittal sections on 2 slides; V. Pl. 871.4: sagittal sections on 2 slides; V. Pl. 871.5: sagittal sections on 4 slides;

V. Pl. 871.6: transverse sections on 4 slides; V. Pl. 871.7: horizontal sections on 3 slides; V. Pl. 871.8: sagittal sections on 1 slide.

Description.—The slides revealed that the animals are pigmented on dorsal and ventral body surface. The sections also unequivocally showed the pharynx to be pigmented. The mouth opening is located at the hind end of the pharyngeal pocket.

The numerous small testes are situated ventrally, from directly behind the ovaries extending to almost the posterior body end. The ovaries are located at some distance behind the brain.

The vasa deferentia recurve at the level of the penis bulb, penetrating it from the lateral sides. Within the bulb the ducts expand in diameter and within the penis papilla they fuse to form a broad ejaculatory duct. The intrapenial parts of the vasa deferentia and the ejaculatory duct are lined with a well developed, nucleate epithelium and are surrounded by a thin layer of circular muscle. The penis papilla is lined with a flat, infranucleate epithelium. Ejaculatory duct and penis epithelium are pierced by ducts of numerous eosinophilic glands, while cyanophilous glands open into the intrabulbar seminal vesicles.

The narrow male atrium communicates with the common atrium; there is no distinct female atrium. The atria are lined with an infranucleate epithelium. Especially the posterior wall of the common atrium is pierced by openings of numerous eosinophilic glands; the glandular elements being broadly distributed in the surrounding parenchyma.

The bursal canal is more or less "angled"; the short section of the canal that sharply turns towards the dorsal part of the atrium receives the openings of erythrophilic shell glands. The bursal canal is lined with an infranucleate, ciliated epithelium. The musculature of the bursal canal either consists predominantly of circular muscles (as in preparations V. Pl. 871.1 and 871.5) or contains intermingled circular and longitudinal fibres (as in preparation V. Pl. 871.3). The infranucleate oviducts join to form a very short common oviduct that opens into the rear wall of the bursal canal, just dorsally to the angled section of the canal.

In specimen V.Pl.871.1 remnants of a spermatophore project from the ejaculatory duct through the gonopore.

Discussion

The above description of *G. veneranda* differs in some important details from that given by Martins (1970). Although she described the vasa deferentia as opening ". . . into a single and spacious true seminal vesicle . . . ," the illustration of the copulatory apparatus (Martins 1970, fig. 5) seems to indicate that the ducts open into a sort of intrapenial papilla. However, this suggestion of an intrapenial papilla merely results from an invagination or fold of the irregularly shaped seminal vesicle. In reality the vasa deferentia penetrate separately the lateral wall of the vesicle, as correctly depicted in figs. 6 and 7 of Martins.

According to Martins, the oviducts open separately into the bursal canal. However, detailed study of both sagittal and transverse sections revealed that the oviducts fuse to an extremely short common duct. This situation is already indicated in Martin's fig. 8 but was interpreted differently in her fig. 5 and in the text description of the copulatory apparatus.

The present re-analysis of the type material of *G. veneranda* reveals that the morphology of the reproductive apparatus is strikingly similar to that of *G. chilla,* as described by Marcus (1954) and Hyman (1959). Both species show the spacious intrapenial seminal vesicle, receiving the abundant cyanophilous secretion. According to Hyman (1959) eosinophilous glands open into the vesicle, but this does not agree with my observations and those of Marcus (1954). The only difference to be noted between the *G. veneranda* specimens and *G. chilla* is that the latter was described with numerous glands opening through the entire epithelium of the common atrium. In the *G. veneranda* material the glands were not as abundantly present as described by Marcus or Hyman. According to Marcus these glands are cyanophilic but Hyman described them as eosinophilic, which conforms to my observations.

In view of the above, it is here concluded that *G. veneranda* is essentially similar to *G. chilla* and that therefore *G. veneranda* must be considered a junior synonym of *G. chilla.*

Because Borelli's (1895) description of *Planaria dubia* [=*G. anceps*] is rather superficial and therefore does not allow detailed comparison with the material described in the present paper, it is here accepted that Böhmig's (1902) more comprehensive description applies to Borelli's species. This axiom is open for criticism, of course, since Borelli's material came from Asunción, Paraguay and Böhmig's specimens were collected near Buenos Aires, Argentina (but it must be noted that Böhmig did examine Borelli's preparations). However, the main purpose of the present discussion is to compare my material with (1) Böhmig's account of *G. anceps,* (2) more recent descriptions of the species, and (3) descriptions of taxonomically related species.

Böhmig mentioned for *G. anceps* the following characteristics: (1) recurved vasa deferentia, (2) infranucleate epithelium lining the atrium and the penis papilla, (3) circular muscles around ejaculatory duct and intrabulbar parts of the vasa deferentia, (4) cyanophilous glands discharging into these intrabulbar seminal vesicles, (5) ejaculatory duct receiving the secretion of eosinophilous glands, (6) proximal, anterior section of bursal canal funnel-shaped, (7) posterior two-thirds of bursal canal lined with infranucleate epithelium, (8) oviducts opening separately into bursal canal, (9) large number of eosinophilous glands (different from the shell glands) discharging into the atrium, (10) ventral testes, (11) dorsal surface dark brown with a pale mid-dorsal stripe. Böhmig's diagrammatic reconstruction of the copulatory apparatus of his *G. anceps* specimens has been redrawn by Cazzaniga & Curino (1987, fig. 2).

It is evident that the material of Durán-Troise & De Lustig (1970), as described in the present paper, conforms in many details with Böhmig's account of *G. anceps,* the only possible difference being the openings of the oviducts into the bursal canal. With respect to the openings of the oviducts, however, it must be noted that Böhmig's reconstruction (cf. Cazzaniga & Curino 1987, fig. 2) suggests oviducts opening very closely together into the bursal canal. Furthermore, it is important to note that in one particular *Girardia* species some specimens may have oviducts opening separately (but closely together) into the bursal canal, whereas in other animals the oviducts fuse to form a very short common oviduct. The same phenomenon was mentioned by Cazzaniga & Curino for their specimens of *G. anceps.*

Especially striking similarities between our material and Böhmig's account are the infranucleate epithelia of penis papilla, atrium, and bursal canal. It is therefore disturbing that Böhmig found Borelli's material with nucleate linings of penis papilla and atria (this may cast doubt on the identicality of Böhmig's and Borelli's material; neither does Borelli depict the funnel-shaped section of the bursal canal where it communicates with the bursa). Cazzaniga & Curino also found in their specimens a bursal canal lined with a nucleate epithelium, but the atrium and penis papilla in these animals were provided with an infranucleate lining epithelium. These differences in nucleate/infranucleate epithelia, as reported by various authors, may simply reflect different states of development of the copulatory apparatus, only fully mature individuals with all their epithelia infranucleate. In *Dugesia gonocephala* (Dugès, 1830) De Vries (1984) found that nucleation of the bursal canal depends on the state of development.

Apart from the differences mentioned above, the material of Cazzaniga & Curino is essentially similar to that studied by me. They mention also the infranucleate epithelium of the oviducts, which are surrounded by successively a layer of circular muscle and nuclei. In contrast to my material, Cazzaniga & Curino reported the pharynx to be unpigmented.

In view of the above, it is concluded that the specimens from Buenos Aires analyzed by Durán-Troise & De Lustig correspond with Böhmig's account of *G. anceps* from the same locality and also with the material described by Cazzaniga & Curino from Bahía Blanca. This contrasts with Moretto's (1991) conclusion that *G. anceps* has been recorded incorrectly from Buenos Aires.

The specimens that Kawakatsu & Rovasio (1992) used for their redescription of *G. anceps* differs in the following features from my material, Böhmig's account, and the description by Cazzaniga & Curino: (1) dorsal surface uniform blackish brown, without light mid-dorsal stripe, (2) pharynx unpigmented, (3) mouth opening somewhat anterior of posterior end of pharyngeal pocket (as suggested by their fig. 3B), (4) divided atrium, (5) male and common atrium lined with nucleate epithelium, (6) bursal canal with nucleate epithelium, (7) bursal canal provided with very thick muscle coat. Each of these characters is known to vary between specimens of a single species and it is debatable whether a combination of these features indicates a species that is different from *G. anceps* and possibly from any other known species of *Girardia.*

Several authors have discussed the similarities of *G. anceps* with *G. sanchezi* (Hyman, 1959) and *G. festae* (Borelli, 1898) and the species status of these taxa (Hyman 1959, Cazzaniga & Curino 1987, Moretto 1991, Kawakatsu & Rovasio 1992) [recently, Curino & Cazzaniga (1993) argued that the original spelling *G. festae* was correct and that later emendations to *G. festai* were invalid]. Sluys (1992) considered *G. sanchezi* to be a junior synonym of *G. festae* because both were described with abundant glands opening into the common atrium, unicellular glands opening into the bursal canal, and with penial glands discharging through the epithelium of the penis papilla. Moreover, *G. sanchezi* and *G. festae* were both described with a pale, longitudinal mid-dorsal stripe. However, the present study shows that several of these features occur also in *G. anceps,* suggesting that *G. festae* might in turn be a junior synonym of *G. anceps*. Although *G. anceps* and *G. festae* are similar in several aspects of their reproductive system, *G. festae* is different in that it has unicellular glands piercing the entire length of the nucleate bursal canal, and nucleate linings of penis papilla and atria.

Thus, the conclusion of the present study is that *G. sanchezi* is a junior synonym of of *G. festae* and that *G. festae* and *G. anceps* are valid species. This conclusion is different from that reached by Cazzaniga & Curino (1987) and Kawakatsu & Rovasio (1992) that *G. sanchezi* is a valid taxon. However, the conclusion of these workers was based on a comparison of *G. sanchezi* with *G. anceps,* whereas the present study suggests that *G. sanchezi* is morphologically closer to *G. festae.* There is one feature that argues against *G. sanchezi* being a junior synonym of *G. festae,* thus illustrating the point made in the introduction that species recognition in *Girardia* can be very complex: *G. festae* has recurved vasa deferentia (cf. Sluys 1992, fig. 2) while this is not the case in *G. sanchezi* (cf. Hyman 1959, fig. 5).

Acknowledgments

Prof. Dr. M. Benazzi (Pisa, Italy) is thanked for making available the material of *G. anceps* described in this paper and for depositing the preparations in the Zoological Museum, Amsterdam. Prof. Dr. E. M. Froehlich (São Paulo, Brazil) is thanked for arranging the loan of the type material of *G. veneranda*. Part of this study was prepared while I stayed as a Visiting Professor at the Universidade do Vale do Rio dos Sinos, São Leopoldo, Brazil; UNISINOS and the Brazilian Council for Scientific and Technological Development (CNPq) are thanked for making this visit possible. The research of the author has been made possible, in part, by a grant from the Netherlands Organization for Scientific Research–NWO (Biodiversity in Disturbed Ecosystems Programme).

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Pycnophyes parasanjuanensis, a new kinorhynch (Kinorhyncha: Homalorhagida: Pycnophyidae) from San Juan Island, Washington, U.S.A.

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Abstract.—A new species of kinorhynch, *Pycnophyes parasanjuanensis,* is described and illustrated from muddy sediments from a depth of 20 m at Friday Harbor, Washington (48°33′N, 123°04′W). It constitutes the second species of *Pycnophyes* from the San Juan Archipelago and the Pacific Coast of North America. The new species closely resembles *P. sanjuanensis* Higgins, 1961, the only other representative of this genus from this region. Like *P. sanjuanensis, P. parasanjuanensis* has a wide, sculptured anterior margin of the first tergal plate and large circular zones of thin cuticle on the midsternal and episternal plates. It differs from the sympatric *P. sanjuanensis* and all other congeners in having longitudinal cuticular ridges near the lateral margins of the sternal plates and a fimbriate terminal border on segment 13. In addition, *P. sanjuanensis* differs from *P. parasanjuanensis* by its thick, robust lateral terminal spines with rounded tips.

There have been few papers on Kinorhyncha from the West Coast of the United States. Of the six species described, all but one have been from the San Juan Archipelago, located in the northwest of the state of Washington between Vancouver Island, Canada and the United States mainland. The first kinorhynch reported (Higgins 1960) from this region was *Echinoderes pennaki* Higgins, 1960, a cyclorhagid, found at East Sound Bay of Orcas Island. The second publication (Higgins 1961) on kinorhyncha from this region described three species of homalorhagids, *Pycnophyes sanjuanensis* Higgins, 1961, *Kinorhynchus ilyocryptus* Higgins, 1961, and *K. cataphractus* Higgins, 1961. Boykin (1965), in his unpublished dissertation, addressed the morphology of *K. ilyocryptus.* A second cyclorhagid, *Echinoderes kozloffi* Higgins, 1977 was the subject of a paper by Kozloff (1972) wherein he described the oviposition and hatching of the juvenile stage of this species described a few years later by Higgins (1977). This latter species was found in the intertidal zone of North Bay, San Juan Island. The only other kinorhynch described from the Pacific Coast of the United States is *Echinoderes nybakkeni* Higgins, 1986. This, too, was described from the intertidal zone, from coarse beach sand at Carmel, California.

Methods

The five specimens upon which this study is based were collected by the senior author (AVA) on 21 Jul 1994. They were found in samples of mud taken by a 0.06 m^2 grab at a depth of 20 m, Friday Harbor, San Juan Island, San Juan Archipelago, located in the northwest section of the State of Washington between Vancouver Island and the United States mainland. Living kinorhynchs were extracted from the sediment by the "bubble-and-blot" method (Higgins 1983). Most specimens were fixed in 10% formalin. Some of were transferred to a glycerin-alcohol solution which was allowed to evaporate to glycerin. The glycerin-impregnated specimens then were mounted individually in Hoyer's-125 mounting medium on slides for further examination using phase-contrast and differential interference contrast optics. A few specimens were selected for scanning electron microscopic (SEM) study. These were transferred to a small tube, sealed with 42-μm mesh nylon net, and placed in a small vessel of distilled water. Ethanol was added slowly until the contration was 100 percent; thereafter, the absolute ethanol was replaced several times. The tube and its contents were dried in a critical-point depression apparatus using carbon dioxide. Specimens were removed, mounted on SEM stubs and coated with gold-platinum. A Stereoscan Microscope 250 MK2 was used to study the specimens.

Examination procedures followed the protocol described by Higgins (1983:4–7). Measurements are given in micrometers (μm). Ratios are expressed in percent of the total length (TL) measured on the midline, from the anterior margin of segment 3 (first trunk segment) to the posterior margin of segment 13, exclusive of spines. Maximum sternal width (MSW) is measured at the anteroventral margin of the widest pair of sternal plates as first encountered in measuring each segment from anterior to posterior. Standard width (SE), or sternal width as segment 12, is measured at the anteroventral margin of 12th sternal plates. The locality data from material examined are referred to by the senior author's number (AVA).

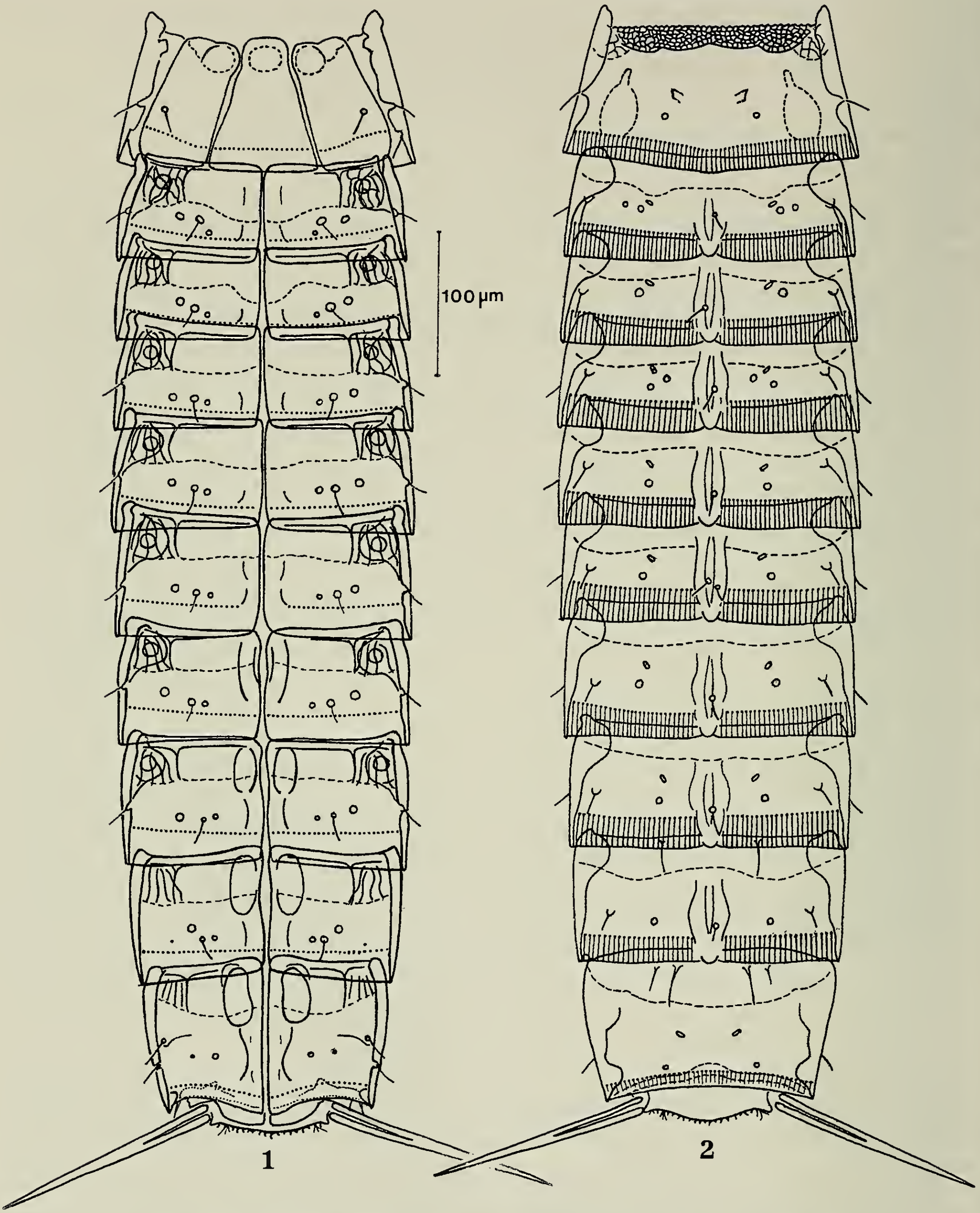
Two specimens of *Pycnophyes parasanjuanensis,* the holotypic female and allotypic male have been deposited in the meiofaunal collection of the Institute of Marine Biology, Vladivostok, Russia. One paratype of *P. parasanjuanensis* is deposited in the Invertebrate Zoology collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. under the catalog number USNM 274223.

Pycnophyes parasanjuanensis, new species
Figs. 1–24

Diagnosis.—Trunk length 740–800 μm; trunk segments slightly increasing in width to segments 7–9, then tapering slightly at segments 11–12; subdorsal placids twice as wide as middorsal placids; anterior margin of first tergite slightly denticulate, shingled or reticulate, with long horn-like lateral processes 22 μm long; posterior margin of terminal tergite clearly fimbriate; lateral terminal spines (LTS) 150–176 μm long, 20–22% of trunk length; middorsal processes obtuse, on segments 4–11, nearly uniform in size, only slightly protruding beyond margin of tergite, each bearing 1–2 sensory setae; midsternal plate trapezoidal, anterior margin about 40% of posterior margin, anterior border of midsternal plate projecting beyond anterior margins of episternites; posterior margins of segments 3–12 with longitudinal rows of minute spherical bodies, becoming less distinct posteriorly; pachycycli of segments 4–10(11) with unclear peg-and-socket articulation ventrally; anteromesial thickenings of ventral pachycycli prominent on segments 10–12 in female and 9–12 in male, not adjacent at ventral midline; sternal plates of segments 4–12 with prominent cuticular ridges near lateral margins.

Description.—Holotypic female (Figs. 1, 2, 7–12), senior author's number AVA FH-1.18, (Figs. 1, 2, 7–12); Allotypic male, (Figs. 3–6, 15–20), senior author's number AVA FH-17; Note: data for allotypic male, if different from those of holotypic female, are in parenthesis and following those female. TL 779 μm (799 μm), MSW-7 178 μm, 23% (22%) of TL; SW 156 μm (152 μm), 20% (19%) of TL; LTS 156 μm (176 μm), LTS/TL 20% (22%); middorsal processes on segments 4–11.

Segment 1: Head withdrawn in holotype.

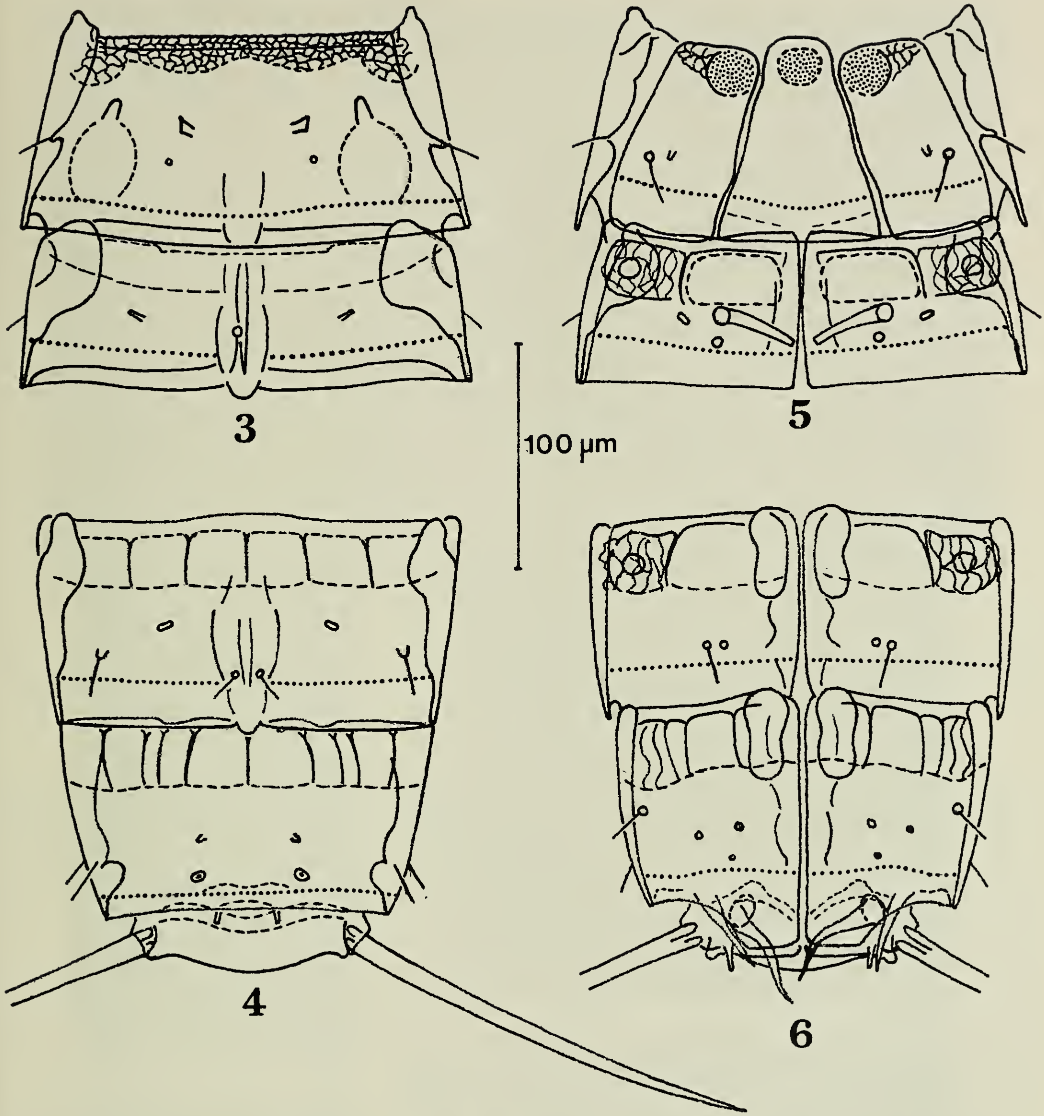


Figs. 1, 2. *Pycnophyes parasanjuanensis,* holotypic female. 1, Ventral view; 2, Dorsal view.

See mouth cone and nine oral syles (OS) in SEM photo of paratypic female, Fig. 21.

Segment 2: Not evident in holotype because of withdrawn head. See neck placids (NP) in paratypic female, Fig. 22.

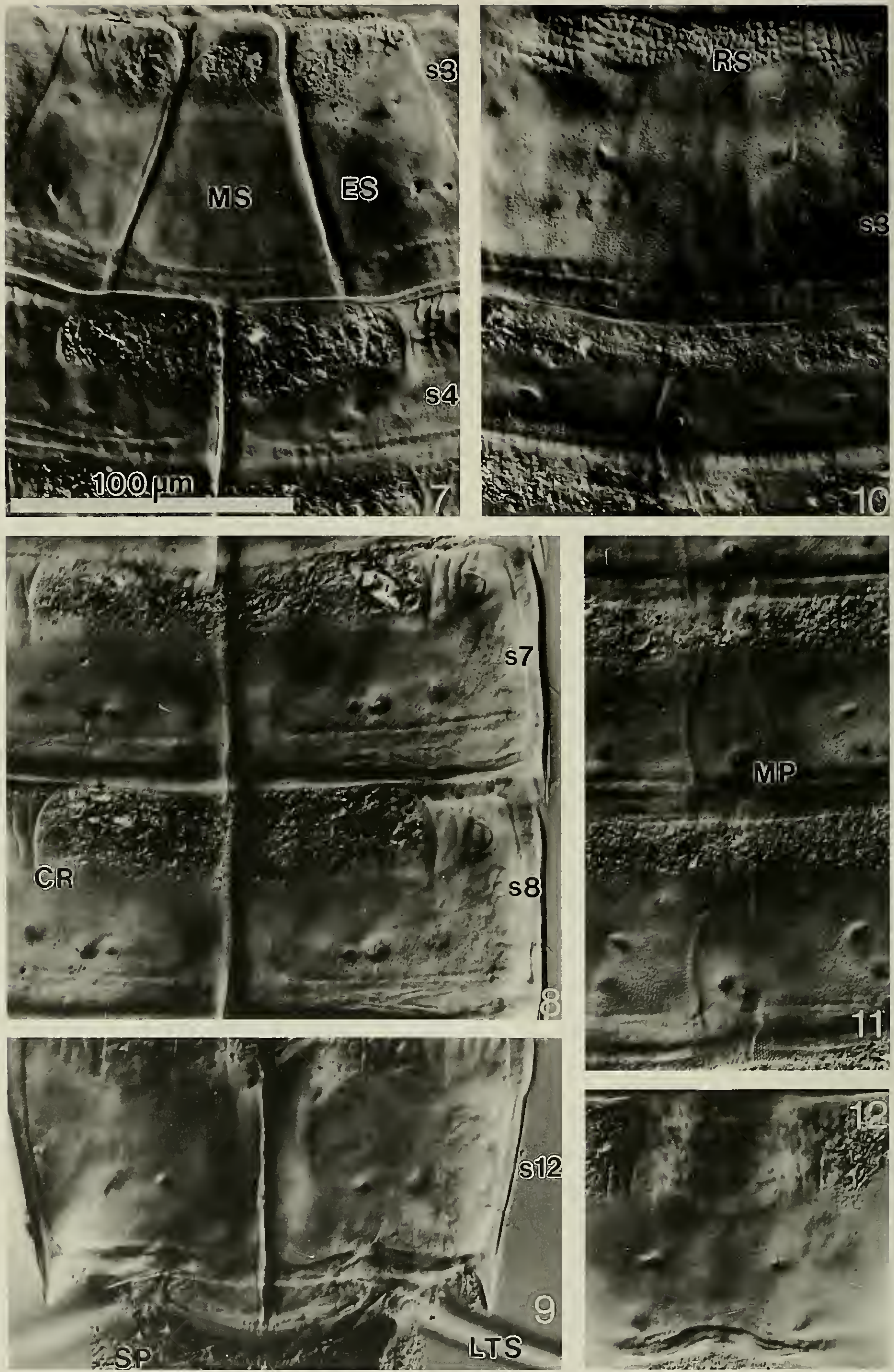
Segment 3: First trunk segment (Figs. 7, 10), length 99 µm (106 µm); with lateral horn-like processes, 22 µm long; anterior margin finely denticulate, shingled or reticulate in appearance; pair of subdorsal tri-



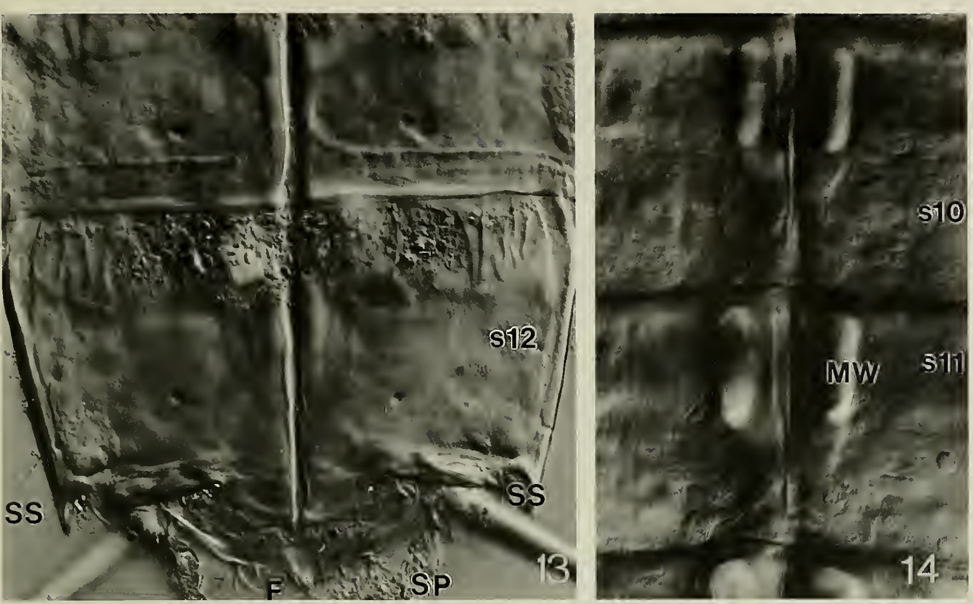
Figs. 3–6. *Pycnophyes parasanjuanensis,* allotypic male. 3, Segments 3, 4, dorsal view; 4, Segments 11–13, dorsal view; 5, Segments 3, 4, ventral view; 6, Segments 11–13, ventral view.

angular muscle scars anterior to midlength of tergite and anterior to large scars of dorsoventral muscles; midsternal plate trapezoidal (Figs. 5, 7, 15; note same in SEM photo of paratypic female, fig. 23), 88 µm basal width tapering evenly to 33 µm about one-sixth the distance from anterior margin and then becoming even, with round area of thin cuticle submarginally; anterior margin of midsternal plate projecting beyond anteromesial margins of episternal plates; each episternite (Figs. 1, 5, 7, 15) with two adjacent areas of thinner cuticle, episternal plates with sensory seta near posterolateral margin; two lateral setae present.

Segment 4: Length 78 µm (80 µm); tergite with two dorsolateral setae, middorsal process obtuse, with seta (male with seta on each side of middorsal process) pachycycli with peg-and-socket articulation ventrally;



Figs. 7–12. *Pycnophyes parasanjuanensis,* holotypic female. 7, Segments 3, 4, ventral view; 8, Segments 7, 8, ventral view; 9, Segments 12, 13, ventral view; 10, Segments 3, 4, dorsal view; 11, Segments 7, 8, dorsal view; 12, Segment 12, dorsal view. All figures to same scale as Fig. 7. Abbreviations: CR, cuticular ridges; ES, episternal plate; LTS, lateral terminal spine; MP, middorsal process; MS, midsternal plate; RS, reticulate sculpturing; SP, spermatophore remainder; s, prefix followed by segment number.



Figs. 13, 14. *Pycnophyes parasanjuanensis,* paratypic female. 13, Segments 11–13, ventral view; 14, Segments 11, 12, midventral thickenings. All figures to same scale as Fig. 7. Abbreviations: F, fimbriate margin of segment 13; MW, Midventral thickenings; SP, spermatophore remainder; SS, sensory seta; s, prefix followed by segment number.

sternites with prominent cuticular ridges laterally and subventral setae; with two lateral setae. (Male with adhesive tube, 44 μm long, anteromesial on each sternite, Figs. 5, 16).

Segment 5: Length 83 μm (81 μm); similar to segment 4 except for lack of lateral setae.

Segment 6: Length 84 μm; similar to segment 5 except for presence of two lateral setae.

Segment 7: Length 89 μm (87 μm) (Figs. 8, 17); similar to segment 6.

Segment 8: Length 92 μm (90 μm); similar to segment 6 except for presence of two setae on middorsal process.

Segment 9: Length 92 μm (95 μm); similar to segment 8 except for more prominent ventromesial pachycycli and only one seta on middorsal process. (Male with prominent anteromesial thickenings of ventral pachycycli.)

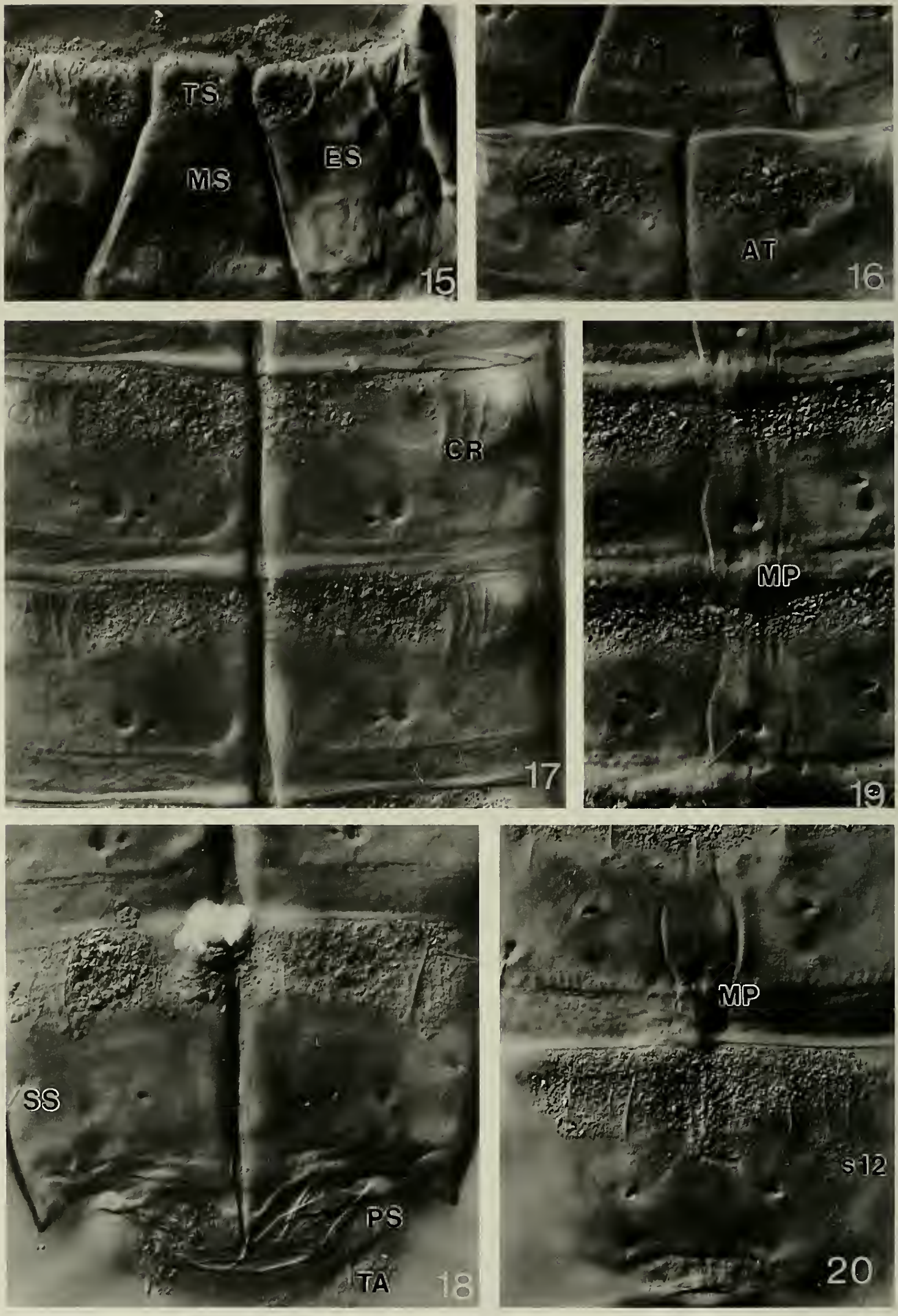
Segment 10: Length 95 μm (99 μm); similar to segment 9 except for presence of well-developed anteromesial thickenings of ventromesial pachycycli (Figs. 1, 6, 14).

Segment 11: Length 99 μm (100 μm); anteromesial thickenings longer and broader than in previous segment, similar to segment 10 except for absence of lateral setae.

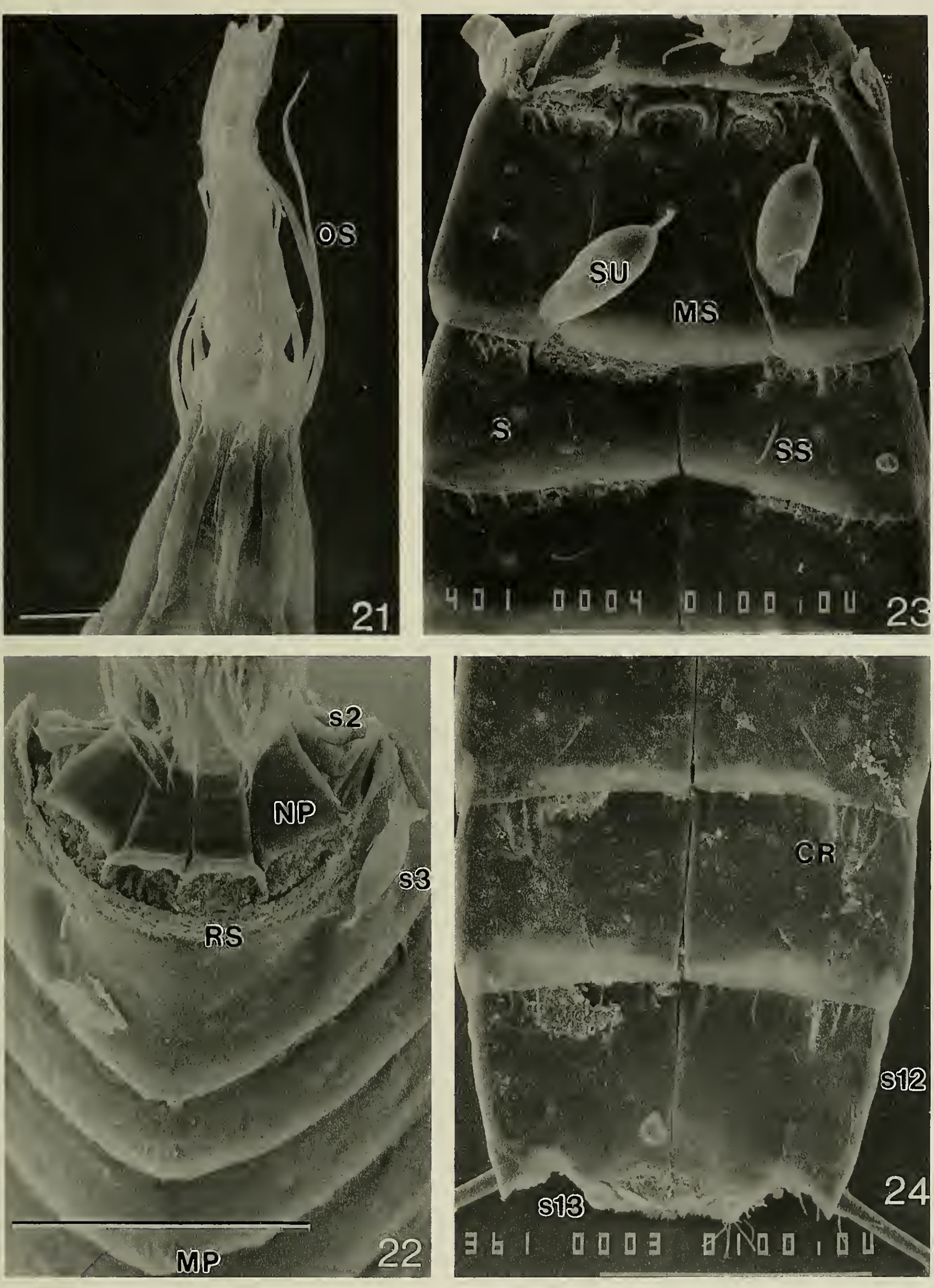
Segment 12: Length 101 μm; no middorsal process (Fig. 20); no dorsolateral setae; anteromesial thickenings longer and broader than in previous segment; sternites with ventrolateral seta; with lateral seta (Fig. 9; also note same segment shown in SEM photo of paratypic female, Fig. 24).

Segment 13: Length 44 μm (43 μm); with two lateroterminal setae (Figs. 1, 4, 9, 13); terminal border of tergite fimbriate Figs. 1, 2, 13); lateral terminal spines 156 μm long. (Pair of penile spines, Figs. 6, 18, near anterolateral margin of each sternite, PS-1 48 μm long, PS-2 35 μm long). (Small protuberance near lateroterminal margin of sternites).

Sexual dimorphism.—The male differs from females in having prominent antero-



Figs. 15–20. *Pycnophyes parasanjuanensis,* allotypic male. 15, Segment 3, ventral view; 16, Segment 4, ventral view; 17, Segments 7–8, ventral view; 18, Segment 12–13, ventral view; 19, Segments 6, 7, dorsal view; 20, Segments 11, 12, dorsal view. All figures to same scale as Fig. 7. Abbreviations: AT, adhesive tubes; ES, episternal plate; MP, middorsal process; MS, Midsternal plate; PS, penile spines; SS, sensory seta; s, prefix followed by segment number; TA, lateral terminal protubrances of segment 13; TS, thin cuticle area.



Figs. 21–24. *Pycnophyes parasanjuanensis,* adult female, SEM photographs, scale equals 100 μm. 21, Protruded mouth cone with oral styles, scale equals 10 μm; 22, Segments 2–5, dorsal view, scale equals 100 μm; 23, Segments 2–5, ventral view, scale equals 100 μm; 24, Segments 10–13, ventral view, scale equals 100 μm. Abbreviations: CR, cuticular ridges; MP, middorsal process; MS, midsternal plate; NP, neck placid; OS, oral styles; RS, reticulate sculpturing; SS, sensory seta; S, sensory spot; SU, ectocommensal suctorian; s, prefix followed by segment number.

mesial thickenings of ventral pachycycli on segments 9–12, two ventral adhesive tubes on segment 4, two lateroterminal protuberances on the margin of sternites of segment 13, two pairs of penile spines (Figs. 6, 18) at the anterolateral margins of segment 13, and two sensory setae on the middorsal process of segment 4.

Paratypic variation.—A single paratypic male, senior author's number AVA FH-1.16 (Figs. 13, 14), TL 740 μm; MSW-7 180 μm (24% of TL), SW 156 μm (21% of TL), LTS 152 μm (20.5% of TL). Paratypic female differs from holotypic female in having two sensory setae on each middorsal process (Fig. 22, MP).

Type material.—Holotype: adult female (AVA FH-1.18), allotype: adult male (AVA FH-1.17), paratype: adult female (AVA FH-1.16 (USNM 274223); Type Locality: Harbor area south of Friday Harbor Laboratories, Friday Harbor, Washington, U.S.A. (48°33′N, 123°04′W); from mud at depth 20 m, collected by A. V. Adrianov, 21 Jul 94.

Other material: Two specimens (Figs. 21–24) mounted for SEM study, from type locality.

Remarks.—Pycnophyes parasanjuanensis, n. sp. resembles only a few other congeners. As it's name implies, it is similar to *P. sanjuanensis* Higgins, 1961. Both species have a wide reticulate-sculptured anterior margin of the first tergite (Figs. 2, 3, 1) (segment 3) and large round zones of thinner cuticle on the midsternal and episternal plates of this same segment (Figs. 1, 5, 7, 15). In addition, both are similar in size, general shape, shape of the midsternal plate and in the arrangement of setae and dorsal processes. However, *P. parasanjuanensis* is easily distinguished from the former species by the shape of the lateral terminal spines (Figs. 1, 2, 4), by the presence of lateral cuticular ridges on the sternal plates (Figs. 1, 6, 8, 17, 24), and by the arrangement of anteromesial thickenings of ventral pachycycli.

Other differences include the width of dorsal placids, and the shape of segment 13. The male of the new species bears lateroterminal protuberances on the caudal margin of the sternites of the terminal segment (Figs. 6, 18). These are unique to this genus, known otherwise in *Kinorhynchus paraneapolitanus* (see Higgins & Adrianov 1991). Two other members of this genus, *P. dentatus* Reinhard, 1881, and *P. robustus* Zelinka, 1928 from European waters, also have a wide sculptured anterior margin of the first tergite, but are distinguished by the arrangement and shape of middorsal processes and anteromesial thickenings of the ventral pachycycli. In contrast to the new species, *P. dentatus* has midventral thickenings on segments 11 and 12 only, and has short lateral terminal spines. *Pycnophyes robustus* has midventral thickenings on segments 8–12 and is further characterized by long lateral terminal spines, 34% of the trunk length, in contrast to *P. parasanjuanensis* (20% of the trunk length). The only other species of *Pycnophyes* having prominent cuticular ridges laterally on sternal plates is *P. corrugatus* Higgins, 1983. This species is distinguished from the new species by the absence of middorsal processes and shape of the areas of thin cuticle on the midsternal and episternal plates.

Pycnophyes parasanjuanensis is the sixth species of Kinorhyncha described from the northwest coast of the United States and from the San Juan Archipelago. It constitutes only the second member of the genus *Pycnophyes* described from the Northeast Pacific Ocean.

Key to Adults of *Pycnophyes*

1. Posterior margin of first tergite (segment 3) with well-developed or subcuticular minute middorsal process 2
– Posterior margin of first tergite always even, without middorsal process 18
2. Middorsal process of first tergite rounded or obtuse 3
– Middorsal process of first tergite spinose, pointed 9
3. Anteromesial thickenings of ventral pa-

chycycli on segments 11–12, adjacent at ventral midline .... *P. greenlandicus* Higgins & Kristensen, 1988

– Anteromesial thickenings of ventral pachycycli midventral thickenings prominent on other segments, adjacent or not adjacent at ventral midline 4

4\. Anteromesial thickenings of ventral pachycycli on segments 6–12 5

– Anteromesial thickenings of ventral pachycycli on segments 9–12 6

5\. Anteromesial thickenings of ventral pachycycli narrowly elongate, most of them longer than half the sternite length, lateral terminal spines about 25% of trunk length .... *P. canadensis* Higgins & Korczynski, 1989

– Anteromesial thickenings of ventral pachycycli shorter than half of sternite length, lateral terminal spines about 10–15% of trunk length .... *P. communis* Zelinka, 1928

6\. Posterior margin of sternite 13 with two midventral conical protrusions extending to the margin of the tergite .... *P. mokievskii* Adrianov 1995

– Posterior margin of sternite 13 without midventral conical protrusions 7

7\. Posteromesial ventral pachycycli of segment 12 prominent, deeply incised anteriorly or elongated posteriorly .. .. *P. spitsbergenensis* Adrianov 1995

– Posteromesial ventral pachycycli not prominent, underdeveloped, not incised, not elongated posteriorly 8

8\. Middorsal processes minute, on segments 3–8(9) .. *P. maximus* Reimer, 1963

– Middorsal processes broadly rounded, on segments 3–12 .... *P. borealis* Higgins & Korczynski 1989

9\. Patches of puncations near lateral margins of sternal plates on segment 4–12 ....*P. iniorhaptus* Higgins, 1983

– Patches of punctations near lateral margins of sternal plates on segments 4–12 absent 10

10\. Middorsal spinous process on segment 12 long, extending well beyond terminal margin .... *P. chukchiensis* Higgins, 1991

– Middorsal spinous process on segment 12 absent or poorly developed 11

11\. Anterior margin of first tergite with wide area of cuticular netting or mosaic pattern; sternal plates of segment 12 with vertical cuticular striations near lateral margins ....*P. dentatus* Zelinka, 1928

– Anterior margin of first tergite without netting or mosaic pattern; sternal plates of segment 12 without cuticular striations near lateral margins 12

12\. Thin area of cuticle at anteromesial margin of episternal plates double or longitudinally divided 13

– Thin area of cuticle at anteromesial margin of episternal plates single or absent 14

13\. Thin area of cuticle at anteromesial margin of episternal plates elongated, about 33% of plate length; anteromesial thickenings of ventral pachycycli of segment 12 widely separated; lateral terminal spines longer than width of segment 12 . . .*P. flaveolatus* Zelinka, 1928

– Thin area of cuticle at anteromesial margin of episternal plates short, less than 20% of plate length; anteromesial thickenings of ventral pachycycli of segment 12 adjacent at ventral midline; lateral terminal spines shorter than width of segment 12 .... *P. calmani* Southern, 1914

14\. Thin area of cuticle at anterior margin of midsternal plate strongly flattened or oval-shaped, round on episternal plates; middorsal processes minute, barely protruding beyond posterior margin of tergite; anteromesial thickenings of ventral pachycycli on segments 11–12 .. .. *P. frequens* Blake, 1930

– Thin area of cuticle at anterior margin of midsternal and episternal plates underdeveloped; middorsal processes elongated; anteromesial thickenings of ventral pachycycli, if present, only on segment 12 15

15\. Segment 2 with 3 dorsal placids .... *P. odhneri* Lang, 1949

– Segment 2 always with 4 dorsal placids 16

16\. Anterior margin of midsternal plate projecting well beyond anteromesial margins of episternal plates; patches of punctations at middorsal processes of tergites ....*P. carinatus* Zelinka, 1928

– Anterior margin of midsternal plate even with, not projecting beyond, anteromesial margins of episternal plates; no patches of punctations at middorsal processes of tergites 17

17. Posterior margin of midsternal plate twice the width of anterior margin .. .. *P. chiliensis* Lang, 1953

– Posterior margin of midsternal plate only slightly wider than anterior margin *P. cryopygus* Higgins & Kristensen, 1988

18. Anterior margin of first tergite scalloped, with one middorsal and two dorsolateral projections, anterior margin between projections concave 19

– Anterior margin of first tergite dentate, coronate (at least seven or more projections) or even 20

19. Tergal plates of segments 4, 5 with middorsal processes .... *P. ponticus* Reinhard, 1881

– Tergal plates of segments 4, 5 without middorsal processes .... *P. kielensis* Zelinka, 1928

20. Anterior margin of first tergite coronate, with prominent middorsal projection and three lateral projections on each side, margin between projections denticulate .....*P. rugosus* Zelinka, 1928

– Anterior margin of first tergite even or evenly dentate without projections ... 21

21. Anterior margin of midsternal plate very narrow, about 25% of posterior margin ......*P. ecphantor* Higgins, 1983

– Anterior margin of midsternal plate relatively broad, about 33–50% of posterior margin 22

22. Anterior margin of first tergite with wide area of reticulate, net-or-mosaic-like pattern 23

– Anterior margin of first tergite without wide area of reticulate, net-or-mosaic-like pattern 24

23. Lateral terminal spines thick, robust and obtuse (not pointed at top); anteromesial thickenings of ventral pachycycli on segments 8–12 .... *P. sanjuanensis* Higgins, 1961

– Lateral terminal spines pointed at top; prominent anteromesial thickenings of ventral pachycycli on segments 10–12 only ... *P. parasanjuanensis*, new species

24. Thin area of cuticle at anterior margin of midsternal plate double, divided into two separated areas .... *P. tubuliferus* Adrianov, 1989

– Thin area of cuticle at anterior margin of midsternal plate single or absent .. 25

25. Lateral terminal spines nearly equal to length of segment 12 .... *P. zelinkaei* Southern, 1914

– Lateral terminal spines longer than combined length of segments 12 and 13 26

26. Thin area of cuticle at anteromesial margin of episternal plates double, divided into two large separated areas: anteromesial thickenings of ventral pachycycli not prominent on any segment ....*P. sculptus* Lang, 1949

– Thin area of cuticle at anteromesial margin of episternal plates, if present, not double; anteromesial thickenings of ventral pachycycli present 27

27. Anteromesial thickenings of ventral pachycycli thin, narrowly elongate, on segments 8–12; anterior margin of first tergite pectinate .... *P. robustus* Zelinka, 1928

– Anteromesial thickenings of ventral pachycycli not narrowly elongate, on other segments; anterior margin of first tergite even or slightly denticulate 28

28. Thin area of cuticle at anterior margin of midsternal plate present 29

– Thin area of cuticle at anterior margin of midsternal plate absent 31

29. Thin area of cuticle at anteromesial margin of episternal plates present; posterior margin of terminal tergite without lateral bulbous protrusions 30

– Thin area of cuticle at anteromesial margin of episternal plates absent; posterior margin of terminal tergite with lateral bulbous protrusions .... *P. emarginatus* Higgins, 1983

30. Sternal plates of segments 11, 12 with strong longitudinal cuticular ridges near lateral margins; anterior margins of tergal and sternal plates without wide areas of cuticular microrelief .... *P. corrugatus* Higgins, 1983

– Sternal plates of segments 11, 12 without cuticular ridges; anterior margins of tergal and sternal plates with wide areas of cuticular microrelief .... *P. egyptensis* Higgins, 1966

31. Thin area of cuticle at anteromesial margin of episternal plates present; anteromesial thickenings of ventral pachycycli on segments 10–12 . . . . *P. longicornis* Higgins, 1983
– Thin area of cuticle at anteromesial margin of episternal plates absent; anteromesial thickenings of ventral pachycycli on segment 12 . . . . *P. beaufortensis* Higgins, 1964

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A new genus and species of ampharetid polychaete from deep-sea hydrothermal vent community in the Azores triple-junction area

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Abstract.—*Amathys lutzi,* a new genus and species of Ampharetinae (Polychaeta: Ampharetidae), is described from active hydrothermal vents on the Lucky Strike segment, close to the Azores triple-junction area of the Mid-Atlantic Ridge. It is found in the same micro-habitat than *Amphisamytha galapagensis* Zottoli, 1983. It differs from all previously known Ampharetinae by the number (17) of thoracic uncinigerous segments.

In 1993, the Lucky Strike expedition (cruise *Atlantis II* 129-6) visited an active hydrothermal field situated at 37°17.538′N and 32°16.490′W in 1626 m. The expedition consisted of six dives of the DSRV *Alvin* and aimed to find and describe active hydrothermal sites and the biological communities associated with venting areas. Based on this first exploration, the *Diva 2* expedition (1994) completed 24 dives of the submersible *Nautile* on the same hydrothermal area. Hydrothermal activity occurs around a lava lake situated in the depression between three cones which form the summit of a seamount, at the center of a long broad ridge segment that extends from 37°00′N to 37°35′N; hydrothermal activity includes flanges with pool temperature ≤200°C to black smokers venting fluids as hot as 333°C (Langmuir et al., 1993, pers. obs.). The dominant organisms in these hydrothermal fields are populations of a new species of mussel (bathymodiolid) that colonizes hydrothermal sulfide edifices and their vicinity. Other less conspicuous components of the fauna include new species of alvinocarid shrimps, peracaridan crustaceans, bythograeid crabs, sea-urchins and several species of polychaetes including a polynoid commensal of mussels (Van Dover et al. 1993). Ampharetid polychaetes were sorted from mussel washings, or found in tubes attached to mussel shell hinges and to sulfide or basaltic rocks.

Materials and Methods

The specimens were collected using *Alvin* and *Nautile* manipulators. The samples were brought to the surface inside insulated boxes and were washed and sieved through a 250-μm mesh. They were sorted partially aboard the mother-vessels, then fixed in buffered formalin and preserved in 80% ethanol after a one day fixation. In the laboratory, specimens are dehydrated to ethyl alcohol absolute, critical point dried, put on stubs and coated with gold. Finally, the specimens were examined using a Philips XL 30 scanning electron microscope.

Order Terebellida
Family Ampharetidae Malmgren, 1865
Subfamily Ampharetinae Chamberlin, 1919
Amathys, new genus

Diagnosis.—Thorax with 20 setigerous segments, of which the last 17 are uncinigerous. Abdomen tapering rapidly with 16–20 uncinigerous segments, no notopodial or neuropodial cirri or vestigial abdominal notopodia. Notopodia of the first setigerous segment reduced. Four pairs of smooth branchiae. A buccal ciliated membrane bearing dorsally clavate and grooved tentacles. Anus terminal without cirri. No modified segment.

Genus.—Amathys

Type species.—Amathys lutzi

Etymology.—Amathys is an anagram of *Samytha.* Gender is male.

Remarks.—This genus differs from all known genera of Ampharetinae by having 17 uncinigerous thoracic segments.

Amathys lutzi, new species

Figs. 1, 2, 3

Etymology.—This species is dedicated to Dr. Richard A. Lutz from Rutgers University, New Jersey, USA in an attempt to express our friendly thanks for several opportunities that he gave us to dive with the DSRV *Alvin* in several Eastern Pacific hydrothermal vent areas.

Material.—Lucky Strike expedition: dive *Alvin* 2606, 1 June 1993 (M. Tivey, L. Saldanha, observers): 5 specimens, dive *Alvin* 2607, 2 June 1993 (C. Van Dover, T. Emerson, observers): 1 specimen. *Diva 2* expedition: dive *Nautile* 912/40-01, 3 June 1994 (A.M. Alayse, observer): 1 specimen; dive *Nautile* 913/41-02, 4 June 1994 (P. Crassous, observer): 15 specimens; dive *Nautile* 915/43-04, 6 June 1994 (D. Desbruyères, observer): 2 specimens (including holotype); dive *Nautile* 916/44-05, 7 June 1994 (F. Barriga, observer): 117 specimens; dive *Nautile* 917/45-06, 8 June 1994 (L. Saldanha, observer): 45 specimens. All specimens from different vent sites within the Lucky Strike area (latitude from 37°17,25′ to 37°17,63′N, longitude from 32°16,50′ to 32°16,90′W, depth from 1622 to 1725 m). All specimens from washings of mussel clumps or tubes attached to mussel shells and sulfide or basaltic rocks. Holotype (USNM 170025), Paratypes (MNHN, Paris, UD 851/A928).

Description.—Body whitish, without color pattern when preserved. Holotype complete, about 14.8 mm in length and 4.3 mm in greatest width, with 38 setigerous segments. Size of paratypes from 1.25 mm to 15.7 mm in length and from 0.25 mm to 4.4 mm in width. Paratype used for SEM observations complete, 6 mm long and 2.1 mm wide. Prostomium indistinctly trilobed, lacking glandular ridges and eye spots but bearing two transversal nuchal slits underlined by secretions and mineral particles (Fig. 2a). Buccal tentacles smooth, entire, clavate, grooved and ciliated (Fig. 2b), inserted on the latero-dorsal part of a folded "feeding" membrane heavily ciliated (Fig. 2c) and sprinkled with organic and mineral aggregates. First two segments (I and II according to Day 1964) achaetous and fused, forming the lower lip. Segment III lacking palae. Thorax with twenty setigerous segments, the last seventeen being uncinigerous. The first setiger, segment IV, with a vestigial notopodium and reduced bundles of capillary setae. Four pairs of smooth, cylindrical branchiae on dorsal surface of segments III-VI, all similar, regularly attenuated. Branchial length about ¼ of the body length in preserved specimens. Branchiophores short and not fused. Small mid-dorsal gap between the two branchial groups but no web. The two outer branchiophores inserted between segments III and IV, the two inner branchiophores in segments V and VI. Notopodia increasing in size from setigerous segments 2 to 5. Notopodium cylindrico-conical, slightly flattened anterio-posteriorly with two series of winged capillary setae (one short, the other approximately 250 μm long). Notosetae capillary slightly unilimbated, covered with continuous layer of minute spinelets when viewed under scanning electron microscope (Fig. 3a, b). Neuropodial lobes (uncinigerous pinnules) from setiger 4, each with a single row of toothed uncini, tips oriented forward (23–30 uncini per row). 17 uncinigerous tori on thoracic segments and 16–20 uncinigerous pinnules on abdominal segments. Thoracic

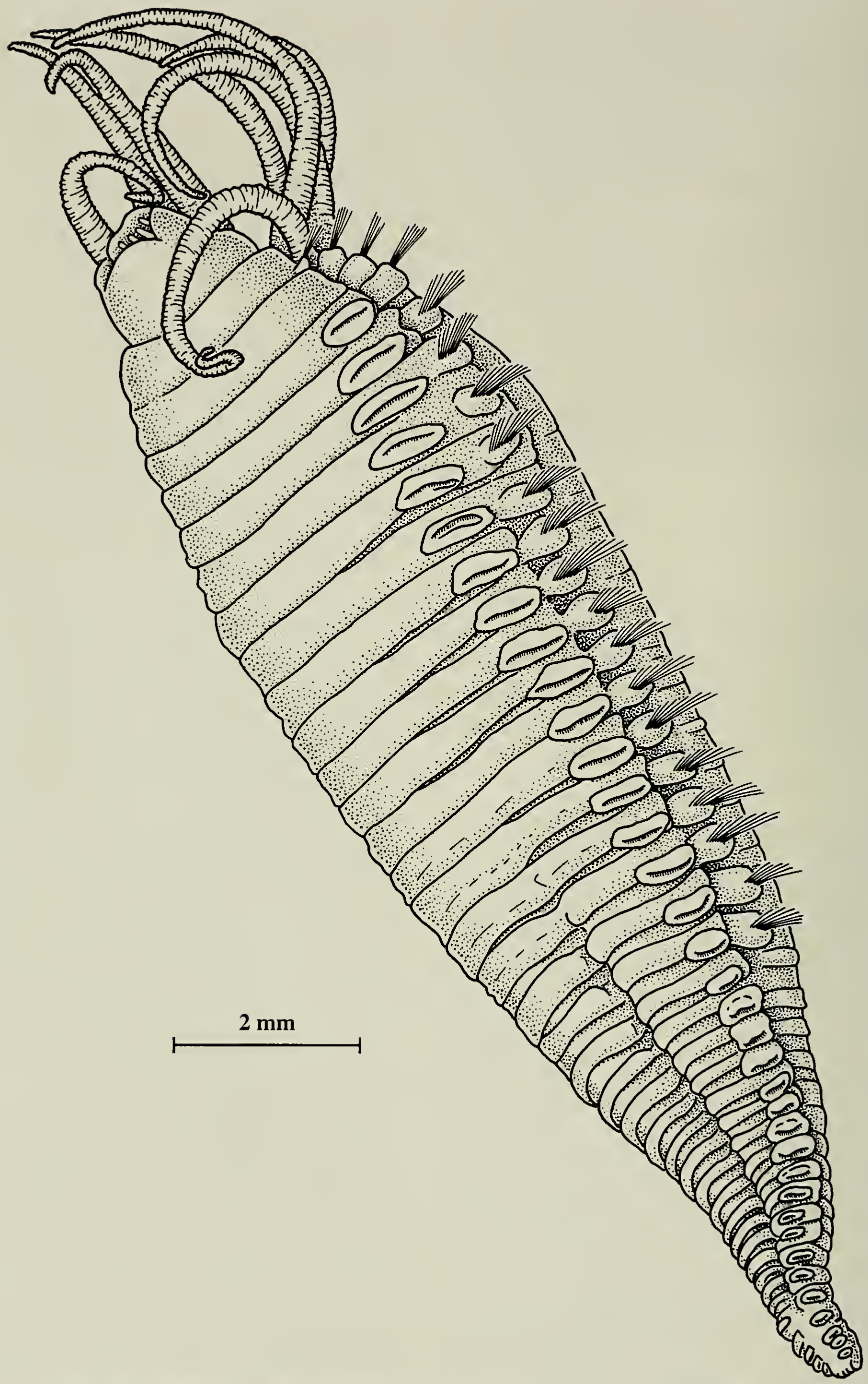

Fig. 1. *Amathys lutzi,* new genus, new species. Entire animal (holotype) in ventro-lateral view.

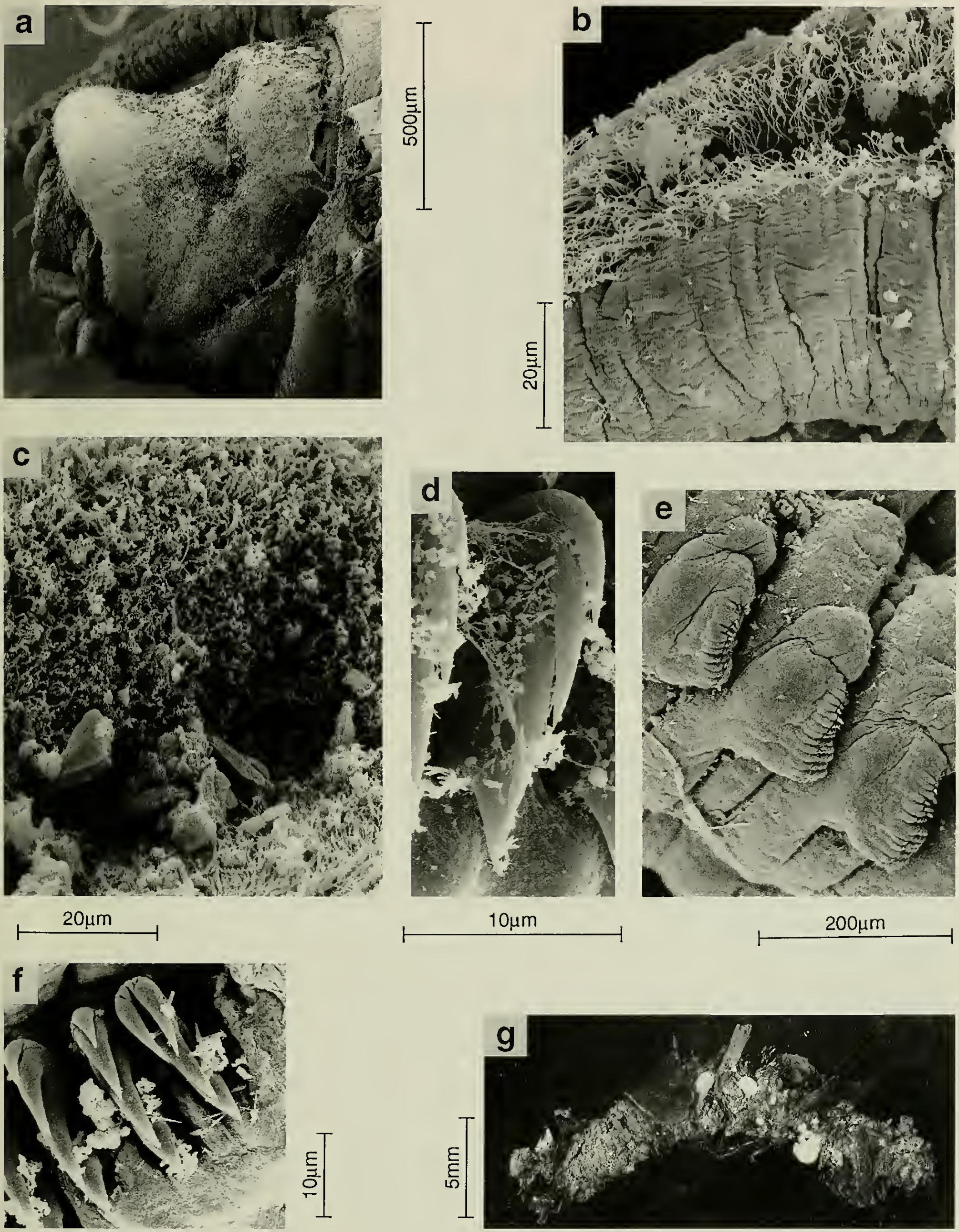

Fig. 2. *Amathys lutzi,* new genus, new species. a, prostomium in dorso-lateral view (left side). b, ciliated groove of a buccal tentacle. c, detail of the ciliated surface of the fold, buccal membrane sprinkled with organic and mineral aggregates. d, thoracic uncinus in lateral view. e, abdominal parapodia in ventro lateral view (left side of the body). f, thoracic uncini with a duplication of the upper tooth. g, tube.

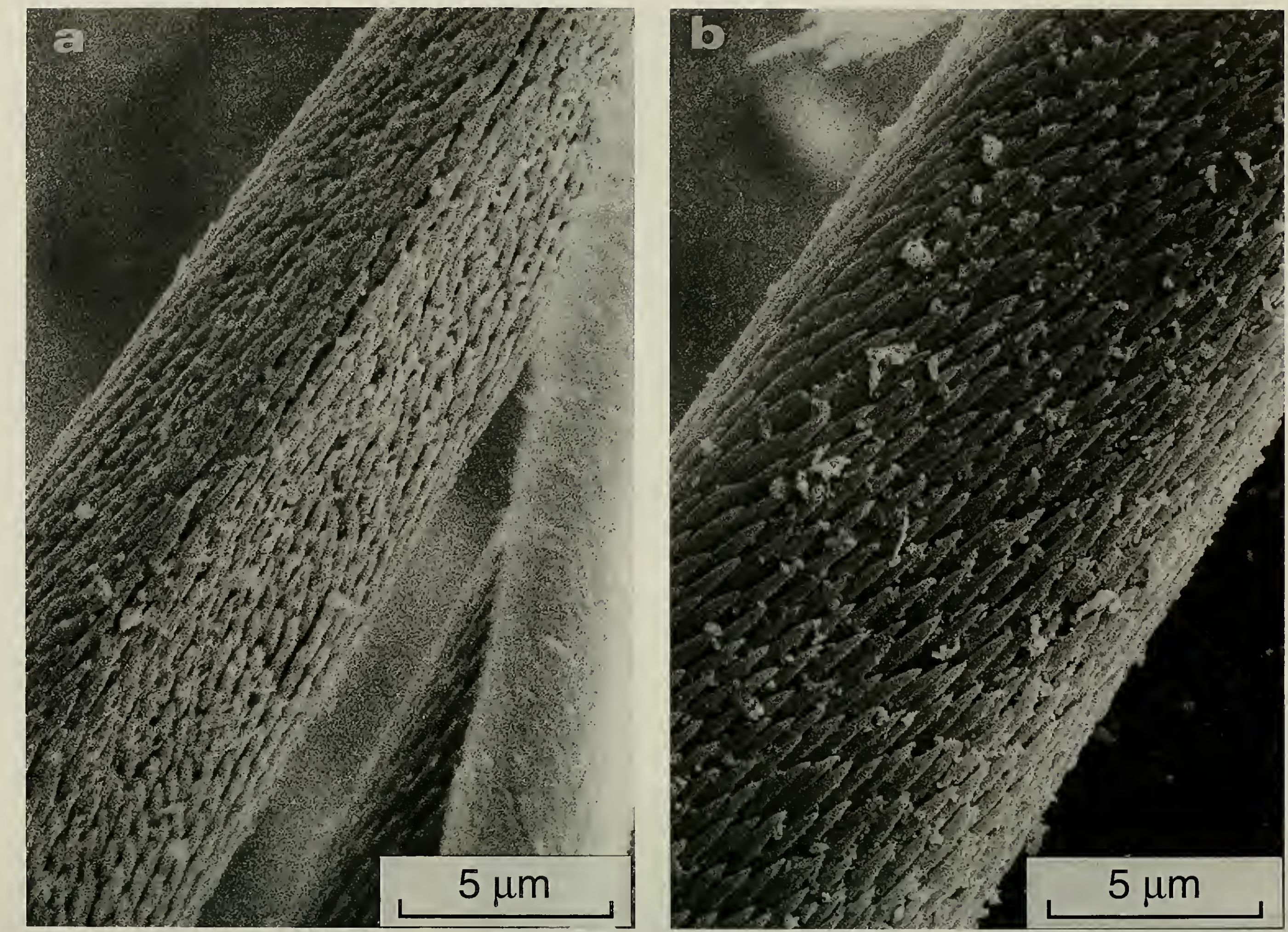

Fig. 3. *Amathys lutzi,* new genus, new species. SEM microphotographs of a thoracic capillary setae. a, distal part of a setae. b, proximal part of the same.

parapodia without cirri. Each thoracic uncinus with a single row of four teeth (Fig. 2d), the upper ones, sometimes but seldom, laterally duplicated (Fig. 2f). Abdominal uncini with same shape and size as thoracic ones. Small teeth present at the base of the main ones laterally on thoracic and abdominal uncini. A rounded glandular pad above each abdominal uncinigerous pinnule (Fig. 2e). Abdominal notopodial lobes absent. Abdomen short (one-third of the body length). Pygidium terminal without circle of papillae or anal cirri. No indication of sexually mature specimens.

Tube.—Mucus lined tubes covered with rusty colored mineral particles, agglomerated with mussel periostracum or byssal threat fragments as well as pieces of gastropod shells; about three times worm length (Fig. 2g). Sometimes, tube simple covered with gray mud.

Discussion.—The morphology of this species is reminiscent of that of *Amphisamytha galapagensis* Zottoli, 1983 and that of *Amphisamytha fauchaldi* Solis-Weiss & Hernández-Alcántara 1994, both found within the Pacific hydrothermal vent environment. In the Atlantic Ocean, McHugh & Tunnicliffe (1994) report, the presence of *Amphisamytha galapagensis* listed as "Ampharetidae gen. sp." by Segonzac (Segonzac 1992); we do not agree with this assumption and we here confirm, after discussion with M. Segonzac, that all specimens (including Segonzac's specimens) from both Snake Pit (M.A.R., 23°20′N) and Broken Spur (M.A.R., 29°10′N) vent fields were damaged and macerated and that their bad shape doesn't allow determination, even at the generic level.

Amathys lutzi, new species, clearly belongs to a group of species having in common a ciliated buccal membrane, grooved ciliated or entire clavate buccal tentacles, no palae, reduced setation on segment IV. This group gathers species having three or four pairs of branchiae, different numbers of thoracic uncinigerous segments, one or two rows of teeth on the thoracic unicini. This collective group gathers together *Amphisamytha galapagensis* Zottoli, 1983, *Amphisamytha fauchaldi* Solis-Weiss & Hernández-Alcántara, 1994, *Amythas membranifera* Benham, 1921 and *Samytha californiensis* Hartman, 1969. *A. lutzi* differs from them by the presence of 17 uncinigerous thoracic segments instead of 14 in *A. galapagensis* and *A. fauchaldi* and the shape of abdominal uncini of the anal part in the former species (Zottoli 1983). This high number of uncinigerous thoracic segments is unusual among Ampharetinae; until the present work it varied within the subfamily from a minimum of 9 (*Mugga* and *Egamella*) to a maximum of 15 (*Weddellia*). Since Day's (1964) revision, the number of thoracic uncinigerous segments has been used by taxonomists as a character that is consistent at the generic level.

Day's revision was justified by the high number of genera (27) and the difficulty of the recognition of genera. Day (1964) proposed to use the number of gills, the number of thoracic uncinigerous segments, the presence of a glandular ridge on the prostomium and the presence of notopodial cirri as generic characters. Since then, 24 new genera were described, all of them still remaining monospecific (see Holthe 1986 for review, Jirkov 1986, Solis-Weiss 1993). In 1979, using multivariable analysis on a phenetical matrix based on Day's taxonomic characters, Chardy & Desbruyères (1979) demonstrated that these characters are only discriminant among a few major shallow water genera like *Amphicteis, Ampharete, Amage* or *Anobothrus* but that they are poorly discriminant in the case of most of the abyssal species which look as a continuum when using Day's characters. Whatever should be the present generic clustering for Ampharetid species, it suffers deeply from the history of sampling which started in shallow waters where evolutive radiation is limited to a few rather well defined genera. Sampling of the deep-sea benthos, which increased rapidly since the Challenger expedition, brought numerous new forms whose morphological patterns do not fall inside the shallow water model variations. In deep-sea species, the different generic characters as cited above evolve independently, thus leading to a continuum of species where generic patterns are difficult to recognize either by aggregation or by dichotomy (Chardy & Desbruyères op. cit.). Unfortunately, most of the new taxa were described on the basis of unique specimens that were often truncated and sometimes damaged during recovery of samples and sieving of abyssal sediment, which led to a difficult situation in the scope of a new revision.

In his recent work on Terebellomorpha, Holthe (1986) proposed to gather *Samytha, Samythella, Eusamytha, Amythas, Demunciger* and *Alkmaria* in a new tribe named *Samythini* for Ampharetinae with tentacles smooth, no glandular ridge in the prostomium. Most of these genera have a rather developed buccal membrane as does *Amathys lutzi.* Surprisingly, Holthe placed *Amphisamytha* among "Ampharetinae with uncertain tribal affinities" when the diagnosis of this genus fits well with the characteristics of the tribus *Samythini.* I propose here to include *Amphisamytha* and *Amathys* inside *Samithini.*

The erection of the new genus *Amathys* is a conservative position which takes into account the classical taxonomic characters as displayed in Day's revision (1964). In that context, the erection of a new genus is fully justified, but, as mentioned by Holthe (1986), ". . . when all genera become monotypic, the generic category has become void of information." Full phylogenetic analyses of morphological and molecular characters may lead to major generic revisions of the Ampharetinae in future.

Acknowledgments

We thank Philippe Crassous (scanning electron microscope) and Violaine Martin (drawings) for technical assistance, Patrick Briand (CENTOB) for sorting specimens and Dr. C. Langmuir, chief scientist of the Lucky Strike expedition, who kindly invited one of us (DD) to participate to the cruise and to dive with the DSRV *Alvin.*

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Description of a new branchiobdellidan species, with observations on three other species, and a key to the genus *Pterodrilus* (Annelida: Clitellata)

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Abstract.—*Pterodrilus annulatus,* a new species, is described from Tennessee, and compared with the west coast species *Cambarincola serratus.* An emended diagnosis of *Pterodrilus* and new observations on the anatomy of *P. cedrus, P. choritonamus* and *P. hobbsi* are presented. A key to the species of the genus, based on external segmental features, is given.

Information on the branchiobdellidan genus *Pterodrilus* was reviewed and extended by Holt (1968). The genus appears to be restricted to the eastern United States and its phylogenetic relationship with other genera was discussed in a synopsis of the Branchiobdellida (Holt 1986). More recently *Pterodrilus* was included in a checklist of North and Central American cambarincolids prepared by Holt & Opell (1993).

Collections of the crayfish, *Orconectes placidens* (Hagen, 1870), from a single site on the Harpeth River south of Franklin, Tennessee, yielded eight species of branchiobdellidans. Usually, at least six of these species were present on a single host. Live branchiobdellidans were relaxed in Perrier Water, fixed in formalin-ethanol-acetic acid (FAA), dehydrated in a graded series of ethanol:water solutions, cleared in methyl salicylate, and mounted on a microscope slide in Canada balsam (Brinkhurst & Gelder 1991). The anatomical nomenclature used in this paper follows that described in Brinkhurst & Gelder (1991) with two exceptions. The spermiducal gland and ejaculatory duct are now referred to as the glandular atrium and muscular atrium respectively so that the terminology becomes consistent with that used in the rest of the Clitellata. Specimens were examined from the collections of Perry C. Holt (PCH), the National Museum of Natural History, Smithsonian Institution (USNM) and the author (SRG).

During the process of identifying the branchiobdellidans from the Harpeth River, a new species of *Pterodrilus* was recognized. To confirm the new species status, type specimens of four species of *Pterodrilus* and *Cambarincola serratus* Holt, 1981 were borrowed from the National Museum and examined. These studies resulted in a clarification of the published descriptions of some of the anatomical features in certain pterodrilids, and the correction of some previously identified specimens. The keys constructed by Holt (1968) and Holt & Opell (1993) for identifying species of *Pterodrilus* utilize both external and internal anatomical features. However, following my examinations of the literature and specimens, a key was devised that used only external anatomical features. This key should greatly simplify the identification of both living and preserved specimens for biologists interested in the genus *Pterodrilus.*

Pterodrilus Moore, 1895

References.—Moore 1895:449–456, Goodnight 1940:58, Holt 1968:1, 3, 1986: 698.

Diagnosis.—Single anterior nephridial pore; vasa deferentia entering glandular atrium entally; body less than 2.0 mm long; dorsal ridge across segment 8, other segments may have ridges and additional finger-like projections; dental formula 5/4; prostate gland arises from ectal to mid region of glandular atrium, and incompletely separated from it; penis muscular, protrusible; spermatheca present (emended by SRG).

Pterodrilus annulatus, new species
Fig. 1A–F, 3G

Type specimens.—Holotype, USNM 169996, and two paratypes, USNM 169997, and 169998 on *Orconectes placidens* (Hagen) removed from the Harpeth River, 6 miles SE of Franklin, Williamson Co., Tennessee (35°59′N, 86°32′W) by S. R. Gelder and R. O. Brinkhurst, 17 Oct 1990.

Diagnosis.—Body about 1.0 mm long, very prominent transverse ridges across the dorsal and lateral surfaces of segments 2 through 8, the last is fan-like, supernumerary muscles present, no dorsal segmental appendages; dorsal lip four slight rises; oral papillae 16; jaws small, lightly sclerotized, dorsal kidney-shaped, ventral quadrangular, dental formula 5/4; glandular atrium subcylindrical, length about ½ and width ¼ diameter of segment; prostate gland length and diameter subequal to glandular atrium, differentiated, ental bulb absent; muscular atrium length about ½ glandular atrium; bursa ovoid, length about ⅓ segment diameter, penial sheath in ental ⅓ of bursa; spermatheca length about 1.2 times diameter of segment, thick-walled ectal duct about ⅓ total length, bulb oval to sacculate, ental process absent.

Etymology.—For the prominent dorsolateral ridges on the body segments.

Description.—Eleven fixed specimens average 1.05 mm in length and range from 0.90 to 1.23 mm long (Fig. 1A). Live, unstressed specimens measure about 1.50 mm long. The body is essentially rod-like with prominent transverse ridges across the dorsal and lateral surfaces of segments 2 through 8. All ridges contain supernumerary muscles (Fig. 1C, sm), with the posterior-most ridge being the largest, and fan-like. Segment 1 may occasionally show a pronounced transverse ridge. However, this is a fixation artifact caused by the head retracting into the segment. The head is greater in diameter than segment 1 and about equal to the posterior attachment disc.

The peristomium consists of two lips: the dorsal usually has four slight rises although the margin may appear smooth, while the ventral lip has a median emargination. There are 16 oral papillae around the mouth. The jaws are small, <⅙ head diameter in width, with sharply pointed teeth and a dental formula of 5/4 (Fig. 1B). The dorsal jaw is kidney-shaped and the ventral jaw is quadrangular when seen in dorsoventral aspect. The pharynx has three sulci and the median is the largest.

The male reproductive organs in segment 6 extend about ¾ of the way dorsad (Fig. 1C). The subcylindrical, glandular atrium is about ½ the diameter of the segment long, and about ¼ wide (short and thick). The epithelial cells contain densely packed granules, and deferent lobes are absent. The prostate gland arises from ectal third of glandular atrium, the length and diameter are subequal to those of the glandular atrium. The ectal portion of the prostate gland contains granular cells and the remainder is lined with highly vacuolated, "differentiated" gland cells. An ental bulb is absent. The muscular atrium length is about ½ that of the glandular atrium, and enters the bursa. The bursa is generally ovoid, and about ⅓ the diameter of the segment in length. The penial sheath is formed from the ental ⅓ of the bursa and partially surrounds the subspherical penis. Although the penis has not been observed in the projected position, it is referred to as "protrusible" following the functional interpretation made by Holt (1986).

The spermatheca length is about 1.2

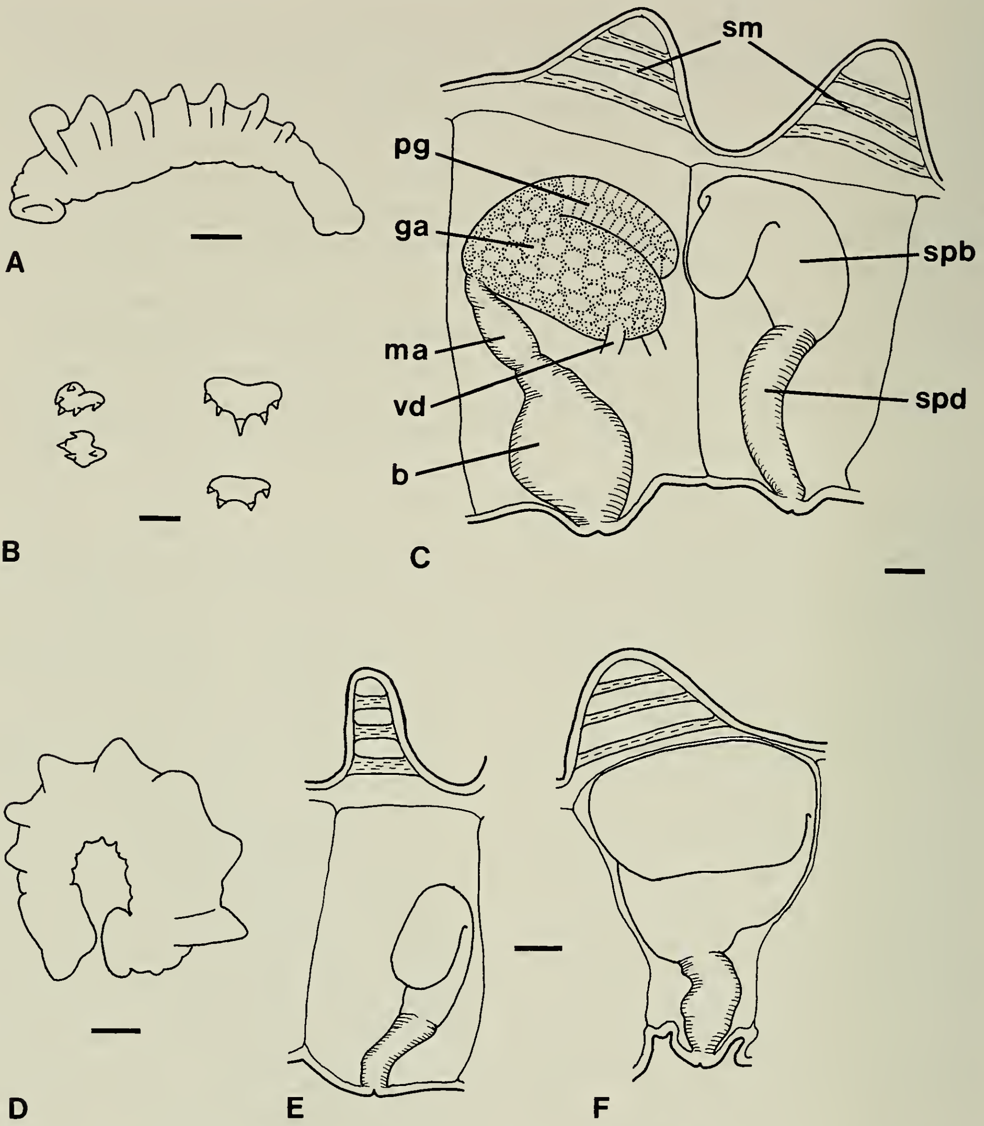

Fig. 1. *Pterodrilus annulatus*: A, Lateral view of holotype, scale bar = 100 μm; B, Oblique lateral and dorsal views respectively of the dorsal and ventral jaws, scale bar = 10 μm; C, Lateral view of the reproductive systems in segments 5 and 6 in the holotype, scale bar = 20 μm; D, Lateral view of a curled paratype specimen, scale bar = 100 μm; E and F, Lateral views of segment 5 in two paratype specimens to show the range in size of the spermatheca, scale bar = 25 μm. Abbreviations: b, bursa; ga, glandular atrium; ma, muscular atrium; pg, prostate gland; sm, supernumerary muscles; spb, spermathecal bulb; spd, spermathecal duct; vd, vas deferens.

times the diameter of segment 5 (Fig. 1C). The thick-walled, ectal duct is about ⅓ the total length of the organ. The bulb is oval, frequently with a recognizable narrowing ental region, but an ental process is absent.

Variations.—The transverse segmental ridges are less obvious when a specimen is fixed in the curled position (Fig. 1D). The shape of the spermathecal bulb ranged from a tubular shape, which happened to be reflexed and contained no spermatozoa (Fig. 1E), to a sacculate bulb that occupied most of the dorsal segment and was filled with spermatozoa (Fig. 1F). All other apparent variations could be accounted for by contraction of the specimen due to its state at the time of fixation.

Other branchiobdellidans on the host.—*Ankyrodrilus legeaus* Holt, 1965; *Cambarincola chirocephala* Ellis, 1919; *C. fallax* Hoffman, 1963; *C. philadelphicus* (Leidy, 1851); *Oedipodrilus oedipus* Holt, 1967; *Pterodrilus hobbsi* Holt, 1968; and *Xironodrilus formosa* Ellis, 1918.

Remarks.—Specimens of *P. annulatus* were observed on the dorsal and lateral surfaces of the carapace, abdomen, and the cephalothoracic appendages of the host. Usually specimens were observed in a cleft or by a bunch of setae supporting large populations of diatoms. *Pterodrilus annulatus* were seen to ingest these diatoms and they appear to form a significant portion of the diet based on the intestinal contents of fixed specimens.

Adjacent to the setal clumps and in the clefts of the exoskeleton, *P. annulatus* was often observed feeding alongside specimens of *P. hobbsi.* The two species showed no aggressive behavior towards one another.

This manuscript was originally submitted for publication in 1993. During the subsequent review period the author obtained a list of the branchiobdellidan species deposited in the National Museum. The collection contained a specimen (USNM 99811) with the unpublished, and therefore unrecognized name of *Pterodrilus annulatus.* This specimen, along with three others from two different species were mounted on the same slide. These branchiobdellidans were subsequently remounted on separate slides. All of these specimen were from lot USNM 99807 (1-769), "Unidentified Branchiobdellids," a collection removed from *Orconectes neglectus neglectus* and *Orconectes ozarkensis* by Perry C. Holt on 7 July 1958, obtained at Wildcat Creek adjacent to U.S. Route 68, Benton County, Arkansas (Worm General Catalog, National Museum of Natural History, Smithsonian Institution, Washington, DC). Two specimens of *P. annulatus* were obtained from this lot and mounted for species confirmation (USNM 169999, USNM 170000). All three branchiobdellidans were of the same species as that already described by the author. To avoid future problems, the author withdrew his manuscript and changes the name of his new species to *P. annulatus.*

Pterodrilus annulatus has an external appearance and size very similar to *Cambarincola serratus* Holt, 1981, reported from Idaho. However, *C. serratus* differs from *P. annulatus* in that the former has a dental formula of 5/5, the differentiated prostate gland arises from the glandular atrium very close to the muscular atrium entrance, the penis fills over two-thirds of the bursal atrium, and the long spermatheca has a subspherical terminal bulb. Although these anatomical differences appear obvious, the effects of fixation and specimen orientation frequently make the differences much more subtle.

Specimens of the crayfish *Orconectes leptogonopodus* and *O. palmeri longimanus* were collected from a site adjacent to U.S. Route 270, 2.3 miles east of Mount Ida, Montgomery County, Arkansas, by P. C. Holt on 23 June 1960. Four branchiobdellidans from this collection were mounted on a slide, USNM 100356 (= PCH 1090), and identified as *Cambarincola serrata* by Holt [all details come from the Worm General Catalogue under USNM 100356]. During the present investigation, these four specimens were remounted on separate slides, USNM 100356, USNM 170002, USNM 170003, USNM 170004, and identified as *P. annulatus.* This correction has maintained the reported distributional separation of the western *C. serratus* and the eastern *Pterodrilus* spp.

Discussion.—Unlike most of the species in the genus, *P. annulatus* can be grouped with *P. choritonamus* and *P. missouriensis,* as they also lack dorsal segmental appendages. The presence of a "differentiated" prostate gland in *P. annulatus* separates it from *P. missouriensis,* but provides a character in common with the rest of the species in the genus.

Holt (1968) reviewed the species of *Pterodrilus* and discussed in great detail the "Primitive *Pterodrilus,*" "Phylogeny of the Genus," and the "Places of Origin and Migration." Observations on *P. annulatus* have not resolved or clarified any of the concepts addressed by Holt, and so no value is seen in discussing these issues here.

Emmended Species Descriptions

Pterodrilus cedrus Holt, 1968
Fig. 2A–B, 3E

Specimens.—Holotype and five paratypes (USNM 36464, = PCH 1396), and USNM 36465-36468.

Brief description.—Body terete 1.0 to 1.3 mm long, low dorsal ridges on segments 2 through 7 and prominent ridge across segment 8 with 5 finger-like projections (Fig. 3E), supernumerary muscles present; dorsal lip smooth; oral papillae present; dental formula 5/4; male genitalia extend upwards just beyond the level of the intestine; glandular atrium length about ⅓ segment diameter; prostate gland ends subterminal to glandular atrium, prostate [vacuolated] differentiated, ental bulb absent; muscular atrium length about two-thirds the glandular atrium; bursa oval, length about ⅓ segment diameter, penial sheath filling ental ½ of bursa; spermatheca length about 1.3 times segment diameter, ectal duct about ⅓ length, bulb tubular to oval, ental process absent.

Variations.—The prominence of the dorsal ridges on segments 2 though 7 depends on the degree of contraction and extent of curvature of the specimen. The shape of the spermathecal bulb varies greatly depending on the amount of sperm present in the lumen and the degree of displacement as it bends over the intestine (Figs. 2A and B).

Hosts.—*Orconectes placidus* (Hagen), *O. rusticus* subspecies, *O. juvenilis* (Hagen) and *Cambarus tenebrosus* Hay from Holt (1968:23).

Distribution.—Clay County, Tennessee from Holt (1968:21).

Remarks.—The holotype and three paratypes show five short finger-like projections which is contrary to the four reported by Holt (1968:21). The length of the muscular atrium is usually about ⅔ that of the spermiducal gland. However, in the holotype it is stretched to be of equal length. The spermatheca has an ectal duct ⅓ to ½ the total length of the organ, and not ⅔ as drawn by Holt (1968:22) in his figure 5a. An examination of the paratypes support the revised ratio.

Pterodrilus choritonamus Holt, 1968
Fig. 3I

The type description reports an ental process on the spermathecal bulb (Holt 1968: 27). However, an examination of the holotype (USNM 36471, = PCH 1395) and two paratype (USNM 35472a,b, = PCH 1395) specimens revealed that an ental process is absent. The ental end of the elongate spermathecal bulb is simply bent over the intestine and gives the appearance of a "process". The presence or absence of a spermathecal ental process is one of the criteria used in branchiobdellidan taxonomy (Holt 1968).

Pterodrilus hobbsi Holt, 1968
Fig. 2C, 3F

Specimens.—Holotype (USNM 36486), five paratypes (USNM 36487), 194 other specimens (USNM 36488-36508), and (SRG 31–35).

Brief description.—body terete, 1.3 to 1.7 mm long, supernumerary muscles absent, dorsal ridge only across segment 8 with 5 finger-like projections (Fig. 3F); dorsal lip smooth; male genitalia extends to dorsad of segment; glandular atrium length about half segment diameter; prostate gland ends subterminal to glandular atrium, prostate [vacuolated] differentiated entirely or

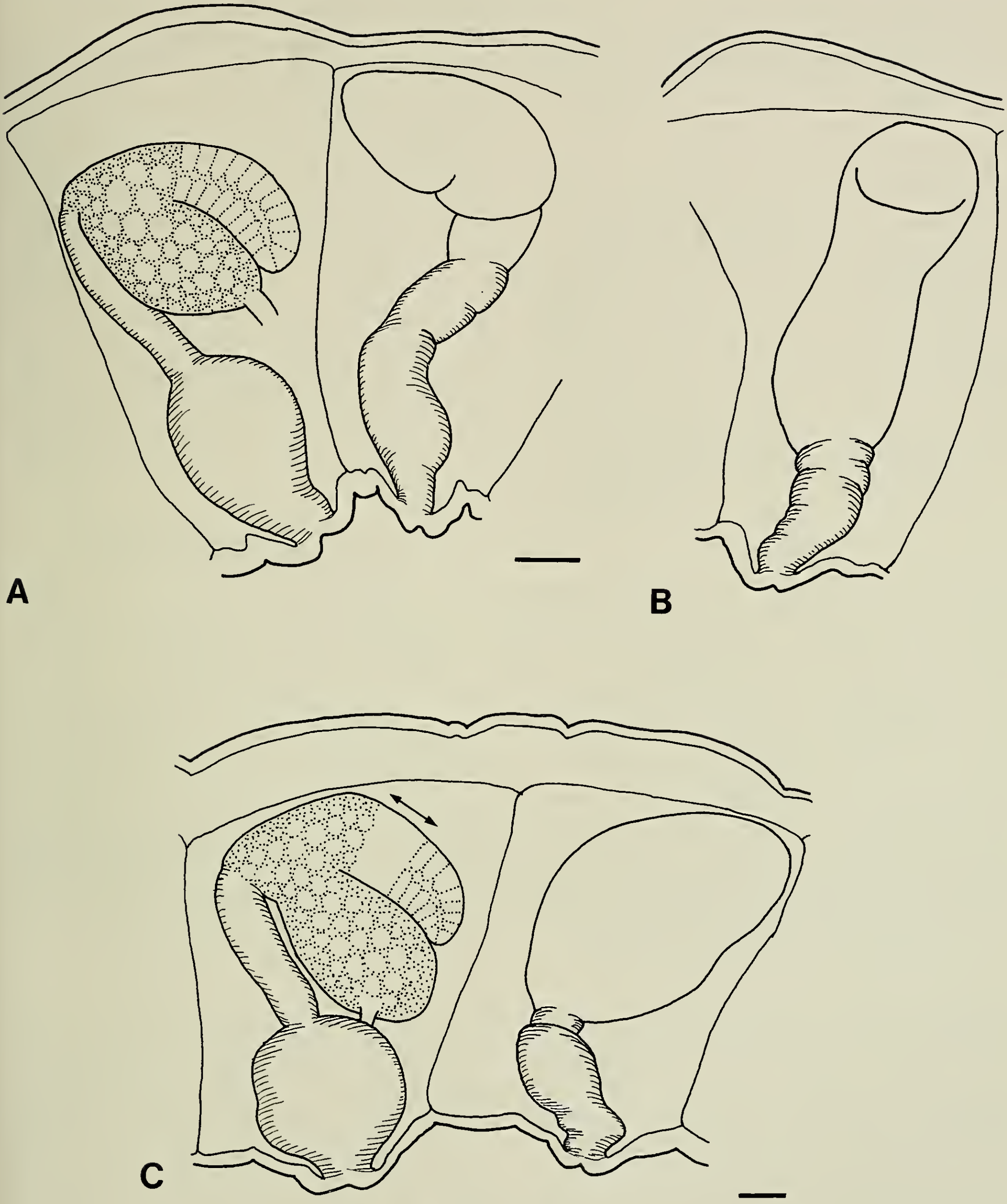

Fig. 2. *Pterodrilus cedrus*: A, Lateral view of the reproductive organs in segments 5 and 6 in the holotype; B, Lateral view of the spermatheca in segment 5 in a paratype, scale bar = 25 μm. *Pterodrilus hobbsi:* C, Lateral view of the reproductive systems in segments 5 and 6 in the holotype, showing the variation in the prostate gland with the double headed arrow, scale bar = 25 μm.

ental ⅔, ental bulb absent; muscular atrium length subequal to glandular atrium, bursa subspherical length ¼ segment diameter, penial sheath filling ental ⅓ of bursa; spermatheca length about 0.8 to 1.1 times segment diameter, duct about ⅓ length, bulb ovoid, ental process absent.

Variations.—The dorsal finger-like pro-

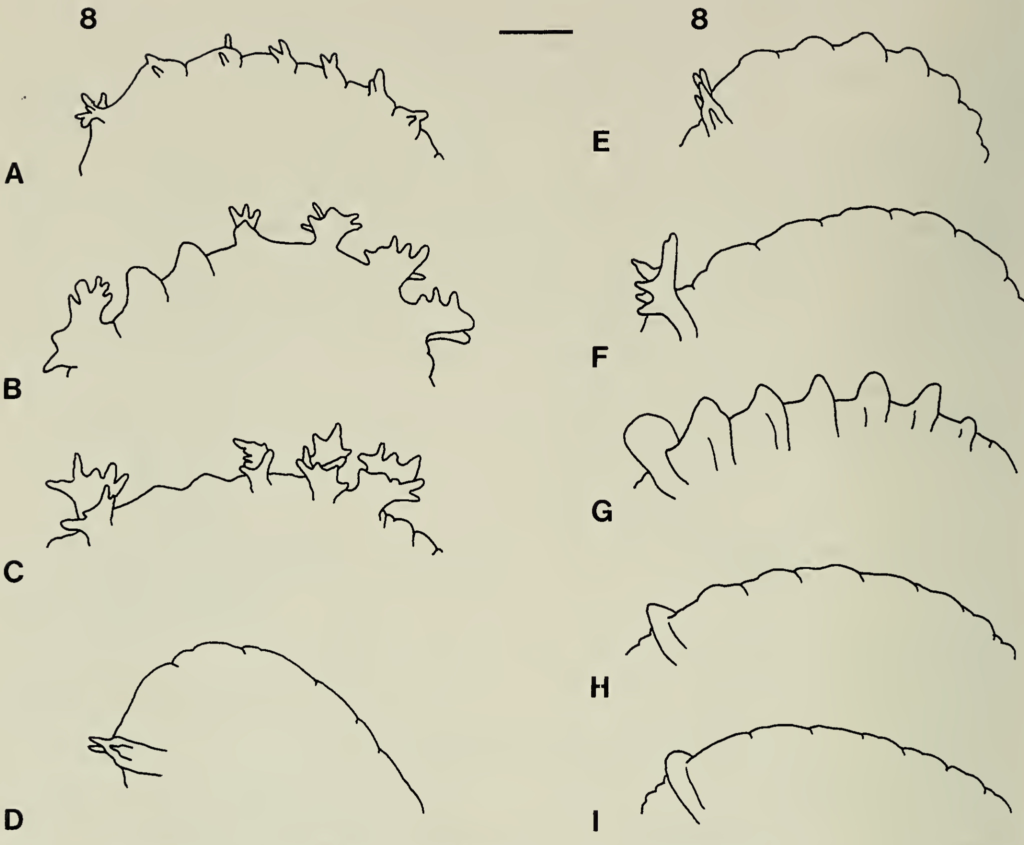

Fig. 3. Lateral view of the dorsal surface of segments 1 to 8 in nine species of *Pterodrilus*: A, *P. distichus*; B, *P. simondsi*; C, *P. alcicornus*; D, *P. mexicanus*; E, *P. cedrus*; F, *P. hobbsi*; G, *P. annulatus*; H, *P. missouriensis*; I, *P. choritonamus* (A, B, and C were redrawn from Holt, 1968), scale bar = approximately 200 μm. Each figure is arranged so that its respective segment 8, as labelled on the top row, is aligned in a column for ease of comparison. Abbreviations: 8, segment 8.

jections vary in length and spacing, therefore this is a dubious character for separating *P. hobbsi* from *P. cedrus*. The glandular atrium and prostate glands also differ slightly in relative length, and the extent of vacuolation in the prostate varies (Fig. 3, double-headed arrow). The size of the spermathecal bulb depends upon the amount of sperm product being stored and may be as small as ¼ the size shown in Fig. 2C.

Hosts.—*Cambarus tenebrosus* Hay, *C. longulus longirostris* Faxon, *C. parvoculus* Hobbs & Shoup, *C. longulus chasmodactylus* James, *C. robustus* Girard, *C. veteranus* Faxon, *C. friaufi* Hobbs, *C. extraneus* Hagen, *C. bartonii cavatus* Hay, *C. sciotensis* Rhoades, *C. distans* Rhoades, *C. bartonii bartonii* (Fabricius), *C. longulus longulus* Girard, *C. latimanus* (LeConte), *C. stratus* Hay, *Cambarus* species, *C. bartonii* subspecies; *Orconectes erichsonianus* (Faxon), *O. juvenilis* (Hagen), *O. rusticus forceps* (Faxon), and *Orconectes* species—from Holt (1968:20) and *Orconectes placidens* (Hagen, 1870).

Distribution.—This is summarized by Holt (1968) in his figure 9 and in a list of river systems and counties. For consistency, a distribution by counties has been compiled from the Worm General Catalogue of the material that Holt (1968:20) deposited in the museum:

Lauderdale County, Alabama; Harlan County, Kentucky; Alleghany County, North Carolina; Anderson, Grainger, Hawkins, Johnson, Lawrence, McMinn, Overton, Roane, Unicoi, and Union counties, Tennessee; Bland, Carroll, Dickenson, Lee, Scott, and Washington counties, Virginia, and a new record from the Harpeth River, Williamson County, Tennessee (see type location of *P. annulatus*).

Remarks.—The description and drawings given here are based on the holotype, and differ from the type description figures given by Holt (1968:18). All of the material examined is consistent with the illustrations given (Figs. 2C, 3F).

Key to species of *Pterodrilus* (Fig. 3)

1a. dorsal projections on any of segments 2–5 2
b. dorsal projections absent from segments 2–5 4
2a. two finger-like projections on segments 2–7 (Fig. 3A) .... *P. distichus*
b. fan-like projections on segments 3–5, and 8 3
3a. fan-like dorsal projections on segment 2 (Fig. 3B) .... *P. simondsi*
b. fan-like dorsal projections absent from segment 2 (Fig. 3C) ...... *P. alcicornus*
4a. dorsal projections on prominent ridge of segment 8 5
b. dorsal projections absent from prominent ridge of segment 8 7
5a. four finger-like projections present (Fig. 3D) .... *P. mexicanus*
b. five finger-like projections present ... 6
6a. ridges on segments 2–7 present (Fig. 3E) ....*P. cedrus*
b. ridges on segments 2–7 absent (Fig. 3F) ....*P. hobbsi*
7a. ridges on segments 2–7 high (Fig. 3G) .... *P. annulatus*
b. ridges on segments 2–7 low (Fig. 3H) .... *P. missouriensis*
c. ridges on segments 2–7 absent (Fig. 3I) .... *P. choritonamus*

Note: In 6b and 7c where ridges are absent, so are the supernumerary muscles. All species identifications made using keys should be confirmed with additional anatomical characters.

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Parkius karenwishnerae, a new genus and species of calanoid copepod (Parkiidae, new family) from benthopelagic waters of the eastern tropical Pacific Ocean

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Abstract.—The last five copepodid stages of a new genus and species of calanoid copepod, *Parkius karenwishnerae*, are described. The basis of the maxilliped of *P. karenwishnerae* is elongate distal to its two medial setae and its medial row of denticles; endopodal segments 2–5 are attenuate, forming a hook-like structure distally, with denticles along the concave margin. These character states are expected to be found in adult females of other species of *Parkius*. Parkiidae, new family, are clausocalanoidean copepods whose adult female has two Bradford's setae on the fifth enditic lobe on the basis of maxilla 2, two medial setae on the basis of the maxilliped, and endopodal segments of the maxilliped with 4, 0, 1, 1, 1 setae. On leg 1 the anterior denticles of Von Vaupel Klein's organ are found proximal to the presumptive boundary of the second endopodal segment.

Species in four families of calanoid copepods (Diaixidae Sars, 1902, Phaennidae Sars, 1902, Scolecitrichidae Giesbrecht, 1892, Tharybidae Sars, 1902) possess Bradford's setae on the terminal part of maxilla 2 and the syncoxa of the maxilliped. These setae are weakly-sclerotized and usually are without setules or with setules clustered at the tip to form a brush-like structure; they often are considered sensory in function and were named by Ferrari & Steinberg (1993) to recognize the contribution of Dr. Janet Bradford to the systematics of these families. The four families are presumed to constitute a monophyletic group within the calanoid copepod superfamily Clausocalanoidea (see Fleminger 1957); we refer to them here as bradfordian families. Presently there are 283 nominal species among 31 genera in these families (Table 1). Because most of the species are found below the epipelagic waters of all oceans, the expectation that new genera will be discovered as deeper pelagic and benthopelagic waters are sampled more thoroughly is fulfilled here with a description of a new species of calanoid copepod with similarly modified setae but with a distinctively modified maxilliped. A new genus and new a new bradfordian family are proposed for this copepod. Because the morphology of maxilla 1, maxilla 2, maxilliped, and endopod of leg 1 is considered important in establishing relationships among bradfordian families, these appendages are redescribed for *Diaixis hibernica* (Scott, 1896) and *Tharybis macrophthalma* Sars, 1902, which are the type species of the type genera of the Diaixidae and Tharybidae respectively.

Methods

Copepods were collected in the eastern tropical Pacific Ocean at Volcano 7 with a multiple sampling opening-closing net system with mouth opening of 40 cm by 40

Table 1.—Genera and number of species in five bradfordian families.

	No. species
Diaixidae Sars, 1902	
Anawekia Othman & Greenwood, 1994	1
Diaixis Sars, 1902	9
Parkiidae new family	
Parkius new genus	1
Phaennidae Sars, 1902	
Brachycalanus Farran, 1905	4
Cephalophanes Sars, 1907	3
Cornucalanus Wolfenden, 1905	8
Onchocalanus Sars, 1905	8
Phaenna Claus, 1863	2
Xantharus Andronov, 1981	1
Xanthocalanus Giesbrecht, 1892	53
Scolecitrichidae Giesbrecht, 1892	
Amallothrix Sars, 1925	46
Archescolecithrix Vyshkvartzeva, 1989	1
Heteramalla Sars, 1907	1
Landrumius Park, 1983	2
Lophothrix Giesbrecht, 1895	9
Macandrewella Scott, 1909	8
Mixtocalanus Brodsky, 1950	1
Parascaphocalanus Brodsky, 1955	1
Pseudophaenna Sars, 1902	1
Puchinia Vyshkvartzeva, 1989	1
Racovitzanus Giesbrecht, 1902	6
Scaphocalanus Sars, 1900	37
Scolecithricella Sars, 1902	26
Scolecithrix Brady, 1883	4
Scolecocalanus Farran, 1936	3
Scopalatum Roe, 1975	6
Scottocalanus Sars, 1905	13
Undinothrix Tanaka, 1961	1
Tharybidae Sars, 1902	
Neoscolecithrix Canu, 1896	4
Parundinella Fleminger, 1957	4
Tharybis Sars, 1902	9
Undinella Sars, 1900	10

cm and net mesh of 183 microns (Wishner & Meise-Munns 1984). During three dives (2146–2148) of the submersible ALVIN, horizontal tows were taken for one hr each, 1–5 m above the bottom at the base of Volcano 7 (13°23′N, 102°27′W) at depths of 2945–3010 m; samples were fixed at depth with gluteraldehyde (Wishner et al. 1995). Specimens were preserved later in the laboratory in 0.5% propylene phenoxytol/4.5% propylene glycol/95.0% water. They were cleared in steps through 50.0% lactic acid/50.0% water to 100% lactic acid and examined with differential interference optics, or stained by adding a solution of chlorazol black E dissolved in 70.0% ethanol/30.0% water and examined with bright-field optics.

The second through sixth copepodid stages are designated CII to CVI; CVI is the adult. Prosome and urosome are Pr and Ur respectively. Thoracic and abdominal somites are numbered according to their appearence during development as interpreted from data of Hulsemann (1991). The first and oldest thoracic somite bears the maxilliped and is fused with the cephalon. The youngest is the seventh; among calanoids it is the only thoracic somite without an appendage. In adult calanoids the seventh is the first somite of the urosome, and in adult females it is fused to the second abdominal somite to form the genital complex. The first and oldest abdominal somite is the most posterior; it bears the caudal rami. The youngest is immediately anterior to the oldest, and the remaining abdominal somites anteriorly increase in age and decrease in numerical designation.

Cephalic appendages are abbreviated A1 = antennule; A2 = antenna; Mn = mandible; Mx1 = maxillule; Mx2 = maxilla. Appendages on thoracic somites are Mxp = maxilliped (thoracopod 1); P1–5 = swimming legs (thoracopods 2–6). The caudal ramus is CR. Designations of appendage segments follow Huys & Boxshall (1991) except for Mx2 and Mxp; exopod = Re; endopod = Ri; medial lobe of a segment = li, lateral lobe = le. Ramal segments of Mx2 are exopodal and the Mxp has at most five endopodal segments (Ferrari 1995).

Ramal segments on thoracopods Mxp and P1–5 are numbered by their appearence during development (Hulsemann 1991, Ferrari & Ambler 1992, Ferrari 1995) and not proximal-to-distal as is the usual case in copepod descriptions. On the Mxp (Figs. 3F, 5D, 8C, J) the distal segment is the first endopodal segment, and the second endopodal segment is immediately proximal to the first. The third endopodal segment is immediately distal to the basis. The fourth endopodal segment is immediately distal to the third. The fifth endopodal segment is the middle segment. The second and first segments of a Mxp with a 5-segmented endopod are more distal and the third and fourth segments are more proximal. The distal segment of a ramus of P1–4 (Figs. 4E, F, 6F, 8E) is the first segment. The second segment is immediately distal to the basis. If present, the third segment is immediately proximal to the distal (or first) segment. For a 3-segmented ramus, the proximal segment is the second segment, the middle segment is the third segment, and the distal segment is the first segment. In the text, the number of setae recorded for ramal segments follows these schemes.

Armament elements of appendages here are termed setae regardless of their position or degree of rigidity. Examples of the position and morphology of setae are shown in the illustrations. Two setae and one aesthetasc on a segment of A1 are designated 2 + 1. Setules are epicuticular extensions of a seta; denticles are epicuticular extensions of an appendage segment; spinules are epicuticular extensions of a somite. Von Vaupel Klein's organ (Ferrari & Steinberg 1993, Ferrari 1995) on P1 (the appendage of thoracic somite 2) consists of the curved basal seta, and sensilla, denticles, or pores on the anterior face of the endopod.

Parkiidae, new family

Diagnosis.—Calanoid copepods with adult females having 3 inner setae on the first exopodal segment on leg 1 and a 1-segmented endopod, and 4 inner setae on the first exopodal segment and a 2-segmented endopod on leg 2. Maxilla 2 with 2 Bradford's setae on the fifth enditic lobe on the basis; with 3 thick, unarmed Bradford's setae and 5 with apical setules on the sixth enditic lobe plus exopod. Maxilliped with 3 Bradford's setae, 2 unarmed and 1 with apical setules, on the syncoxa; with 2 medial setae on its basis; with 4, 0, 1, 1, 1 setae on the endopod. Von Vaupel Klein's organ on leg 1 includes a well-defined group of long, thin denticles on the proximal third of the anterior face of the endopod; these denticles insert in an area proximal to the presumptive boundary of the second segment. Four derived character states of adult females exhaustive for the family are (1) maxilla 2 with 2 Bradford's setae on the fifth enditic lobe on the basis; (2) maxilliped with 2 medial setae on the basis; (3) endopodal segments of the maxilliped with 4, 0, 1, 1, 1 setae; and (4) leg 1 endopod with area of denticles of Von Vaupel Klein's organ in proximal position.

Parkius, new genus

Diagnosis.—Adult parkiid females (1) maxilliped with basis elongate distal to its two medial setae and medial denticle row; (2) with endopodal segments 2–5 attenuate, forming a hook-like structure distally, with denticles along the concave margin.

Type species.—*Parkius karenwishnerae,* by monotypy.

Etymology.—The genus honors Dr. Taisoo Park for his contributions to the phylogeny and taxonomy of calanoid copepods.

Parkius karenwishnerae, new species
Figs. 1–8

Material examined.—A dissected female holotype from dive 2148 at the Zoological Institute, St. Petersburg (ZISP 66823). Remaining copepods (CII—6 specimens; CIII—6 specimens; CIV—2 females and 4 males; CV—2 males; CVI—2 females) comprise one lot of paratypes in the National Museum of Natural History, Smithsonian Institution (USNM 278203). All specimens were collected at the base of Volcano 7 (13°23′N, 102°27′W), 1–5 m above the bottom, at depths of 2945–3010 m.

CVI female.—Length of 3 specimens 1.80 (holotype), 2.04, 2.15; average Pr length/Ur length = 3.6.

Pr (Fig. 1A): 5 segments; 1st a complex of 5 cephalic somites + Th1 and 2; Th3–6 simple and articulated; posterior margin of Th6 extended.

Ur (Fig. 1A–C): 4 segments; 1st a genital complex of Th7 and Abd2 (Fig. 1B, C) seminal receptacles curve dorsally and anteriorly; Abd3, 4, 1 articulated.

Rostrum (Fig. 1D): a simple plate with a pair of thin filaments; labrum and paragnath as illustrated.

A1 (Fig. 1E–G): 24 articulated segments with 3, 6 + 1, 2 + 1, 2, 2 + 1, 2, 2 + 1, 4 + 1, 1, 1, 2 + 1, 1, 2 + 1, 2, 2, 2, 2, 1 + 1, 1, 1, 2, 2, 2, 4 + 1 setae + aesthetascs.

A2 (Fig. 2A, B): coxa with 1 seta and a row of long denticles; basis with 2 setae. Re 6-segmented with 0, 1, 1, 1, 1, 4 setae. Ri 2-segmented with 1, 13 (6 terminal, 7 subterminal) setae.

Mn (Fig. 2C, D): coxa with 2 areas of denticles; basis with 3 setae. Re 5-segmented with 1, 1, 1, 1, 2 setae. Ri 2-segmented with 2, 9 setae.

Mx1 (Fig. 3A–C): le with 8 setae. Re 1-segmented with 8 setae and several denticles; baseoendopod with sets of 4, 2, 3, and 5 setae. Li 2, 3 both with 4 setae. Li 1 with 9 apical and 2 posterior setae; denticles on anterior surface.

Mx2 (Fig. 2E, F): li 1–4 of coxa each with 4, 3, 3, 3 setae each; li5 on basis with 4 setae, 2 are Bradford's setae without setules. Li6 + Re an indistinctly segmented complex with 8 Bradford's setae; terminal 3 setae thick without setules, 5 shorter with apical setules.

Mxp (Fig. 3D–F): syncoxa with denticles on disto-medial margin and 8 setae (1 short Bradford's with apical setules and 2 long Bradford's without apical setules). Basis elongate with medial row of denticles followed by 2 setae arising from an unsclerotized area; indistinct disto-medial lobe with 2 setae. Ri 5-segmented with 4, 0, 1, 1, 1 setae; intersegmental arthrodial membranes indistinct. Ri 2–5 attenuate, forming a hook-like structure with denticles along concave margin.

P1 (Fig. 4A, B): coxa with medial denticles; basis with medial seta and denticles. Re 3-segmented with 5 (3 medial, 1 terminal, 1 lateral), 1 (lateral), 2 (medial and lateral) setae; Re1 with lateral denticles and Re2 and 3 with medial denticles. Ri a 1-segmented complex with 5 setae (3 medial, 2 terminal). Von Vaupel Klein's organ with an area of long, thin denticles on proximal one-third of anterior face of Ri. A breaking plane on most inner setae of Ri; 2 breaking planes on most inner setae of Re.

P2 (Fig. 4C, D): coxa with medial seta and denticles. Basis unarmed. Re 3-segmented with 8 (4 medial, 1 terminal, 3 lateral), 2 (medial and lateral), 2 (medial and lateral) setae; posterior face of Re1 and 3 with distally polarized denticles. Ri 2-segmented with 5 (2 medial, 2 terminal, 1 lateral), 1 (medial) setae; posterior face of Ri1 with distally polarized denticles. A breaking plane on most inner setae of Ri; 2 breaking planes on most inner setae of Re.

P3 (Fig. 4E, F): coxa with medial seta and denticles. Basis unarmed Re 3-segmented with 8 (4 medial, 1 terminal, 3 lateral), 2 (medial and lateral), 2 (medial and lateral) setae; posterior face of Re1-3 with distally polarized denticles. Ri 3-segmented with 5 (2 medial, 2 terminal, 1 lateral), 1 (medial), 1 (medial) setae; posterior face of Ri1–3 with distally polarized denticles. A breaking plane on most inner setae of Ri; 2 breaking planes on most inner setae of Re.

P4 (Fig. 4G, H): coxa with medial seta, and medial and posterior denticles. Basis with posterior denticles. Re 3-segmented with 8 (4 medial, 1 terminal, 3 lateral), 2 (medial and lateral), 2 (medial and lateral) setae; posterior face of Re1–3 with distally polarized denticles. Ri 3-segmented with 5 (2 medial, 2 terminal, 1 lateral), 1 (medial), 1 (medial) setae; posterior face of Ri1–3 with distally polarized denticles. A breaking plane on most inner setae of Ri; 2 breaking planes on most inner setae of Re.

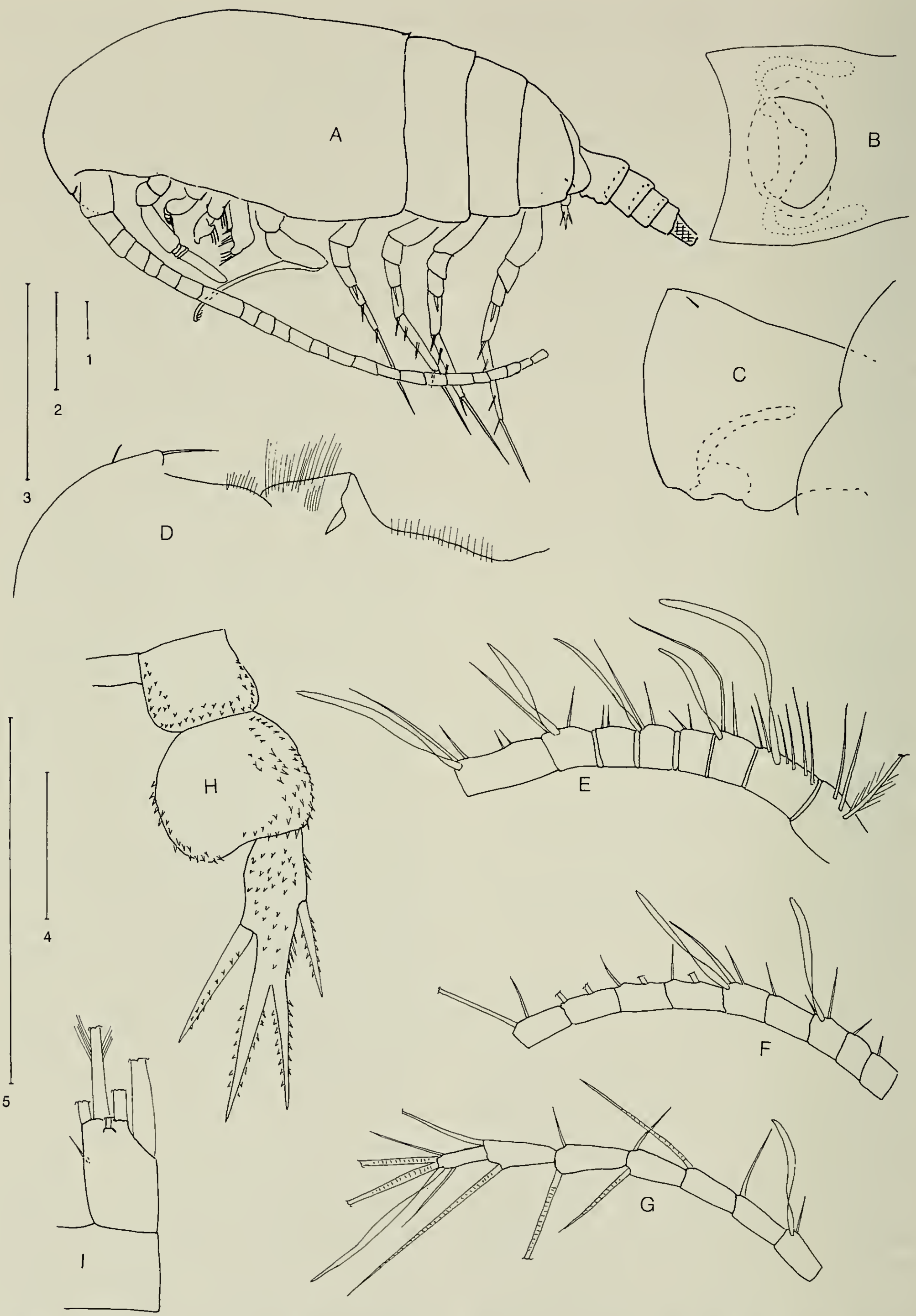

Fig. 1. *Parkius karenwishnerae,* new genus and species, CVI female: A, animal, left lateral (CR cross-hatched); B, genital complex, ventral; C, genital complex, right lateral; D, rostrum, labrum and labium, right lateral; E, A1 free segments 1–8; F, A1 free segments 9–17; G, A1 free segments 18–24; H, P5; I, CR. Wavy line cutoff indicates broken setae. Line 1 = 0.1 mm (A); line 2 = 0.1 mm (D, E, F, G); line 3 = 0.1 mm (I); line 4 = 0.1 mm (B, C); line 5 = 0.1 mm (H).

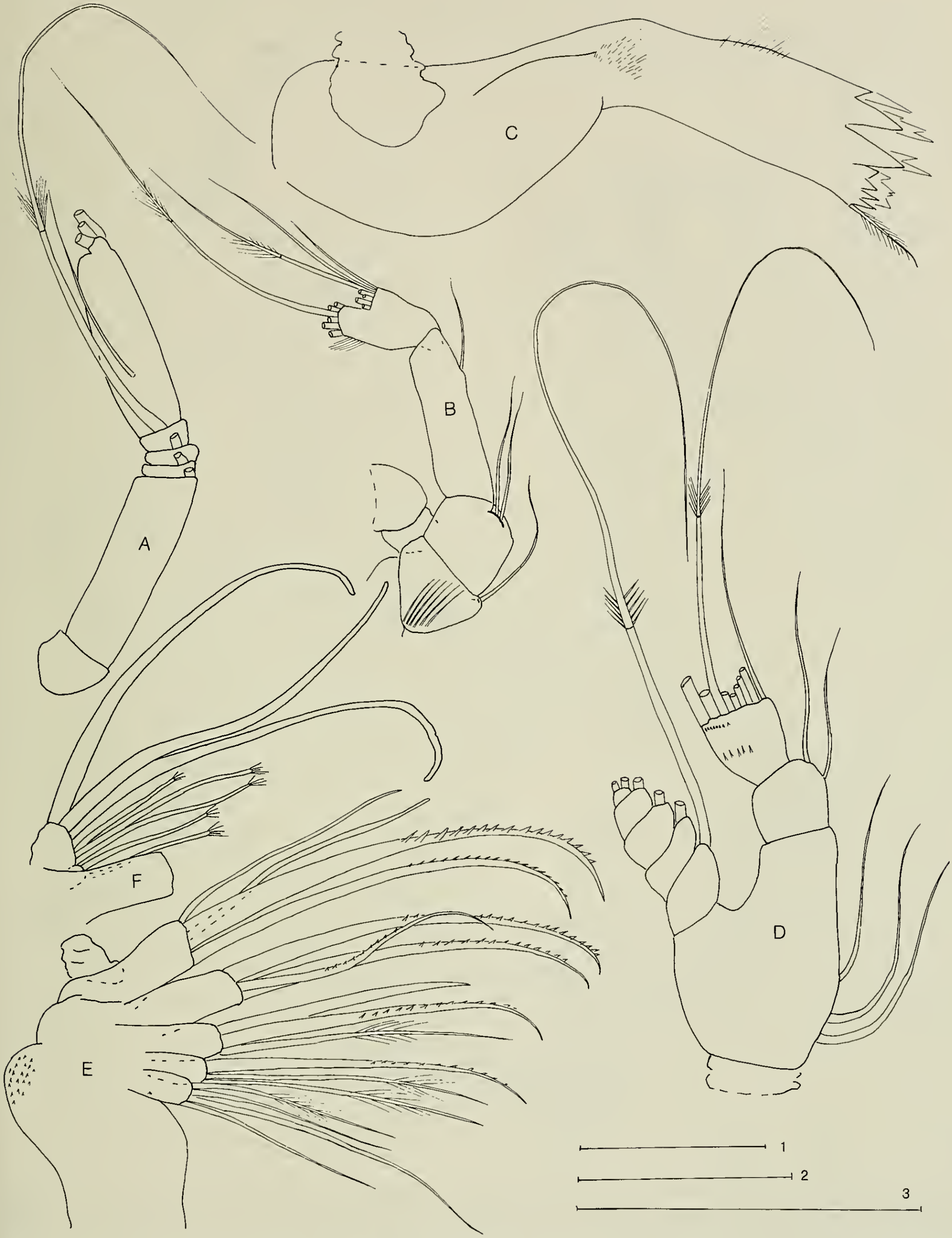

Fig. 2. *Parkius karenwishnerae,* new genus and species, CVI female: A, A2, Re; B, A2, coxa, basis and Ri; C, Mn, gnathobase, anterior; D, Mn, palp, anterior; E, Mx2, li 1–4 on coxa and li 5 on basis, posterior; F, Mx2, li 5 on basis (without setae) and li 6 + Re, posterior. Line 1 = 0.1 mm (A), B; line 2 = 0.1 mm (E), F; line 3 = 0.1 mm (C, D).

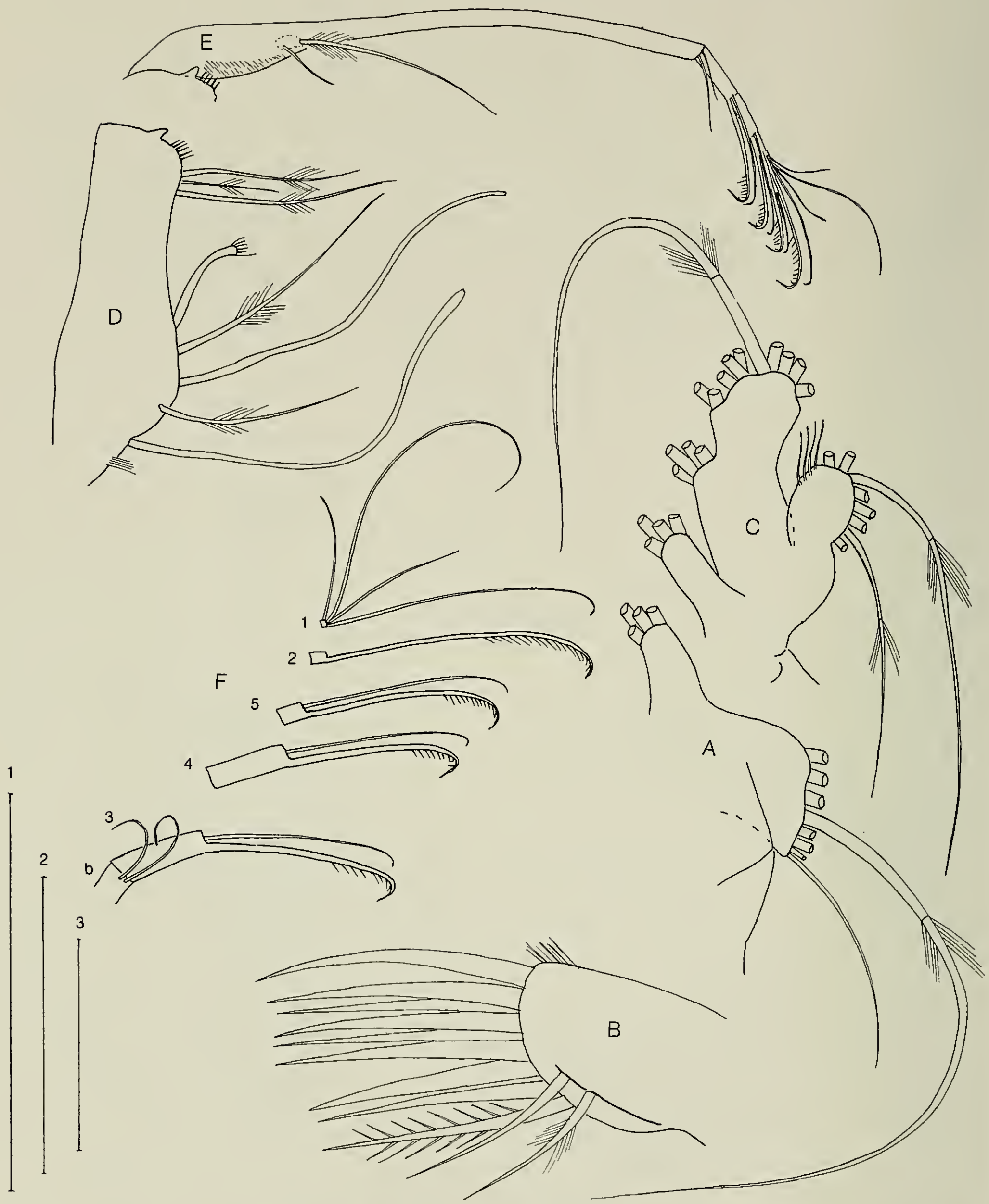

Fig. 3. *Parkius karenwishnerae,* new genus and species, CVI female: A, Mx1, syncoxa with li 1 detached, posterior; B, Mx1, li 1, posterior; C, Mx1, palp, posterior; D, Mxp, syncoxa; E, Mxp, basis and Ri; F, Mxp, detached segments of Ri (b = distal tip of basis; numbers to right indicate relative appearence of ramal segments during development). Line 1 = 0.1 mm (F); line 2 = 0.1 mm (A, B, C); line 3 = 0.1 mm (D, E).

P5 (Fig. 1H): coxa and basis without setae, with posterior denticles. Re 1-segmented with 2 setae (medial and lateral); apically with 2 attenuate points.

CR (Fig. 1I): 3 large, terminal setae, 1 large, postero-lateral seta, 1 small seta on a distomedial, ventral lobe, and 1 small seta on a dorsal lobe.

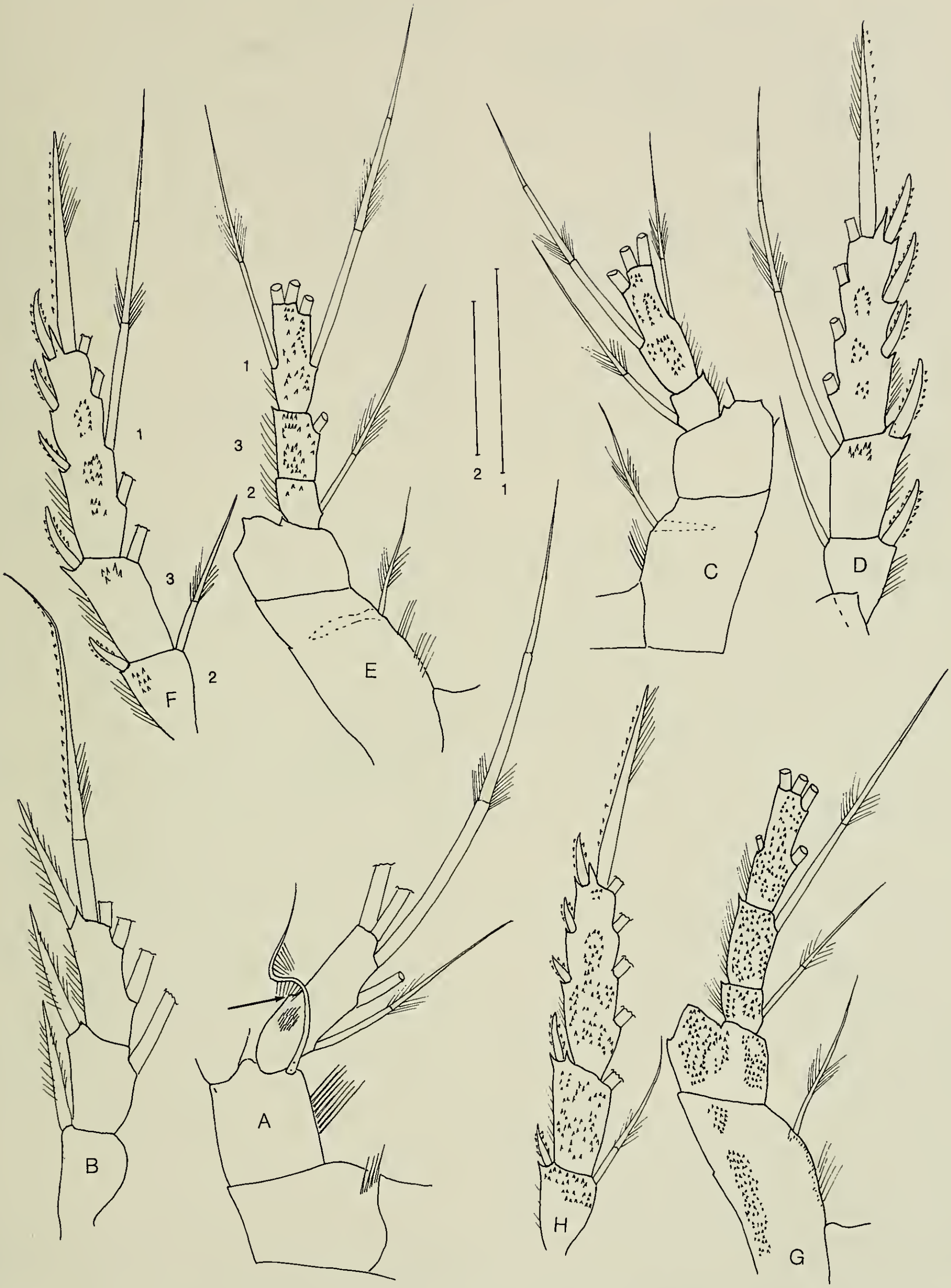

Fig. 4. *Parkius karenwishnerae,* new genus and species, CVI female: A, P1, coxa, basis and Ri, anterior (arrow indicates approximate position of presumptive boundary between Ri1 and Ri2, between proximal two medial setae); B, P1, Re, anterior; C, P2, coxa, basis and Ri, posterior; D, P2, Re, posterior; E, P3, coxa, basis and Ri, posterior (numbers to left indicate relative appearence of ramal segments during development); F, P3, Re (numbers to right indicate relative appearence of ramal segments during development), posterior; G, P4, coxa, basis and Ri, posterior; H, P4, Re, posterior. Wavy line cutoff indicates broken setae. Line 1 = 0.1 mm (A, B); line 2 = 0.1 mm (C–H).

CVI male.—Not found.

CV male.—Differs from CVI female as follows: length of 2 specimens 1.96, 2.11 mm; average Pr length/Ur length = 3.5.

Ur (Fig. 5A): 4 segments; Th7 and Abd 2, 3, 1 articulated.

A2 (Fig. 5B): Ri terminal segment with 12 setae (6 terminal, 6 subterminal).

Mn (Fig. 5C): Ri2 with 8 setae.

Mxp (Fig. 5D): Ri 4-segmented with 4, 0, 1, 1 setae.

P1: denticles on anterior face of Ri absent.

P5 (Fig. 5E): Re 2-segmented with 1 (medial), 1 (lateral) setae. Ri 1-segmented, apically attenuate.

CV female.—Not found.

CIV female.—Differs from CV male as follows: length of 2 specimens 1.37, 1.50 mm; average Pr length/Ur length = 3.7.

Pr (Fig. 5F): 6 segments; 1st a complex of 5 cephalic somites + Th1; Th2–6 articulated; posterior margin of Th6 extended.

Ur (Fig. 5F): 3 segments; Th7 and Abd2, 1 articulated.

A1 (Fig. 6A, B): 24 segments; proximal 8 segments with 3, 3 + 1, 1, 1, 1 + 1, 1, 1, 2 + 1 setae+aesthetascs.

Mn (Fig. 5G): Ri2 with 7 setae.

P1 (Fig. 6C): Re 2-segmented with 7 (4 medial, 1 terminal, 2 lateral), 1 (lateral) setae. Coxa without medial denticles.

P2 (Fig. 6D): Re 2-segmented with 9 (5 medial, 1 terminal, 3 lateral), 2 (medial and lateral) setae. Ri with fewer distally polarized denticles.

P3 (Fig. 6E): Re 2-segmented with 9 (5 medial, 1 terminal, 3 lateral), 2 (medial and lateral) setae. Ri 2-segmented with 6 (3 medial, 2 terminal, 1 lateral), 1 (medial) setae; posterior face of Ri2 without distally polarized denticles.

P4 (Fig. 6F): Re 2-segmented with 9 (5 medial, 1 terminal, 3 lateral), 1 (lateral) setae. Ri 2-segmented with 6 (3 medial, 2 terminal, 1 lateral), 1 (medial) setae.

P5 (Fig. 5H): Re 1-segmented with 1 (lateral) seta.

CIV male.—Differs from CIV female as follows: length of 4 specimens 1.47, 1.48, 1.53, 1.57 mm; average Pr length/Ur length = 3.9.

A1 (Fig. 6A, B): segments 14–16 on right appendage each with 2 setae.

P5 (Fig. 5I): Re 1-segmented with 1 (lateral) seta. Ri 1-segmented unarmed.

CIII.—Differs from CIV male as follows: length of 6 specimens 1.12, 1.14 (3 specimens), 1.16, 1.26; average Pr length/Ur length = 3.8.

Ur (Fig. 7A): 2 segments; Th7 and Abd1 articulated.

A1 (Fig. 7B–D): 23 articulated segments with 3, 1, 1, 1 + 1, 0, 1, 1 + 1, 0, 1, 1, 1, 1, 1, 1, 1, 1, 1 + 1, 1, 1, 2, 2, 2, 4 + 1 setae + aesthetascs.

A2 (Fig. 8A): Ri terminal segment with 10 setae (5 terminal, 5 subterminal).

Mn (Fig. 8B): Ri2 with 6 apical setae.

Mx1 (Fig. 7E): Le with 7 setae. Re 1-segmented with 6 setae; baseoendopod with sets of 3, 3, and 5 setae. Li1 with 9 apical setae, 1 apical seta reduced in size.

Mxp (Fig. 8C): disto-medial lobe of basis with 1 seta. Ri 4-segmented with 4, 0, 0, 0 setae.

P2: Re denticles absent; sparse on Ri.

P3 (Fig. 8D): Re 2-segmented with 7 (4 medial, 1 terminal, 2 lateral), 1 (lateral) setae; posterior face of Re1 without distally polarized denticles; Re2 without denticles. Ri2 distally polarized denticles sparse.

P4 (Fig. 8E): coxa unarmed. Re 1-segmented with 7 (3 medial, 1 terminal, 3 lateral) setae. Ri 1-segmented with 6 (3 medial, 2 terminal, 1 lateral) setae.

P5 (Fig. 7F): a simple unarmed lobe on medial face of Th6.

CII.—Differs from CIII as follows: length of 6 specimens 0.91 (2 specimens), 0.93 (2 specimens), 0.95, 1.05 mm; average Pr length/Ur length = 3.5.

Pr (Fig. 8F): 5 segments; Th2–5 articulated; posterior edge of Th5 in shape of simple papilla.

Ur (Fig. 8F): 2 segments; Th6 with lateral lobes and Abd1 articulated.

A1 (Fig. 7G, H): 19 articulated segments

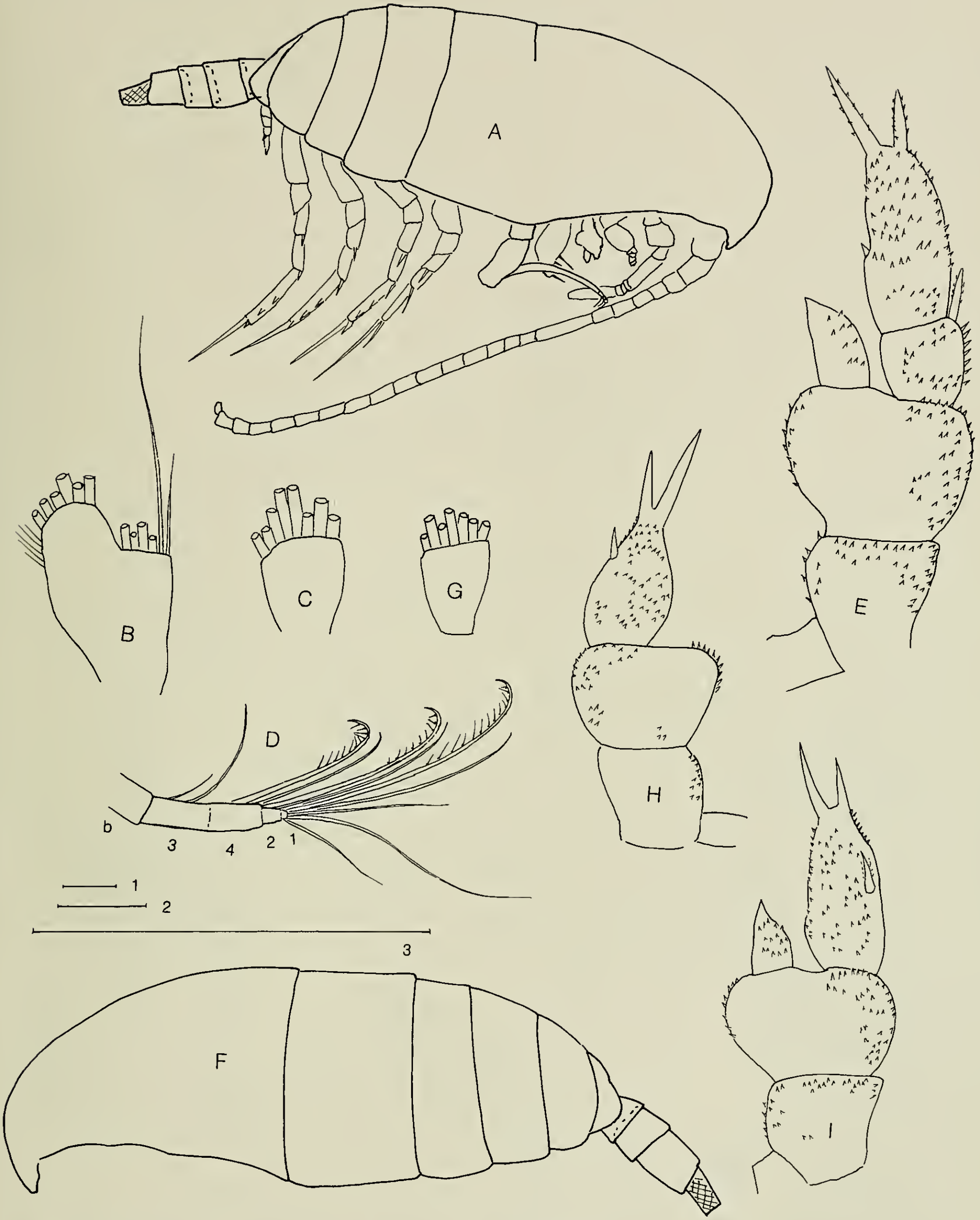

Fig. 5. *Parkius karenwishnerae,* new genus and species, CV male: A, animal, right lateral (CR cross-hatched); B, A2, Ri2; C, Mn, Ri2; D, Mxp, Ri (b = distal tip of basis; numbers below indicate relative appearence of ramal segments during development); E, P5. CIV female: F, animal, left lateral (CR cross-hatched); G, Mn Ri2; H, P5. CIV male: I, P5. Line 1 = 0.1 mm (A); line 2 = 0.1 mm (F); line 3 = 0.1 mm (B–E, G–I).

with 3, 2 + 1, 0, 1, 0, 1, 0, 1, 0, 1, 0, 1, 1, 0, 1, 2, 2, 2, 4 + 1 setae + aesthetascs.

A2 (Fig. 8G): Ri terminal segment with 9 (5 terminal, 4 subterminal) setae.

Mn (Fig. 8H): Ri2 with 5 setae.

Mx1 (Fig. 7I): Le with 6 setae. Li 2 with 3 setae. Li1 with 7 apical setae.

Mxp (Fig. 8I, J): syncoxa with 7 setae

Fig. 6. *Parkius karenwishnerae,* new genus and species, CIV female: A, schematic of A1, free segments 1–10; B, A1, free segments 11–18 (# indicate setae which are present only on right A1 of CIV male); C, P1, Re, anterior; D, P2, Re, posterior; E, P3, Re and Ri, posterior; F, P4, Re and Ri, posterior (numbers to right of Re and left of Ri indicate relative appearence of ramal segments during development). Line 1 = 0.1 mm (A, B); line 2 = 0.1 mm (C, E, F); line 3 = 0.1 mm (D).

Fig. 7. *Parkius karenwishnerae,* new genus and species, CIII: A, animal, right lateral (CR cross-hatched); B, A1, free segments 1–14; C, A1, free segments 15–19; D, free segments 20–23; E, Mx1, posterior; F, P5 (tip of arrow) near posterior edge of Th6 and Th7 (#). CII: G, A1, free segments 1–12; H, A1, free segments 13–19; I, Mx1, posterior; J, P4 at posterior edge of Th5 (Th6 with #). Wavy line cutoff indicates broken setae. Line 1 = 0.1 mm (A); line 2 = 0.1 mm (B–D, G, H); line 3 = 0.1 mm (E, F, I, J).

Fig. 8. *Parkius karenwishnerae,* new genus and species, CIII: A, A2, Ri2; B, Mn, Ri2; C, Mxp, Ri (b = distal tip of basis; numbers to left indicate relative appearence of ramal segments during development); D, P3, Re, posterior; E, P4, posterior (numbers to right of Re and left of Ri indicate relative appearence of ramal segments during development). CII: F, animal, left lateral (CR cross-hatched); G, A2, Ri2; H, Mn, Ri2; I, Mxp, syncoxa; J, Mxp, Ri (b = distal tip of basis; numbers to left indicate relative appearence of ramal segments during development); K, P2, Re, posterior; L, P3, posterior. Wavy line cutoff indicates broken setae. Line 1 = 0.1 mm (F); line 2 = 0.1 mm (D, E, I, K, L); line 3 = 0.1 mm (A–D, H, J).

(only 2 in disto-medial set); Ri 3-segmented with 4, 0, 0 setae.

P2 (Fig. 8K): Re 2-segmented with 7 (4 medial, 1 terminal, 2 lateral), 1 (lateral) setae.

P3 (Fig. 8L): coxa unarmed. Re 1-segmented with 7 (3 medial, 1 terminal, 3 lateral) setae. Ri 1-segmented with 6 (3 medial, 2 terminal, 1 lateral) setae.

P4 (Fig. 7J): a bilobe bud on posterior edge of Th5; dorsal lobe with 3 weakly-sclerotized setae, ventral lobe with 2 weakly-sclerotized setae; lobes and setae directed dorsally.

Etymology.—This new species honors Dr. Karen Wishner for her many and varied contributions to the biology of the oceans.

Remarks.—Adult females of *P. karenwishnerae* share with species of the calanoid superfamilies Ryocalanoidea, Spinocalanoidea, and Clausocalanoidea, a 1-segmented endopod on leg 1, and a 2-segmented endopod on leg 2. Adult males of species of the latter two superfamilies have non-geniculate antenna 1, a character state we have been unable to determine for the new species. Adult females of *P. karenwishnerae* share with species of the Clausocalanoidea three inner setae on the first exopodal segment of leg 1 and four inner setae on the first exopodal segment of leg 2 (Park 1986). Adult females of *Parkius* share: with diaixids, tharybids, phaennids and scolecitrichids, Bradford's setae on the sixth enditic lobe on the basis plus exopod of maxilla 2; with diaixids and scolecitrichids three apical Bradford's setae without setules and five more with apical setules on this segment complex; with diaixids, phaennids and scolecitrichids distally and/or radially polarized denticles on the posterior surfaces of some ramal segments of legs 2–4; with most scolecitrichids two Bradford's setae on the fifth enditic lobe on the basis of maxilla 2. The combination of the following derived character states separates Parkiidae from the other bradfordian families: maxilla 2 with two Bradford's setae on the fifth enditic lobe on the basis; maxilliped with two medial setae on the basis; and 4, 0, 1, 1, 1 setae on its endopodal segments (reduced by truncation during development); and one leg 1 anterior denticles of Von Vaupel Klein's organ proximal to the presumptive boundary of the second endopodal segment.

The shapes of maxillipedal segments are diagnostic for *Parkius*; an elongate basis distal to the medial row of denticles and distal to the two medial setae; endopodal segments 2–5 of the maxilliped attenuate, forming a hook-like structure distally, with denticles along the concave margin.

Neither homologies of Bradford's setae at various positions on maxilla 2, nor the transformation sequence of those setae have been hypothesized. We do not know the ancestral state for numbers of Bradford's setae on the sixth enditic lobe of the basis plus exopod of maxilla 2 although presence of one sclerotized seta on *Tharybis macrophthalma* may be a primitive condition. We believe that the presence of four sclerotized setae on the fifth enditic lobe on the basis is primitive, and that two Bradford's setae on that lobe is a derived character state. Phylogenetic hypotheses about species within bradfordian families await careful collecting, better preservation and complete descriptions of appendage armament. Of particular value to our understanding of relationships among the species are the armament of maxilla 1, presence of Bradford's setae on the fifth and sixth enditic lobes and exopod of maxilla 2, shape and armament of maxilla 2, armament of the maxilliped, structure of Von Vaupel Klein's organ, presence of radially polarized denticles on legs 2–4, homologies of segments and setae of leg 5.

Segmental and setal homologies.—The number of segments and associated setae on the ramus of maxilla 2 of the ancestor to the bradfordian families is difficult to infer based on our present knowledge of clausocalanoideans. Presumed older calanoids like *Pleuromamma xiphias* or *Ridgewayia klausruetzleri* with two enditic lobes on the basis (the fifth and sixth enditic lobes) have seven exopodal setae (Ferrari 1985, Ferrari 1995). Presence of eight setae on the distal segments of many species in the bradfordian families apparently is correlated with reduction in size of the sixth enditic lobe. The hypothesis accepted here is that the sixth lobe, apparently with at least one of its setae, are included in the exopod and group of eight Bradford's setae, although the homologies of each of these setae cannot as yet be determined. The tip of maxilla 2 then is a complex of exopodal segments plus the sixth enditic lobe on the basis whose setation is complete early in the copepodid phase of calanoid development. This hypothesis is supported by the fact that, in general, setation of enditic lobes and exopodal segments are complete early in calanoid copepodid development (Ferrari 1995).

A medial row of denticles is found on the proximal portion of the basis of the maxilliped of many copepods. Usually this row ends at the level of the second of three medial setae. On *P. karenwishnerae* these denticles and only two medial setae, occupy the proximal one-fourth of the basis; the distal portion of the basis is elongate. Some species of the phaennid genus *Onchocalanus* have a maxilliped with an elongate basis (Park 1983). However, in *O. trigoniceps, O. paratrigoniceps, O. magnus,* and *O. cristatus* the area of elongation is not homologous to *P. karenwishnerae* because it apparently results from the proliferation of cells immediately distal to the medial denticle row so that cells producing the three medial setae of the basis are included in the area of elongation. In *Parkius karenwishnerae* this area of elongation apparently results from the proliferation of cells distal to the two medial setae as well as the medial denticle row, so that cells producing the two medial setae are not included in the area of elongation.

Table 2.—Setation of the maxilliped of *Parkius karenwishnerae* and *Scopalatum vorax* for stages CII–CVI and of *Ridgewayia klausruetzleri* for stages CI–CVI. Beginning with CII, setation of the endopod of the scolecitrichid, *S. vorax*, is identical to the presumed older calanoid, *R. klausruetzleri. P. karenwishnerae* exhibits delayed appearance of the fifth endopodal segment, no seta at the formation of endopodal segments 2–4, and truncation of post-formation setal addition on three endopodal segments. Lobes of the syncoxa (s1–s4), the basis (b) and its distomedial lobe (l), and the endopodal segments (*n1–n5* numbered by developmental stage) are arranged from left, proximally, to right, distally. a = segment not formed.

Parkius karenwishnerae

	s1	s2	s3	s4	b	l	*n3*	*n4*	*n5*	*n2*	*n1*
CI	?	?	?	?	?	?	*?*	*?*	*?*	*?*	*?*
CII	1	2	2	3	2	1	*0*	*a*	*a*	*0*	*4*
CIII	1	2	2	3	2	1	*0*	*0*	*a*	*0*	*4*
CIV	1	2	2	3	2	2	*1*	*1*	*a*	*0*	*4*
CV	1	2	2	3	2	2	*1*	*1*	*a*	*0*	*4*
CVI	1	2	2	3	2	2	*1*	*1*	*1*	*0*	*4*

Scopalatum vorax

	s1	s2	s3	s4	b	l	*n3*	*n4*	*n5*	*n2*	*n1*
CI	?	?	?	?	?	?	*?*	*?*	*?*	*?*	*?*
CII	1	2	1	3	2	2	*1*	*a*	*a*	*1*	*4*
CIII	1	2	1	3	3	2	*1*	*1*	*a*	*2*	*4*
CIV	1	2	1	3	3	2	*2*	*2*	*1*	*2*	*4*
CV	1	2	1	3	3	2	*3*	*3*	*2*	*3*	*4*
CVI	1	2	1	3	3	2	*4*	*4*	*3*	*4*	*4*

Ridgewayia klausruetzleri

	s1	s2	s3	s4	b	l	*n3*	*n4*	*n5*	*n2*	*n1*
CI	0	1	2	2	2	1	*a*	*a*	*a*	*1*	*4*
CII	1	2	4	3	3	2	*1*	*a*	*a*	*1*	*4*
CIII	1	2	4	3	3	2	*1*	*1*	*a*	*2*	*4*
CIV	1	2	4	3	3	2	*2*	*2*	*1*	*2*	*4*
CV	1	2	4	3	3	2	*3*	*3*	*2*	*3*	*4*
CVI	1	2	4	3	3	2	*4*	*4*	*3*	*4*	*4*

Table 2 compares setation during copepodid development of the maxilliped of *P. karenwishnerae,* the related scolecitrichid *Scopalatum vorax,* and *R. klausruetzleri,* a presumed older calanoid. Ferrari & Steinberg (1993) incorrectly figured and described *S. vorax* with three setae on the proximal (third) endopodal segment at CIV; the correct number for that stage is two. There are no differences between *S. vorax* and *R. klausruetzleri* in segmentation or setation of the endopod. However, *S. vorax* has three fewer setae on a lobe of the syncoxa and the addition to the basis of the third medial seta is delayed until CIII. *Parkius karenwishnerae* has two fewer setae on the homologous syncoxal lobe, a third medial seta is never added to the basis, the addition of the second seta to the disto-medial lobe of the basis is delayed until CIV, and the addition of the fifth endopodal segment is delayed until CVI. These changes are neotenic because appearances of segments or setae are delayed until late in development or delayed so that they do not appear at all. There is no seta present at the formation of endopodal segments 2–4 of *P. karenwishnerae,* and only one of three plus three post-formation setae are added to endopodal segments 3 and 4. The pattern of endopodal setation exhibited by *R. klausruetzleri* and *S. vorax* appears to have been truncated in *P. karenwishnerae,* resulting in a reduction in setal number on the endopod. An alternate hypothesis of neotenic reduction, i.e., delaying setal addition, is not supported by the pattern for *P. karenwishnerae* because final setal numbers are reached at CIV rather than CVI. Thus two developmental processes, neoteny and truncation, may be responsible for setal addition to the maxilliped of *P. karenwishnerae.*

The morphology of Von Vaupel Klein's organ suggests that the 1-segmented endopod of leg 1 of *P. karenwishnerae* is a segment complex. The development of leg 1 of *P. karenwishnerae* is incompletely reported here, but we assume that its morphology at CI is similar to *Drepanopus forcipatus* with 1-segmented exopod and endopod (Hulsemann 1991), and without presumptive structures of Von Vaupel Klein's organ (also see Ferrari, 1995, for development of *R. klausruetzleri*). On *D. forcipatus, S. vorax* or *P. karenwishnerae* this endopod does not add segments or setae later in development; however, structural elements of Von Vaupel Klein's organ (tubercle and curved basal seta) presumabley are added during the molt to CII. At this stage in development of presumed older calanoids like *R. klausruetzleri,* which continue to add segments and setae to leg 1 endopod during development, the endopod is 2-segmented. For CII of *R. klausruetzleri* the boundary between the second (proximal) and first (distal) endopodal segments of a 2-segmented endopod has formed between the 2 medial setae of the endopod of CI, and the tubercule of Von Vaupel Klein's organ is located near that boundary. Later in development the tubercule is located near the boundary of the second (proximal) and third (middle) endopodal segments of the 3-segmented endopod at CV of *R. klausruetzleri* and *P. xiphias.* Based on the position between the two proximal inner setae of this presumed homologous denticule bearing tubercule, we believe that the 1-segmented endopod of leg 1 of *D. forcipatus,* species of *Euchirella* and *Pseudochirella* mentioned by Von Vaupel Klein (1972), and *S. vorax* is a complex of cells of the first and second endopodal segments which are not separated by an arthrodial membrane. The 1-segmented ramus of *P. karenwishnerae* also is a segment complex, but without a distinct tubercle. The homologous denticles are located away from the boundary of the presumed second and first segments. The alternate hypothesis, that the 1-segmented endopod of leg 1 is simply the first endopodal segment of CI, would require Von Vaupel Klein's organ to have evolved independently among calanoids with 1-segmented and with 2- or 3-segmented endopods on leg 1.

The pattern of development of legs 1–4 of *P. karenwishnerae* is identical to *S. vorax* although Ferrari & Steinberg (1993) incorrectly described the second exopodal segments of leg 4 of CIV male and of leg 3 of CIII with two setae (they have one seta), and the endopod of leg 4 which at CIII was incorrectly described and illustrated with five setae (there are six; the proximal, medial one was not shown). The ramus on female leg 5 appears to be an exopod, because it is morphologically similar to the outer ramus of the male. Distal structures on the exopod of female leg 5 exopod of *P. karenwishnerae* and both rami of the male do not articulate with the segment but instead appear to be attenuations of the segment.

Bradford (1973) and Bradford et al. (1983) have made significant contributions to our understanding of the specialized clausocalanoidean families Phaennidae and Scolecitrichidae despite the fact that the morphology of many described species is incompletely known. Most of the species live in deep water and thus few specimens have been available for study; adult males are usually rare. In addition, the ramal segments of legs 1–4 are often broken during capture, and Bradford's setae, which are weakly-sclerotized, may become distorted over time in ethanol, a commonly used preservative. A better understanding of relationships among bradfordian families has been hampered by incomplete descriptions of species in the families Diaixidae and Tharybidae. Here maxilla 1, maxilla 2, maxilliped and endopod of leg 1 are redescribed for *Diaixis hibernica* (Scott 1896) and *Tharybis macrophthalma* Sars 1902, which are the type species of the type genera of their respective families.

Diaixidae Sars, 1902
Diaixis Sars, 1902
Diaixis hibernica (Scott 1896)

Material examined.—CVI 5 females and 2 males plus several other copepodids from Raunefjord, Norway (60°16′N, 5°10′E) collected by Audun Fosshagen on 4 April 1995 with a Beyer epibenthic sampler (180 micron mesh) at 120 m have been deposited in the U.S. National Museum (USNM 278204).

CVI female.—Mx1 (Fig. 9A) Le with 8 setae. Re 1-segmented with 8 setae; baseoendopod with sets of 3, 3, 3, and 3 setae. Li2 with 2 setae, Li3 with 3. Li 1 with 8 apical setae.

Mx2 (Fig. 9B, C): Li 1–4 on coxa each with 4, 3, 3, 3 setae each; li5 on basis with 4 setae, 1 weakly-sclerotized without setules. Li2 + Re an indistinctly segmented complex with 8 Bradford's setae; terminal 3 thick without setules, 5 thinner with apical setules.

Mxp (Fig. 9D–E): syncoxa with denticles on disto-medial margin and 9 setae (1 Bradford's with setules along its length and 2 Bradford's with narrow base and without apical setules). Basis with medial row of denticles and 3 medial setae; disto-medial lobe with 2 setae. Ri 5-segmented with 4, 4, 4, 4, 3 setae.

P1 (Fig. 9F, G): Von Vaupel Klein's organ with an area of long, thin denticles laterally on anterior face of Ri. There are also 3 areas on denticles on the posterior face of Ri.

CVI male.—Differs from CVI female as follows. Mx1 (Fig. 10A) Le with 4 setae. Re 1-segmented with 7 setae; Ri with 1 medial and 4 apical setae. Li1–3 unarmed.

Mx2 (Fig. 10B): Li 1–3 on coxa with numerous small denticles; li 4 with a sclerotized seta and denticles; li5 on basis with 1 Bradford's seta without setules. Li2 with 1 Bradford's seta with setules; Re indistinctly segmented with 5 Bradford's setae; terminal 3 thick without setules, and 2 shorter with apical setules.

Mxp (Fig. 10C): syncoxa with 4 setae (1 Bradford's with apical setules). Basis with medial row of denticles and 2 medial setae.

Remarks.—We examined from The Natural History Museum in London one lot (B.M. 1911.11.8 37900–907) of *Scolecithrix hibernica* labelled types by A. Scott and "Feby 1896" from the Irish Sea which contained CVI 4 females, 5 males; CV 1 female, 2 males, and one lot from the Zoological Museum of the University of Oslo (F 20677) labeled "*Diaixis hibernica* A. Scott, sted. Bundefj., dt. G. O. Sars" which contained CVI 12 females, 1 male; CV 5 females, 2 males. We did not dissect specimens from either lot, but adult females from both lots agree with Raunefjord specimens in morphology of the posterior margin of the prosome and of the genital complex; we believe all specimens are conspecific. For adult females of both lots, we were able to verify the general shape of

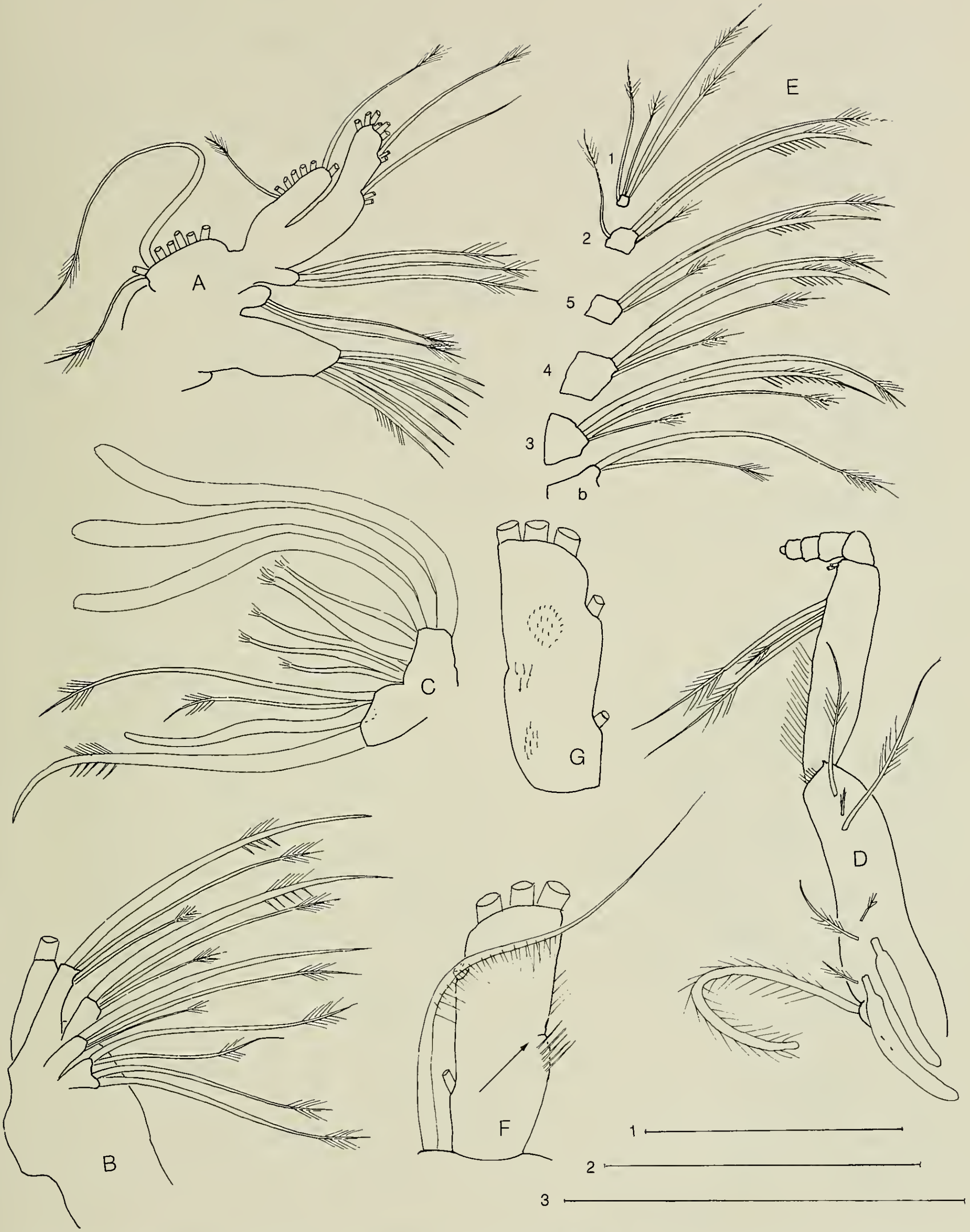

Fig. 9. *Diaixis hibernica* (Scott, 1896), female: A, Mx1, posterior; B, Mx2, li1–4 on syncoxa, posterior (li5 with one seta with circular cutoff also shown); C, Mx2, li5 on basis and li6 + Re, anterior; D, Mxp (setation of Ri not shown); E, Mxp, Ri (b = distal tip of basis; numbers to left indicate relative appearence of ramal segments during development); F, P1, Ri, anterior (arrow indicates approximate position of presumptive boundary between Ri1 and Ri2, between proximal two medial setae); G, P1, Ri, posterior. Line 1 = 0.1 mm (A–D); line 2 = 0.1 mm (E); line 3 = 0.1 mm (F, G).

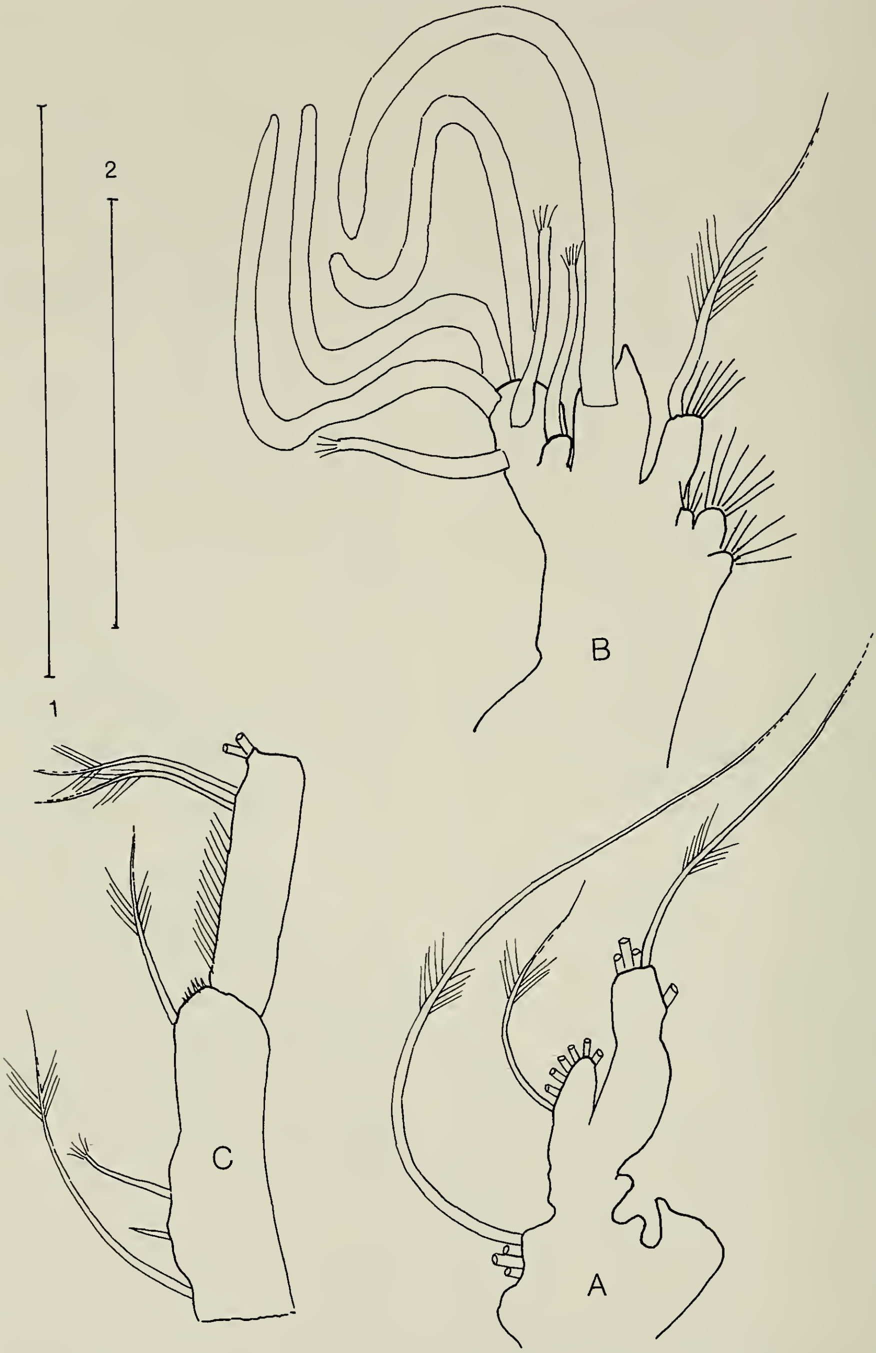

Fig. 10. *Diaixis hibernica* (Scott, 1896), male: A, Mx1, posterior; B, Mx2; C, Mxp, coxa and basis. Line 1 = 0.1 mm (A, B); line 2 = 0.1 mm (C).

Fig. 11. *Tharybis macrophthalma* Sars, 1902: A, Mx1, anterior; B, Mx1, tip of li1, posterior; C, Mx2, li1–4 on syncoxa, posterior; D, Mx2, li5 on basis and li6 + Re, anterior; E, Mxp, syncoxa; F, basis and Ri (setation of Ri not shown); G, Mxp, Ri (b = distal tip of basis; numbers to right indicate relative appearence of ramal segments during development); H. P1, Ri, anterior (arrow indicates approximate position of presumptive boundary between Ri1 and Ri2, between proximal two medial setae). Line 1 = 0.1 mm (E, F); line 2 = 0.1 mm (A, B); line 3 = 0.1 mm (C, D, G); line 4 = 0.1 mm (H).

Mx1 and setation of the exite, the armament of li6 plus Re of Mx2, and setation of basis and presence of 19 setae on Ri of Mxp which agree with Raunefjord specimens.

Tharybidae Sars, 1902
Tharybis Sars, 1902
Tharybis macrophthalma Sars, 1902

Material examined.—CVI 9 females and 10 males from Raunefjord, Norway (60°16′N, 5°10′E) collected by Audun Fosshagen on 4 April 1995 with a Beyer epibenthic sampler (180 micron mesh) at 120 m have been deposited in the U.S. National Museum (USNM 278205).

CVI female.—Mx1 (Fig. 11A, B): Le with 9 setae. Re 1-segmented with 5 setae; baseoendopod with sets of 3, 2, 2, and 3 setae. Li 2 with 3 setae, Li3 with 4. Li 1 with 9 apical (5 thick with setules, 4 thin and unarmed) and 4 posterior setae.

Mx2 (Fig. 11C, D): Li 1–4 of coxa each with 4, 3, 3, 3 setae each; li5 on basis with 4 sclerotized setae. Li2 + Re an indistinctly segmented complex with 8 setae; terminal 3 Bradford's setae without setules, 4 Bradford's setae with apical setules, and 1 sclerotized seta with setules.

Mxp (Fig. 11E–G): syncoxa with denticles on disto-medial margin and 9 setae (1 short Bradford's with apical setules). Basis elongate with medial row of denticles followed by 3 setae; disto-medial lobe with 2 setae. Ri 5-segmented with 4, 4, 4, 4, 3 setae.

P1 (Fig. 11H): Von Vaupel Klein's organ with lateral margin of Ri extended distally; denticles medial and lateral to the extension, and on the anterior face of Ri below the basal seta.

CVI male.—Mx1, Mx2, Mxp, and P1 similar to female.

Remarks.—We examined one lot from the Zoological Museum of the University of Oslo (F 20610) labeled "*Tharybis macrophthalma* G. O. Sars, sted. Drobak, dt. G. O. Sars" which contained CVI 5 females, 2 males; CV 1 male. We did not dissect these specimens but adult females agree with Raunefjord specimens in morphology of leg 5 and the genital complex; we believe specimens from both areas are conspecific. For adult females we were able to verify the armament of li6 plus Re of Mx2, and setation of coxa and basis, and the presence of 19 setae on Ri of Mxp.

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Occurrence of anomuran crabs (Crustacea: Decapoda) in hydrothermal vent and cold-seep communities: a review

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Abstract.—Crabs of the family Lithodidae are frequently encountered in the vicinity of deep-sea hydrothermal vents and cold-seeps. Together with crabs of the families Galatheidae and Chirostylidae, they are the main contributors to the scavenging/predatory fauna of these highly productive areas, and a potential vector for the export of organic carbon to the surrounding deep-sea communities. A review of the literature indicates that anomuran crabs have been reported from such environments since their discovery, and occur virtually anywhere a reducing habitat is found. These three families are represented by at least eight genera, with at least 14 species occurring in hot vent areas, and eight in cold-seep associated communities.

Two species of lithodid crabs have recently been reported from the south Barbados accretionary prism cold-seeps at depths of 1200–1700 m (Macpherson 1994). In addition to the description of a new species, *Paralomis arethusa,* Macpherson mentioned that his new species and *Lithodes manningi* Macpherson, 1988, were the first records of the family Lithodidae to be found in hydrothermal vent and cold-seep areas. However, a review of the literature showed that occurrence of lithodid crabs in such environments has been known at least since 1985 (Suess et al. 1985). The taxonomic literature on deep-sea hydrothermal vent and cold-seep organisms often lacks ecological data, and ecological surveys frequently present vague taxonomic information. This review is intended to demonstrate that the Anomura are a particularly well represented group in deep-sea chemosynthetically-based ecosystems, and to present a literature survey of the species and accompanying information relevant to biogeographic studies.

Vents and seeps are environments where biomass and biological production are high compared to that of the surrounding abyssal plains, due to utilization of the expelled reduced compounds by chemoautotrophic microorganisms that constitute the first step of a trophic web independent from sea-surface production. Although organisms exclusively dependent on fluid emissions usually dominate these communities and live close to the expelled fluids, other inhabitants of the neighboring deep-sea environment are attracted by the high food supply and enter these environments. Like anomurans, most of these organisms are filter-feeders, scavengers, or predators. As top predators/scavengers, anomurans are rivalled only in some cases, in particular by the hydrothermal-endemic brachyuran crab family Bythograeidae.

Infraorder Anomura

Superfamily Paguroidea (sensu Forest 1987)

This superfamily comprises the Lithodidae and two families of hermit crabs, Paguridae and Parapaguridae. Only one hermit crab has been reported to date from cold seeps of the Barbados accretionary prism, at depths of 1000–2000 m (K. Olu, pers. obs.), and another one from Monterey Bay seeps at 600–1000 m (J. P. Barry, pers. comm.). The Barbados specimen seems to belong to the genus *Parapagurus* (M. de Saint Laurent, pers. comm.). Although the Monterey Bay hermit crab has not been identified, it is possible that it is also a parapagurid, which are common at these depths.

Family Lithodidae

The first report of the occurrence of Lithodidae in hydrothermal vent or cold-seep habitats, is a "large crab," clearly a lithodid, illustrated in a sketch of the benthic community associated with cold-seeps along the lower Oregon subduction zone at 2037 m depth (Suess et al. 1985, Kulm et al. 1986). Subsequently, Carey et al. (1988) observed *Lopholithodes foraminatus* from a shallower part of this subduction zone. Whether the "large crab" and *L. foraminatus* are the same species is not stated. Tunnicliffe & Jensen (1987) proposed that the deeper water species from the lower zone could be the same *Paralomis* sp. they found at hydrothermal vents in the Juan de Fuca Ridge.

In total, four lithodid crabs have been identified to the species level from cold-seep areas, and the status of four others remains uncertain. The Lithodidae are represented at hydrothermal vents by two species and six occurrences not yet clearly assigned to species. Two of the described species (*Paralomis arethusa* and *P. jamsteci*) are until now known only from reducing environments. No lithodid species is definitely known from both vents and seeps.

Genus *Lithodes* Latreille, 1806
Lithodes manningi Macpherson, 1988

One specimen was collected at 1236 m depth in cold seeps of the Barbados accretionary prism, and was identified by Macpherson (1994). The species is known from depths of 640–777 m in the Caribbean (Macpherson 1988).

Two species of lithodid crabs found at seeps of the Monterey Bay, at 600–1000 m, have been assigned tentatively to the genus *Lithodes* (J. P. Barry, pers. comm.). These crabs are not considered as seep-endemics.

Genus *Lopholithodes* Brandt, 1848
Lopholithodes foraminatus (Stimpson, 1859)

As previously mentioned, Carey et al. (1988) observed dense aggregations of *Lopholithodes foraminatus* while exploring apparently extinct seepage areas of the upper Oregon subduction zone, at a depth of ca. 250 m. There is no mention of this species at active seeps, but it could be the same species as the "large crab" observed at 2037 m by Suess et al. (1985). However, this occurrence would be much deeper than the known depth range of *L. foraminatus,* which is known from British Columbia to southern California, at 0–547 m (Hart 1982).

Genus *Neolithodes* Milne Edwards & Bouvier, 1894
Neolithodes diomedeae (Benedict, 1894)

This species represents the first reported occurrence of Lithodidae in hydrothermal vents. Grassle (1986) described it as the most common crab found at the active hydrothermal vents, at 2000 m, in the Guaymas Basin, Gulf of California. It is known from southern California to South Georgia, at depths of 640–2450 m (Macpherson 1988).

Genus *Paralithodes* Brandt, 1848

Based on submersible observations, Sagalevich et al. (1992) reported *Paralithodes* sp., at 350–400 m, on the periphery of active hydrothermal vents on the summit of Piyp Volcano, in the Bering Sea, on dense populations of actinians.

Genus *Paralomis* White, 1856

This is the best represented of the lithodid genera in chemosynthetically-based communities. At least four species have been reported, including two exclusively from reducing habitats. Considering the numerous reports of "*Paralomis* sp." found in the literature, more species are likely to be discovered in the future.

Paralomis arethusa Macpherson, 1994

Paralomis arethusa is one of two lithodid crabs known from cold-seep communities of the Barbados accretionary prism at 1691 m depth. This species is known only from this location (Macpherson 1994).

Paralomis cubensis Chace, 1939

Sassen et al. (1993) produced a photograph of a "crab" (clearly a lithodid) crawling on tubeworms and mussels at the Green Canyon methane seep, on the upper continental slope of the Gulf of Mexico, at 620 m. It was subsequently identified as *Paralomis cubensis.* It is considered as a "vagrant" species of the Gulf of Mexico seeps by Carney (1994), and is not commonly in direct contact with the seep community. *P. cubensis* is known from east Florida to Brazil, at 329–730 m (Macpherson 1988).

Paralomis jamsteci Takeda & Hashimoto, 1990

In hydrothermal areas of the Okinawa Trough, lithodid crabs have been observed on the Minami-Ensei Knoll, at 700 m, where a new species was described as *Paralomis jamsteci* (Hashimoto et al. 1990, Takeda & Hashimoto 1990). This species is living among mytilid beds, near vent openings (Hashimoto et al. 1995). Two other yet unidentified species of *Paralomis* also occur at the Minami-Ensei vents (Hashimoto et al. 1995).

Paralomis multispina (Benedict, 1894)

Horikoshi & Ishii (1985), Hashimoto et al. (1987, 1989), and Ohta (1990b) have described cold-seep communities of Sagami Bay in Japan, at depths of 900–1200 m, where large *Paralomis multispina* and the clams *Calyptogena soyoae* are the dominant species. *P. multispina* is known from Japan to California, at 500–1665 m (Hart 1982).

Paralomis verrilli (Benedict, 1894)

Paralomis verrilli is believed to be the species found at hydrothermal vents of the Iheya Ridge, at 1400 m, in the Mid-Okinawa Trough (S. Ohta, pers. comm.; Ohta 1990a; Kim & Ohta 1991; Hashimoto et al. 1995). Although still to be confirmed, this occurrence would not be surprising as *P. verrilli* is usually found at depths of ca. 1500–3500 m around Japan and from the Bering Sea to California (S. Ohta, pers. comm.). Crabs tentatively assigned to this species were also reported from the Sagami Bay cold-seeps, but in much lower numbers than the dominant *P. multispina* (J. Hashimoto, pers. comm.).

Additional occurrences of Paralomis *species.*—Several authors have reported the occurrence of lithodid crabs as belonging to the genus *Paralomis.* Most reports have been based on collected specimens. Two yet unidentified species of *Paralomis* occur at the Minami-Ensei vents (Mid-Okinawa Trough), living on mytilids or around bacterial mats, together with the vent endemic *P. jamsteci* (Hashimoto et al. 1995). In the hydrothermal areas of the North-Fiji back-arc basin (2000 m) the "white-coloured lithodid crabs" observed by Jollivet et al. (1989), were later identified as belonging to the genus *Paralomis,* and have also been sampled at 1800 m in venting areas of the Lau back-arc basin (Desbruyères et al. 1994). On the Juan de Fuca ridge in the northern Pacific, the lithodid crab observed and sampled at 1600 m on the Axial Seamount hydrothermal vent area by Tunnicliffe & Jensen (1987), is a species of *Par-*

alomis that co-occurs with the brachyuran majid crab *Macroregonia macrochira.* These authors suggested that this lithodid might be the same species found at the Oregon cold-seeps by Suess et al. (1985). This *Paralomis* sp. and *Paralomis verrilli* (if confirmed) would then be the only lithodid species that occur in both vent and seep environments. Galkin & Moskalev (1990b) also observed a crab closely related to *Paralomis* on the Juan de Fuca ridge.

Remarks on Lithodidae.—The Lithodidae do not seem to be physiologically dependent on the chemosynthetic production of vents or seeps. E. Escobar-Briones (pers. comm.) recently observed that although *Neolithodes diomedeae* was seen near bacterial mats and hydrothermal vent structures in the Guaymas Basin, it appears to mainly feed on organic matter of photoautotrophic origin. The opportunistic behavior of this deep-sea scavenger is, however, believed to contribute to the export of hydrothermal material to the surrounding abyssal environment. In other hydrothermal and cold-seep settings, direct evidence exists of lithodid crabs feeding on chemoautotrophic symbiont-containing fauna. Tunnicliffe & Jensen (1987) reported that pieces of vestimentiferan tubes were found in the stomachs of *Paralomis* sp. at Axial Seamount vents. Observations of *P. multispina* and *P. jamsteci* feeding upon live vesicomyid and mytilid bivalves are mentioned by Hashimoto et al. (1989) and Takeda & Hashimoto (1990) in Sagami Bay cold-seeps and Okinawa vents. Suess et al. (1985) described a large lithodid in the Oregon seeps as actively feeding on vesicomyid clams. The *Lithodes* spp. from Monterey Bay seep communities are known to have attacked unsuccessfully vesicomyid clams (J. P. Barry, pers. comm.). Another type of feeding has been proposed for *P. multispina* by Horikoshi & Ishii (1985), who observed this crab actively scooping up and "feeding" on the black reduced mud within the clam beds of Sagami Bay cold-seeps. Most frequently, the Lithodidae occur in greatest densities at vents and seeps. As there appears to be no other advantage in getting close to such a toxic milieu than the increased food-supply (particularly near hydrothermal vents with high concentrations of hydrogen sulfide and heavy metals, low oxygenation and pH), they can be considered at least to partially feed on chemosynthetically-derived material.

Cold-seep Lithodidae described to date range in depths from 250 to 2037 m. However, one occurrence is known from cold-seep communities of the Nankai Trough, Japan subduction zone, at 3800 m (M. Sibuet, pers. comm.). At hydrothermal vents, the depth range is 350–2000 m. The geographical distribution of these observations is worldwide, with some noticeable exceptions: no Lithodidae have ever been observed near hydrothermal vent areas of the East Pacific Rise (EPR), the Galápagos Rift, nor the Mid-Atlantic Ridge. The crab mentioned by Guinot & Macpherson (1987) from the EPR at 12°35′N, although probably a lithodid, cannot be assigned to a hydrothermal context. It was indeed observed on an off-axis seamount located 18 km from the ridge axis and even farther from the nearest known vent site in this area (P. Chevaldonné, pers. obs.).

Superfamily Galatheoidea

This superfamily includes four families, two of which are represented at deep-sea hydrothermal vents and cold seeps.

Family Galatheidae

Galatheid crabs have been found associated with hydrothermal environments since the first submersible expeditions explored the Galápagos Rift vents (Corliss & Ballard 1977). They have also been known to occur in cold-seep settings since the discovery of this type of community (Paull et al. 1984). Galatheids are familiar members of vent and seep communities but often do not attract as much attention as other spectacular organisms such as the Vestimentifera and large bivalves. Also, because most galatheid crabs appear similar, to the non-specialists, observations on them are numerous but often vague. Only three of the 11 definite species known so far have been reported from cold-seep communities, and one, *Munidopsis crassa,* from both hydrothermal and seep environments. Reports of the latter, however, seem suspect as one is from the Mid-Atlantic Ridge, and another from the Peru margin. Many occurrences are mentioned only as "galatheid crabs," so much more species are likely to be described in the future.

Genus *Munida* Leach, 1820

Munida magniantennulata Baba & Türkay, 1992

This species was originally described from three specimens collected at hydrothermal vents of the Lau back-arc basin in the southwest Pacific, at a depth of 1750–2000 m (Baba & de Saint Laurent 1992, Baba & Türkay 1992). It was subsequently found in collections from a non-vent environment off Australia (Baba 1994).

Munida microphthalma Milne Edwards, 1880

In the seepage areas of the Barbados accretionary prism, at 1700–2000 m, two different species of Galatheidae have been observed (K. Olu, pers. obs.). Only one has been collected and identified as *M. microphthalma* (M. de Saint Laurent, pers. comm.). Jollivet et al. (1990) earlier reported *Munidopsis* sp. from the same area. They either misidentified *M. microphthalma* from their towed camera pictures, or observed the second and bigger species, which might be a *Munidopsis. Munida microphthalma* has been reported from the Atlantic, south of Iceland to Ascencion Island, in the Gulf of Mexico, the Carribbean, and the Bay of Biscaye, at depths of 194–2129 m (Wenner 1982).

Genus *Munidopsis* Whiteaves, 1874

This is the most commonly encountered galatheid genus in reducing environments, including at least 10 species, of which six are known so far only from hydrothermal vents. Many authors have reported *Munidopsis* sp. or *Munidopsis*-like galatheid crabs, so again, the list of species is likely to expand.

Munidopsis alvisca Williams, 1988

This so far exclusively hydrothermal-associated species was described by Williams (1988) from widely separated venting areas. *Munidopsis alvisca* occurs at the periphery of hydrothermal areas on the Explorer and Juan de Fuca ridges, at 1545–1800 m, in the northeastern Pacific, and at 2000 m in the Guaymas Basin, Gulf of California (Khodkina 1991). Van Dover et al. (1990) also reported a galatheid crab which might be *M. alvisca,* from vents of the Escanaba Trough on the Gorda Ridge.

Munidopsis beringana Benedict, 1902

A galatheid sampled from cold-seeps of the Middle America Trench at 3700–4000 m west of Mexico has been assigned to *Munidopsis beringana* (E. Macpherson, pers. comm.). The galatheid crabs observed at shallower seep communities (2900 m) might belong to this same species (K. Olu, pers. obs.). There is still some doubt on the determination of this species, as the collected specimens present some variations from other *M. beringana.* This occurrence is also out of the known geographical and depth range of this species, usually found from the Bering Sea to Oregon, at 2800–3276 m (Ambler 1980).

Munidopsis crassa Smith, 1885

As previously mentioned, this species is believed to be present both in cold-seep and hydrothermal settings. Segonzac (1992) reported it from the Snake Pit hydrothermal area, at 3480 m, on the Mid-Atlantic Ridge.

Olu et al. (1996) recently reported *Munidopsis crassa* from cold-seeps of the Peru margin, at 3000–3600 m, although unidentified galatheids were also observed at 5040 m. A comparative examination of Atlantic and Peru specimens is needed to confirm these findings. *M. crassa* was previously only known from the Atlantic, at 2679–5315 m (Wenner 1982).

Munidopsis diomedeae (Faxon, 1895)

Munidopsis diomedeae was observed near hydrothermal vents of the Guaymas Basin, Gulf of California, at 2000 m depth (Khodkina 1991), along with *M. alvisca.* One of these two species might be the *Munidopsis* sp. mentioned by Lutz (1992) from cold seepages in the same area. *M. diomedeae* is common in the Gulf of California, and is known from California to Chile, at 768–3790 m (Haig & Wicksten 1975).

Munidopsis lauensis Baba & de Saint Laurent, 1992

Munidopsis lauensis occurs with *Munida magniantennulata* at deep-sea vents of the Lau back-arc basin, in southwest Pacific, at 1750 m. It is also found at 2000 m in hydrothermal sites of the nearby North-Fiji back-arc basin (Baba & de Saint Laurent 1992). To date, this species is exclusively known from hydrothermal areas.

Munidopsis lentigo Williams & Van Dover, 1983

This hydrothermal vent endemic is considered a "high temperature" species (Williams & Van Dover 1983) as it seems to be the galatheid that lives closest to high temperature fluid venting. It has been found only at vent sites of the East Pacific Rise at 21°N, 2600 m depth.

Munidopsis marianica Williams & Baba, 1989

Munidopsis marianica is another apparently vent-endemic from the 3600–3700 m deep hydrothermal sites of the Mariana back-arc basin, western Pacific, where it lives in 10–25°C waters among dense carpets of actinians (Williams & Baba 1989, Hessler & Lonsdale 1991).

Munidopsis sonne Baba, 1995

Munidopsis sonne is only known from two specimens collected at active vents of the North Fiji Basin, at 1992 m (Baba 1995).

Munidopsis starmer Baba & de Saint Laurent, 1992

Munidopsis starmer also seems restricted to hydrothermal vents (Baba & de Saint Laurent 1992) and occurs at vent sites of the North-Fiji Basin, at 2750 m. In the same area, *M. lauensis, M. sonne,* and two species of Chirostylidae are also present.

Munidopsis subsquamosa Henderson, 1885

Munidopsis subsquamosa is believed to be a complex of deep-sea cosmopolitan species (Van Dover 1986), which explains its considerable geographic range. Although this complex clearly needs a complete reexamination and taxonomic work at the molecular level, we will simply call it here *M. subsquamosa.* It was the first galatheid species observed in a chemosynthetically-based community, and is found at almost every vent location in the eastern Pacific, in a depth of ca. 2600 m (de Saint Laurent 1984, Hessler et al. 1985, Van Dover et al. 1985). At 21°N on the East Pacific Rise (EPR), it occurs with *M. lentigo,* but inhabits colder waters. It is the only species observed at 13°N (EPR) and sites of the Galápagos Rift, and has also been collected from the EPR at 10–12°N (Van Dover & Hessler 1990) and 9°50′N (Kaartvedt et al. 1994). At the latter location, Lutz (1992) suggested that there might be two different species of *Munidopsis.*

Additional occurrences of Munidopsis

species.—Many reports of "*Munidopsis* sp." exist from a great variety of hydrothermal and seepage areas. Hydrothermal occurrences include the EPR at 17–20°S (Van Dover & Hessler 1990); three locations in the Mid-Okinawa back-arc basin, the Iheya Ridge at 1400 m (Ohta 1990a, Kim & Ohta 1991), the Izena Caldron at 1400 m (Hashimoto et al. 1995), and the Minami-Ensei Knoll at 700 m (Hashimoto et al. 1990, 1995); Manus back-arc basin in the southwest Pacific at 2500 m (Galkin 1992); TAG area on the Mid-Atlantic Ridge (Galkin & Moskalev 1990a); and Broken Spur area farther north on this same ridge (Murton et al. 1995). Reports from cold-seeps include the Nankai Trough in the Japanese Trench at 3800 m (Laubier et al. 1986), cabonate seeps of Enshu-nada, Japan, at 1000–1220 m (Ohta et al. 1995), and the Laurentian Fan at 3850 m (Mayer et al. 1988).

In Monterey Bay, cold-seep communities occur at two different bathymetric levels, at 3000–3600 m (Embley et al. 1990) and 600–1000 m (J. P. Barry, pers. comm.). At least two different species have been observed so far, possibly of two different genera. At deeper sites, a single species has been found and tentatively assigned to the genus *Munidopsis* by Embley et al. (1990), but could also be a species of *Munida* according to J. P. Barry (pers. comm.). At shallower seeps (600–1000 m), two different species of Galatheidae are known, one of which might be the same species observed deeper, and the other apparently is a seep endemic that might belong to the genus *Munidopsis* (J. P. Barry, pers. comm.).

In the Gulf of Mexico seep communities, MacDonald et al. (1989) reported a possibly undescribed species of *Munidopsis* from the Bush Hill site, at 540 m, on the Louisiana Slope. At different seepage depths on the slope (400–1000 m and 2200 m), Carney (1994) indicated two *Munidopsis* spp. (including one seep endemic), different from the "background" galatheids. One of these is probably the Bush Hill species. *Munidopsis* spp. are much more common than the chirostylid *Eumunida picta* that also occurs at the 400–1000 m sites, and they live in close association with mytilid bivalves and vestimentiferan tubeworms. At 3270 m, in cold-seeps of the Florida Escarpment, Hecker (1985) has reported a large and numerous white *Munidopsis* sp. that has not been seen far outside the seep communities.

Unconfirmed reports of *Munidopsis*-like galatheids include those from the hydrothermal vents of the Piyp volcano, at 800 m, in the Bering Sea (Sagalevich et al. 1992). In the region of the Barbados accretionary prism, *Munidopsis*-like galatheids have also been observed associated with cold seeps on mud volcanoes, at 4710–4980 m (K. Olu, pers. obs.), and galatheids tentatively assigned to *Munidopsis* were reported by Jollivet et al. (1990), at shallower cold-seep sites (1000–2000 m), in the southern part of the prism.

Family Chirostylidae

Chirostylid crabs are represented in chemosynthetic communities by two genera and three species. This family is frequently overlooked by non-specialist observers when reporting the occurrence of "galatheids."

Genus *Eumunida* Smith, 1883
Eumunida picta Smith, 1883

This species is considered as a rare vagrant in cold-seeps of the Louisiana slope, at 400–1000 m depth (Carney 1994). It has been reported from Massachusetts to Colombia, at 200–600 m (de Saint Laurent & Macpherson 1990).

Genus *Uroptychus* Henderson, 1888

Baba & de Saint Laurent (1992) have described two new species only known from vents of the North-Fiji Basin.

Uroptychus bicavus Baba & de Saint Laurent, 1992

Uroptychus bicavus is known from a depth of 2750 m.

Uroptychus thermalis Baba & de Saint Laurent, 1992

Uroptychus thermalis occurs at depth of 2000 m.

Additional occurrences of Galatheoidea.—Several authors have reported the occurrence of "galatheid crabs" or "squat lobsters" that cannot be assigned with certainty to a family. These reports are from hydrothermal areas of the EPR at 21°30′S (Renard et al. 1985), 23°30′S and 26°S (Marchig & Gundlach 1987), the Gulf of Aden (Juniper et al. 1990) and the Edison Seamount in the southwestern Pacific (Herzig et al. 1994), and from cold seeps of Enshu-nada, Japan, at 1000–1220 m (Ohta et al. 1995).

Remarks on Galatheidae and Chirostylidae.—Like Lithodidae, Galatheidae and Chirostylidae are generally not considered to be dependent on the chemically reduced fluids emitted at vents and seeps. Their representatives are often restricted to the periphery of the sites, where they are believed to be opportunistic species taking advantage of increased productivity. However, there is a significant number of species that seem to be endemic to hydrothermal vents or cold-seeps, and some of them even appear to be adapted to this harsh environment, not just the periphery. Van Dover (1986) observed that gravid females of the hydrothermal *Munidopsis subsquamosa* seemed to live under higher temperature conditions than males. Although this species is not restricted to vent areas, this behaviour was interpreted as a possible adaptation to improve reproductive efficiency. Galatheids also seem to adapt relatively well to hypoxic conditions, such as those encountered in reducing habitats. In some British Columbia fjords, for instance, dense aggregations of *Munida quadrispina* are consistently found at low oxygen levels, where most other invertebrates of the fjords cannot compete for food and space (Burd & Brinkhurst 1984). Stable isotope analyses led Van Dover & Fry (1989) and E. Escobar-Briones (pers. comm.) to characterize *Munidopsis subsquamosa* and *M. alvisca,* of the Galápagos and Guaymas hydrothermal vents, as having a mixed diet partly including a sulfur-based source of carbon. Similar analyses on the Iheya Ridge *Munidopsis* sp. also show at least a partial nutritional dependence on chemosynthetic processes (Kim et al. 1989, Kim & Sakai 1991). At the Monterey Bay cold-seeps, an apparently seep endemic galatheid is found grazing on mats of the filamentous bacteria *Beggiatoa,* and is even covered with the bacterial filaments (J. P. Barry, pers. comm.).

Galatheids and chirostylids might also act as vectors for the export of organic matter of hydrothermal origin in the deep sea. They might disperse more efficiently than lithodids, due to their swimming abilities, and can also easily detect new food sources. Two shark carcasses placed 100 m from a vent site at 13°N on the EPR (Fig. 1) attracted hundreds of *Munidopsis subsquamosa* within a day (D. Desbruyères, pers. comm.). These characteristics might also favor dispersal of non-planktonic developmental stages of vent and seep species. Carney (1994) reported that *Munidopsis* sp. of the Gulf of Mexico seepage areas are often covered with juvenile mussels, and may be an important means of post-settlement dispersal for seep endemic sessile taxa. Such phoretic processes might also occur in hydrothermal polychaetes (Tunnicliffe & Jensen 1987, Zal et al. 1995).

Galatheidae are found in virtually every hydrothermal or cold-seep environment, as well as in other types of reducing habitats such as whale carcasses (Bennett et al. 1994, Wada et al. 1994) or decomposing wood (Williams & Baba 1989). They do not seem to be limited by depth, as their occurrence is reported from as deep as 5040 m, in the deepest cold-seep communities

Fig. 1. Attraction of *Munidopsis subsquamosa,* a galatheid crab commonly found in deep-sea hydrothermal vents of the eastern Pacific, to shark carcasses deposited 100 m from a vent site at 13°N, on the East Pacific Rise (2600 m).

(Olu et al. 1996). They are also associated with the shallowest occurrence of vestimentiferans known to date, at 82 m, in the cold-seep site of Kagoshima Bay, Japan (Hashimoto et al. 1993).

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A new species of *Aniculus* Dana (Decapoda: Anomura: Diogenidae) from Hawaii

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Abstract.—A new and spectacular, but rarely seen, species of the hermit crab genus *Aniculus* Dana (*Aniculus hopperae*) is described and illustrated. It is compared and contrasted with *Aniculus maximus* Edmondson, the only other species of the genus known from the Hawaiian Islands and with *A. retipes* Lewinsohn, a species to which it is most morphologically related.

While diving at Pupukea on the north shore of the Hawaiian island of Oahu during June of 1995, the junior author collected an unfamiliar hermit crab inhabiting a drupe shell, *Drupa rubusidaeus* Röding, 1798 (aperture length about 2 cm). At a depth of about 8 m, the shell lay on boulder and rubble bottom adjacent to the low limestone cliffs of the shoreline containing a system of deep undercuts and small caves.

A brief literature search by the junior author revealed no named species to which it could be referred. However, a photograph of a similar animal from a popular book on hermit crabs (Giwojna 1978: 57) bore the following caption: "This species of *Dardanus* with red legs and claws and orange eye-stalks and antennae, hails from Hawaii."

The photographer, Scott Johnson, contacted by telephone, was able to locate an additional photograph of the species in question, taken at Makua, Oahu on a ledge at a depth of 8–10 m, a site on the western shore similar to that at Pupukea where the holotype was collected.

The Pupukea specimen was kept alive in a plastic container full of seawater that was changed every other day until it could be photographed in natural surroundings, then preserved in 70% alcohol and sent to the senior author. It has now been deposited in the collection of the National Museum of Natural History, Smithsonian Institution (USNM). A second specimen, subsequently collected, has been deposited in the collection of the Bernice P. Bishop Museum (BPBM). Shield length (SL), measured from the midpoint of the anterior carapace margin to the midpoint of the posterior margin of the shield provides an indication of size.

Aniculus hopperae, new species
Figs. 1–3

Dardanus species: Giwojna, 1978: 57, unnumbered figure.

Holotype.—♂ (SL = 6.32 mm), Pupukea, Oahu, Hawaii, 8 m, 18 Jun 1995, coll. J. Hoover; USNM 275921.

Paratype.—♂ (SL = 2.96 mm), Pupukea, Oahu, 10 m, 7 Oct 1995, coll. R. Holcom; BPBM S11284.

Description.—Shield (Figs. 1A, 2A) longer than broad, with few shallow depressions, but not divided into distinct lobes. Mesogastric region delimited posteriorly only by pair of furrows forming weak V; with deep transverse post-rostral furrow. Rostrum triangular, acute, approximately reaching level of well developed, spinose

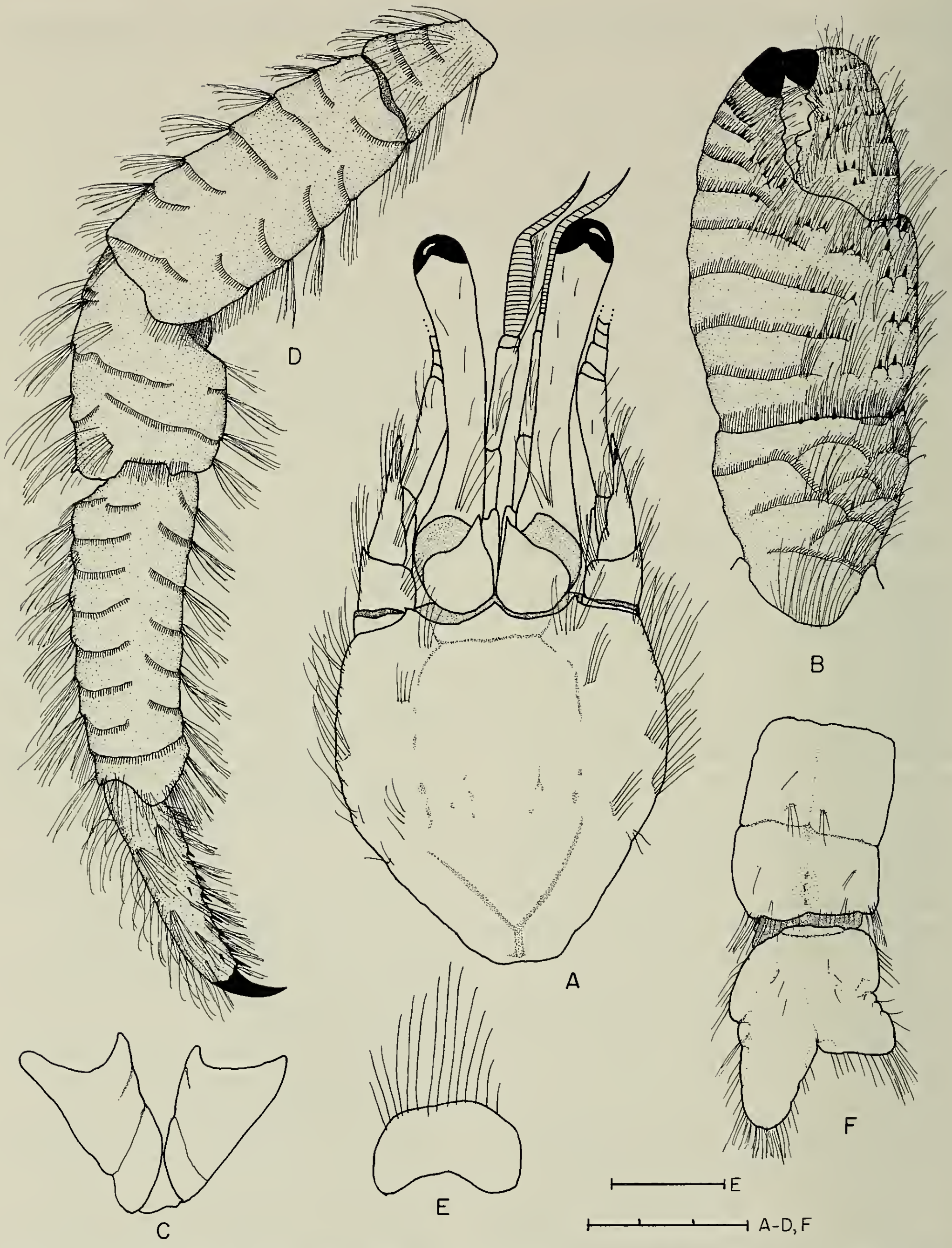

Fig. 1. *Aniculus hopperae,* new species. Holotype, USNM 275921: A, shield and cephalic appendages; B, carpus and chela of left cheliped (outer face); C, coxae of chelipeds (ventral view); D, third left pereopod (lateral view); E, anterior lobe of sternite of third pereopods; F, tergite of sixth abdominal somite and telson (dorsal view). Scales equal 3.0 mm (A–D, F) and 1.0 mm (E).

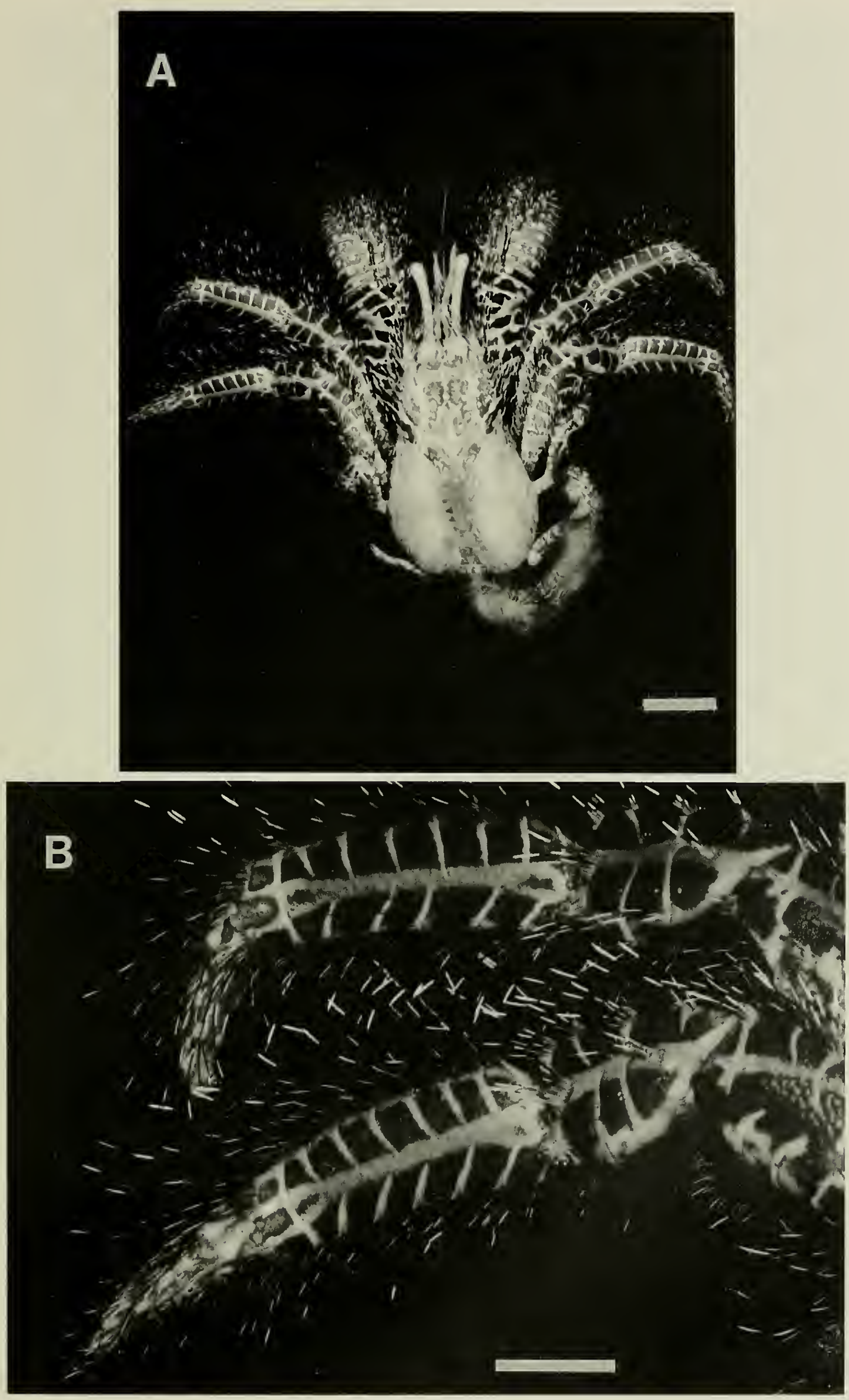

Fig. 2. *Aniculus hopperae,* new species. Holotype, USNM 275921: A, whole animal (dorsal view); B, left second and third pereopods (lateral view). Scales equal 4.0 mm (A) and 2.0 mm (B).

lateral projections. Ocular peduncles unequal in length, left longest, slightly longer than shield, bulbous basally, appreciably thinner medially; corneae not dilated. Ocular acicles very well developed, triangular, with simple terminal spine.

Antennular peduncles reaching to distal third of ocular peduncles. Ultimate and penultimate segments with scattered long, stiff setae. Basal segment with scattered stiff setae, and minute spinule on laterodistal margin.

Antennal peduncles shorter than antennular peduncles, reaching little beyond proximal half of ocular peduncles. Fifth, fourth and third segments unarmed, but with scattered long stiff setae, most abundant at ventrodistal margin of third. Second segment with dorsolateral distal angle produced, with small terminal spine practically obscured by long stiff setae; dorsomesial distal angle unarmed, mesial margin with long stiff setae. First segment with 3 or 4 spinules on ventrolateral margin distally. Antennal acicle subtriangular, elongate, reaching well beyond proximal margin of ultimate peduncular segment, with terminal spine obscured by tuft of long setae and additional tufts of similar setae mesially and laterally. Antennal flagellum long, overreaching outstretched chelipeds and ambulatory legs; each article with 1 or 2 minute setae.

Chelipeds (Figs. 1B, C, 2A, 3A, B) and ambulatory legs short. Chelipeds equal, similar; overreaching distal margin of corneae by half length of palm; tips of dactyls and fixed fingers reach slightly beyond proximal margins of dactyls of second pereopods and mid-length of dactyls of third. Dactyls slightly longer than palm; cutting edges of both dactyl and fixed finger with few large calcareous teeth, terminating in very prominent corneous hoof-like claws; dorsal and mesial surfaces of dactyls each with transverse rows of striae armed with small corneous spines and stiff setae, continuing onto ventral surfaces as rows of striae set with short stiff setae. Palms with short, transverse rows of 1 to 4 corneous-tipped tubercles on dorsal surface in mesial fourth, remainder of palm and fixed finger with transverse striae almost completely circumscribing dorsal, lateral and mesial surfaces and set with rows of quite short setae ventrally and laterally, becoming longer and supplemented with corneous spinules on dorsal surface of fixed finger and medianly on dorsal surface of palm. Carpi approximately equaling length of palms; striae of dorsal surfaces not disposed in regular transverse lines but rather in network of curves inset with short stiff and few longer stiff setae, dorsomesial distal angles each with 1 prominent corneous-tipped spine and 3 corneous spinules on dorsodistal margin; mesial, lateral and ventral surfaces with transverse, sometimes short or interrupted, striae inset with short stiff setae. Meri subtriangular; dorsal margins with transverse rows of striae inset with short setae, extending onto lateral and ventral surfaces, dorsally accompanied by tufts of long setae; ventromesial margins each with 2 or 3 very small spines distally, ventral surfaces at mesial angles each with cluster of corneous-tipped spinules. Ischia each with 2 transverse striae inset with short setae on ventral surface. Coxae (Fig. 1C) each with very short stria mesially.

Second and third pereopods (Figs. 1D, 2B) similar from left to right, third pair slightly shorter than second; dactyls with tufts of long stiff setae on all surfaces, propodi, carpi, meri and ischia with tufts of long setae predominately dorsally and ventrally. Dactyls 0.75 to 0.80 length of propodi; dorsal surfaces of both second and third, and mesial and lateral faces of third each with irregular rows of corneous spinules; ventral margins each with 7 or 8 corneous spines. Propodi slightly longer than carpi and approximately equal to length of meri; 1 continuous transverse stria inset with short setae circumscribing dorsal, lateral and ventral surfaces distally, followed posteriorly by series of striae interrupted medially on lateral surfaces; mesial faces

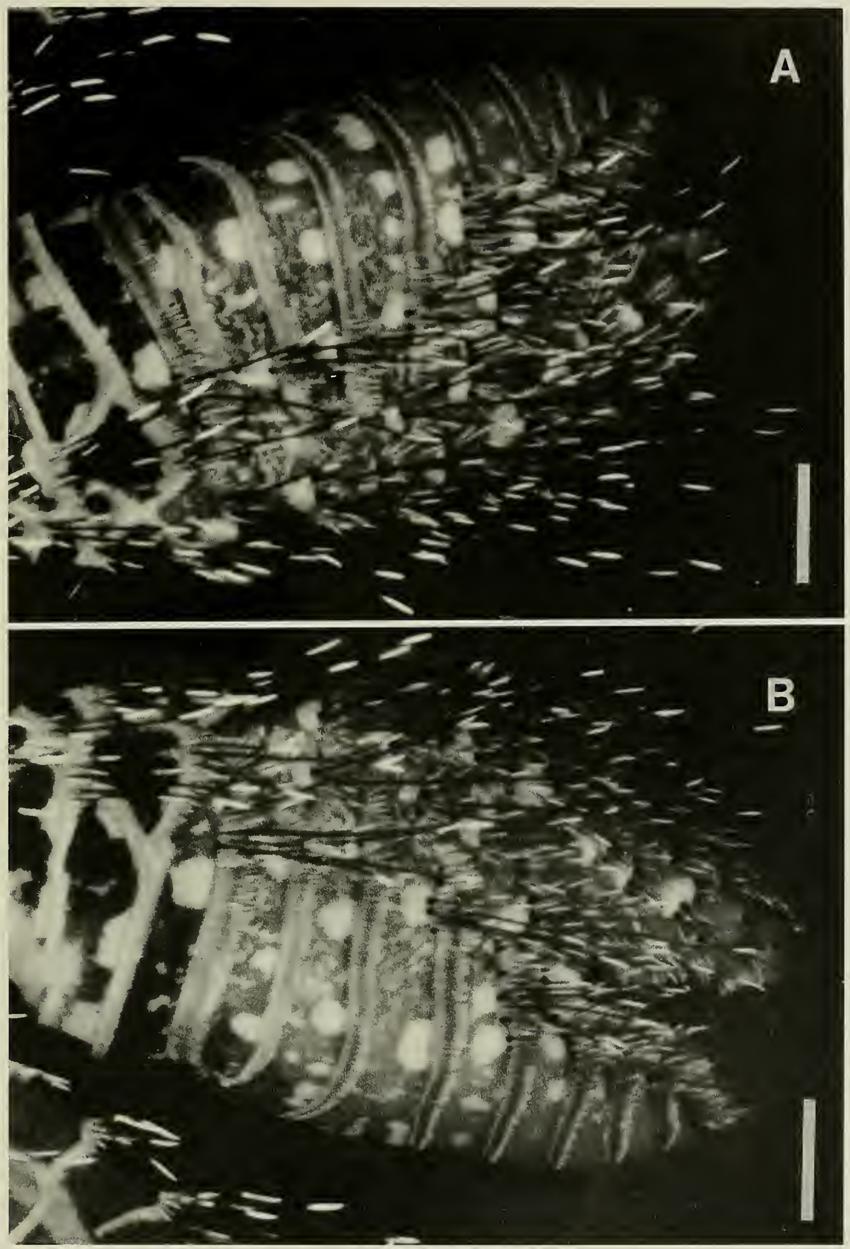

Fig. 3. *Aniculus hopperae,* new species. Holotype, USNM 275921: A, chela and carpus of left cheliped (dorsal view); B, chela and carpus of right cheliped (dorsal view). Scales equal 2.0 mm.

with scattered tufts of setae; ventrodistal margins each with 1 or 2 corneous spinules. Carpi with few transverse striae incompletely circumscribing dorsal, lateral and mesial surfaces; dorsodistal angles each with corneous-tipped spine. Meri each with transverse striae circumscribing dorsal, lateral and ventral surfaces, interrupted medianly on lateral faces; striae of second pair much less distinct than third; second each with small spine at ventrolateral distal angle. Anterior lobe of sternite of third pereopods (Fig. 1E) subrectangular, with long marginal setae.

Tergites of abdominal somites 1–5 membraneous but clearly delineated and ornamented with long greenish- or whitish-tipped red marginal setae; tergite of sixth (Fig. 1F) with dorsal longitudinal median furrow of anterior lobe very weakly marked, continued on posterior lobe as ovate depression and longitudinal series of deep pits posteriorly. Telson (Fig. 1F) with transverse suture not much more distinct that supplemental lateral notches; posterior lobes asymmetrical, subtriangular, left slightly to appreciably longer than right; with narrow median cleft; terminal margins with long setae, longest at external angles.

Color.—Long setae overall red proximally, greenish-white distally, short setae of striae greenish or yellowish-white; spines white with black corneous tips; claws and corneous spines black. Shield mottled red and white with purple tint medianly and anterior to post-rostral furrow. Ocular peduncles yellow; ocular acicles mottled red and white, with white terminal spinule. Antennular peduncles and flagella light yellow. Proximal segments of antennal peduncle and acicle mottled red and white; ultimate segment and flagella light purple. Chelae of chelipeds brilliant red with scattered white specks and splotches. Carpi brownish red with specks and splotches of white. Meri with lighter patches of brownish-red or mottled red and white on white background. Dactyls of ambulatory legs red with white patches. Propodi each with irregular longitudinal white band dorsally and ventrally; mesial faces mottled red and white; lateral faces red with white striae and median longitudinal band of purple. Carpi each with longitudinal white stripe on ventral surface; mesial faces mottled red and white; dorsal and lateral surfaces red, striae white, striae of lateral faces separated by longitudinal band of purple. Meri mottled red and white; longitudinal purple band of carpi continued on lateral faces dorsolaterally.

Distribution.—At present known only from two locations on Oahu, Hawaii; 8–10 m.

Etymology.—This species is named in honor of Dr. Carol N. Hopper, Director of Education at Honolulu's Waikiki Aquarium, an enthusiastic advocate of Hawaii's marine invertebrates, and an inspiration to the many young aspiring marine biologists who attend her classes.

Affinities.—*Aniculus hopperae* is immediately distinguished from the other resident Hawaiian species of the genus, *A. maximus* Edmondson, 1952, by its color, the sculpturing of the shield, the arrangement of striae on the ambulatory legs, and the armature of the tergite of the sixth abdominal somite. In *A. maximus,* the general color is intense orange or golden yellow with the striae set off by red-violet, the setae are yellow and the bristles red-tipped; the shield is marked by a series of furrows that clearly delineate the rhomboid mesogastric region common to most species of *Aniculus*; the transverse striae on the lateral faces of the propodi of the ambulatory legs are continuous; and the anterior lobe of the tergite of the sixth abdominal somite is armed with a cluster of spinules on either side of the midline. In contrast, the general color of *A. hopperae* is brilliant red, the striae often are white and the long setae are red, tipped with greenish white; the shield lacks any clear delineation of the mesogastric region; the striae of the lateral faces of the propodi of the ambulatory legs are interrupted by a broad smooth longitudinal band of purple; and the tergite of the sixth abdominal somite has an unarmed anterior lobe.

Forest (1984:59) remarked that *A. retipes* Lewinsohn, 1982 ". . . occupe une position incontestablement isolée par rapport aux autres espèces du genre." Those characters which set *A. retipes* apart included the lack of a delimited mesogastric region and the interruption of the striae on the lateral faces of the propodi of the ambulatory legs by a smooth longitudinal band. *Aniculus hopperae* shares both of these characters with *A.*

retipes. Additionally the tergite of the sixth abdominal somite has an unarmed anterior lobe in both species; however, that is a character common to all species except *A. maximus. Aniculus retipes* and *A. hopperae* are readily distinguished by their color patterns, as well as the different patterns of the striae on the carpi of the chelipeds. The ocular peduncles of *A. hopperae* are uniformly yellow, where as those of *A. retipes* have longitudinal red stripes. *Aniculus retipes,* particularly specimens from Phuket, Thailand, have appreciably longer antennular peduncles (Forest 1984:52, fig. 51) than seen in *A. hopperae.*

Remarks.—Like *A. hopperae,* the majority of the seven other described species of *Aniculus* are known from relatively few specimens. Only *A. aniculus* (Fabricius, 1787) and *A. ursus* (Olivier, 1811) can be considered common. However, most species have broad, albeit sporatic, distributions. For example, the other Hawaiian species, *A. maximus,* has also been reported from the Marquesas and Seychelles Islands. Similarly, the closely related *A. retipes* is known from the Red Sea to Zanzibar in the western Indian Ocean, to the west coast of Malaysia in the east, and in the western Pacific from the South China Sea and Banda Sea of Indonesia to Samoa (Forest 1984).

Twenty photographs of the living holotype were distributed to members of the Hawaiian Malacological Society, dive charter operators, Waikiki Aquarium staff and other likely acquaintances in the hope that further specimens and ecological data would come to light. Subsequently, John L. Earle, a long-time Oahu shell collector, informed the junior author that the crab was familiar to him, although not encountered very often. He could not cite an exact location or depth but said that he usually collected in the rubble at the bottom of a drop-off near Makua, Oahu at a depth of about 23 m. The drop-off contains numerous undercuts and caves. In the absence of additional information, the authors postulate this species to be an uncommon inhabitant of exposed rocky Hawaiian shores at a depth of 8 to 23 m or more, in the vicinity of caves and ledges (where it may shelter during the enormous winter surf). It is almost certainly not an intertidal species; this biotope has been well sampled on Oahu for many years. Like many hermit crabs, it is probably most active at night.

Acknowledgments

The authors gratefully acknowledge the collection of the second specimen by Ron Holcom and the ecological information provided by John Earle. This is a scientific contribution from the Shannon Point Marine Center, Western Washington University.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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Description of a new porcellanid, *Petrolisthes gertrudae* from the southeastern Caribbean Sea (Crustacea: Decapoda: Porcellanidae)

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Abstract.—A new species of the genus *Petrolisthes* Stimpson, 1858, *P. gertrudae,* from the West Indies is described. The new species belongs to a group of *Petrolisthes* species characterized by the complete lack of spines on the carapace and pereopods 1–5. The new species can be easily distinguished from other species of that group by the convex shape of the carpal lobe of the chelipeds, and by the pubescence which covers the outer margins of the chelae.

The porcellanid fauna of the Caribbean Sea can be considered fairly well known, and has been documented in a series of publications treating species from the southern Caribbean (Gore 1970, 1974, 1982; Gore & Abele 1973, 1976; Werding 1977, 1978a, 1978b, 1982, 1986). Werding (1986) considered the species inventory of the western Atlantic as almost complete. A total of 43 species is now known from the western Atlantic, including three endemics from the coast of Brazil.

The study of collections in the National Museum of Natural History, Smithsonian Institution, revealed the presence of an undescribed species from the southeastern Caribbean. The specimens were collected by P. Hummelinck in 1931, at Bonaire (Dutch West Indies), and by W. L. Schmitt in 1956, at Guadeloupe (French West Indies).

All type specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). The measurements given refer to carapace length (CL) and carapace width (CW) respectively.

Family Porcellanidae

Petrolisthes gertrudae, new species

Figs. 1, 2

Material.—Holotype: ovigerous female, Guadeloupe, West Indies, Pointe a Pitre, Rat Islands, exposed reef, submerged weedy rock, Smithsonian Bredin Caribbean Expedition, 30 Mar 1956, leg. W. L. Schmitt USNM 275965. Paratypes: 1 ovigerous female, same data as holotype USNM 275966; 1 ovigerous female, Bonaire, West Indies, Kralandijk, in colonies of *Zoanthus sociatus,* 31 Oct 1930, leg. P. Hummelinck USNM 275967.

Measurements.—Holotype: CL 3.38 mm, CW 3.51 mm. Paratype from Guadeloupe: CL 4.29 mm, CW 4.35 mm; paratype from Bonaire: CL 3.45 mm, CW 3.64 mm.

Range of length/width of carpus of cheliped: 1.35–1.44; range of egg diameter: 0.65–0.72 mm.

Description.—Carapace subquadrate and about as long as broad; lateral margins nearly parallel behind epibranchial angle. Surface almost smooth, without setae, covered anteriorly with fine granules and behind epibranchial angle with fine plicae; grooves marking regions distinct. Frontal region strongly deflexed, produced, slightly trilobate, median lobe broad, triangular with shallow median groove. Flanks between side walls and legs with fringe of plumose setae. Orbits shallow, outer orbital angle slightly produced. No epibranchial spine.

Inner part of ocular peduncle expanded to a longitudinal crest.

First movable segment of antennae an-

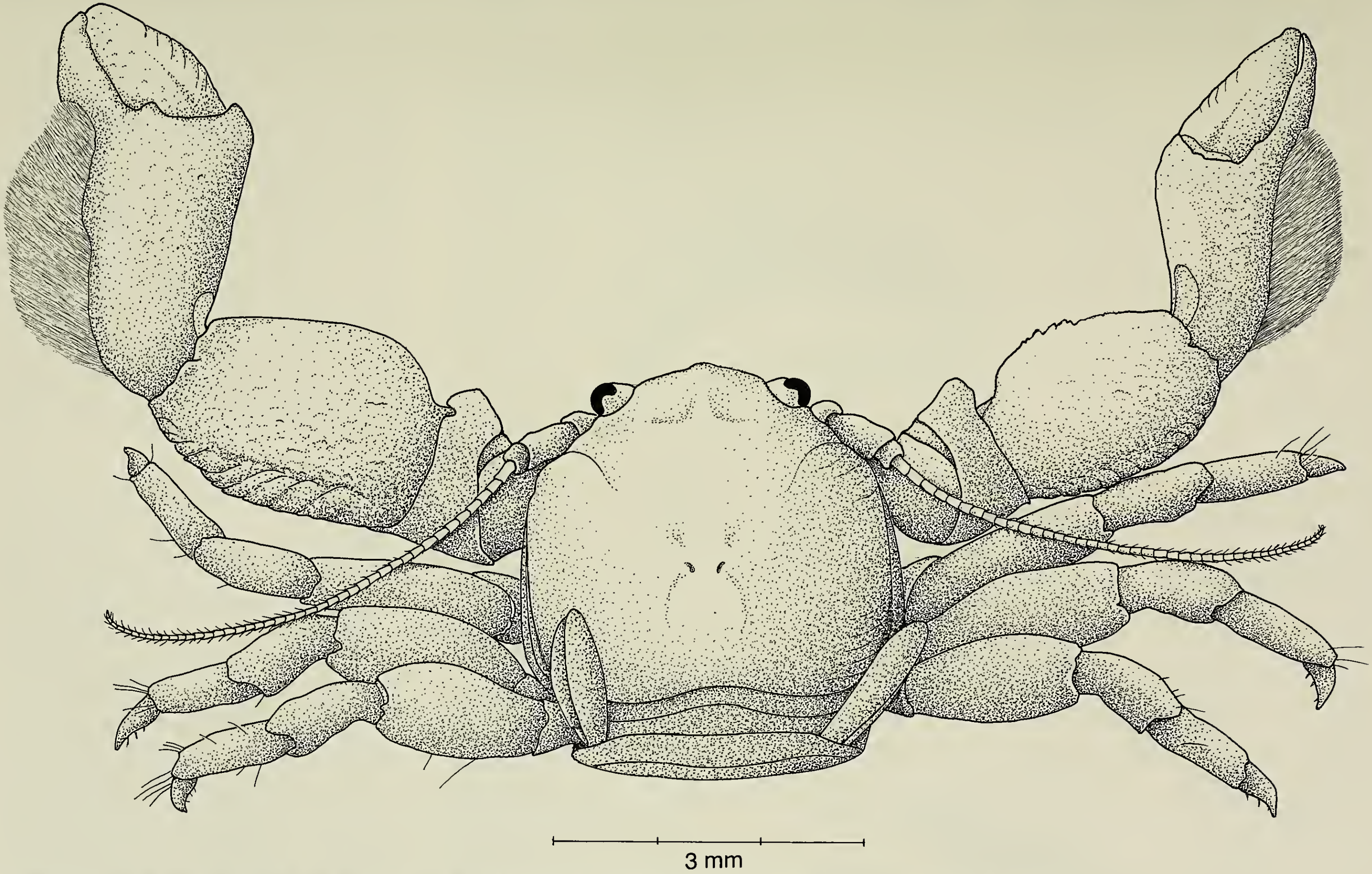

Fig. 1. *Petrolisthes gertrudae*, new species. Female holotype from Guadeloupe, West Indies, dorsal view USNM 275965.

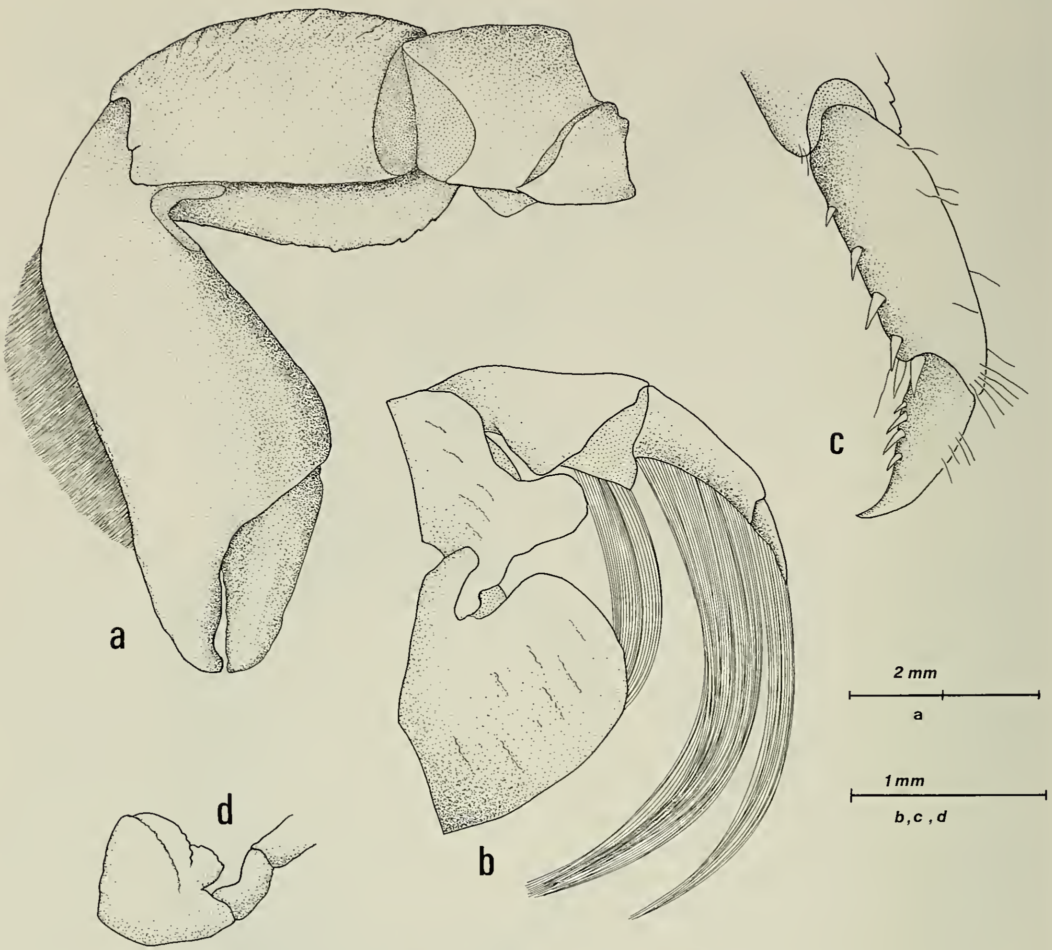

Fig. 2. *Petrolisthes gertrudae*, new species. Female paratype from Guadeloupe, West Indies USNM 275966. a, left cheliped ventral view; b, right third maxilliped, external view; c, propodus and dactylus of first right walking leg, ventral view; d, basal segment of right antennula, ventral view.

teriorly extended to form low, granular crest; second irregularly granulate; third nearly smooth. Flagellum thick, setose. Outer surface of ischium of third maxilliped slightly rugose.

Chelipeds subequal; merus and carpus without setae, dorsal surface with large flattened granules. Merus with broad granular lobe on anterior margin. Carpus less than ½ as long as wide, anterior margin extended, forming rounded lobe, strongly convex at proximal ⅔; proximal portion sometimes armed with fine, irregular denticulation along edge; with shallow longitudinal groove marking broad rounded crest on dorsal surface near the posterior margin, crest composed of large transversally oriented granules; outer distal angle rounded. Surface of manus with similar granulation, upper side with large longitudinal elevation extending to gape of fingers; outer border with longitudinal depression, forming rounded crest at outer margin; outer margin distally straight or slightly curved outward, pollex bent upward; with thick tuft of long feathered setae covering outer margin leaving free only proximal portion and distal half of pollex. Fingers curved at tips, cutting edges without prominent teeth, fingers meeting for entire length or slightly gaping, gape lacking pubescence.

Walking legs with surface granulation similar to that of chelipeds; unarmed, with scattered plumose setae. Propodus with 3 movable spines distally, and 2 or 3 additional ones on inner margin variing inconsistently among legs. Dactylus with 4 movable spines on inner margin.

Abdomen with dense fringe of plumose setae on entire outer margin; telson consisting of 7 plates.

Variations.—The paratype specimen from Bonaire exhibits a more accentuated granulation on the surface of the carapace, and specially at the extremities, than the two specimens from Guadeloupe. The anterior lobe of the carpus of the chelipeds is somewhat depressed by a longitudinal groove.

Habitat.—The specimen collected by P. Hummelinck was found in a colony of the zoanthid *Zoanthus sociatus* Ellis, a species which settles on the wave surf zone of the rocky intertidal. The specimens by W. L. Schmitt were found on an exposed reef. The species seems to be confined to the upper littoral.

Etymology.—The species is named in honor of my wife, Mrs. Gertrud Werding, for her help and understanding during all the years that I have been working on crustaceans.

Discussion

Petrolisthes gertrudae, new species, belongs to a group of species which is mainly confined to the eastern Pacific, where it is represented by 17 tropical and temperate species (Haig 1960). The group is characterized by the complete lack of spines on the carapace and pereopods, including the chelipeds. The carpus of the chelipeds is unarmed, with the exception of minute spinules in some species. The group was represented until now in the western Atlantic by *P. quadratus* Benedict, *P. tridentatus* Stimpson, and *P. tonsorius* Haig. The new species is clearly distinguished from all other species of the group by the convex lobe of the anterior margin of the carpus of the chelipeds which, in some cases, is slightly dentate, and the dense pubescence on the outer border of the manus absent in other representatives of the group.

Acknowledgments

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Nannotheres moorei, a new genus and species of minute pinnotherid crab from Belize, Caribbean Sea (Crustacea: Decapoda: Pinnotheridae)

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Abstract.—*Nannotheres moorei* is described from a small pteriid bivalve mollusk taken in the Caribbean Sea off Belize. This minute, ovigerous pinnotherid crab can be distinguished by its size and the 2-segmented palp on its third maxilliped. With a carapace width of about 1.5 mm in a sexually mature female, it may be the smallest known species of crab.

The minute crab described below was found on the edge of the shell of its host by Donald R. Moore, University of Miami, who gave it to us for study. The unique holotype is in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Abbreviations used below include: cb, carapace breadth; m, meters; mm, millimeters; Mxp3, third maxilliped; P1–P5, pereopods (P1 is the cheliped, P2–P5 the walking legs); Plp, pleopod.

Nannotheres, new genus

Diagnosis.—Adult female: size very small, carapace length less than 2 mm. Carapace soft, subcircular, lacking both sharp anterolateral border and longitudinal sulci anteriorly on dorsal surface. Front projecting only slightly, deflected. Mxp3 with ischium and merus indistinguishably fused; exopod present; palp 2-segmented, proximal longer than distal, segments articulated end-to-end; distal segment very short, rounded distally. Walking legs similar, dactyli simple, subequal. Abdomen of 7 somites, in ovigerous female expanded well beyond bases of walking legs and mouthparts.

Male: Unknown.

Type species.—*Nannotheres moorei*, new species, by present designation and monotypy.

Etymology.—From the Greek, *nannos*, small, and *tereo*, to guard, as used in the name *Pinnotheres*. The gender is masculine.

Host.—A bivalve mollusc of the family Pteriidae, *Malleus candeanus* (d'Orbigny). Waller & Macintyre (1982:490) reported that "In the vicinity of Carrie Bow Cay, Belize, specimens of *Malleus candeanus* are common from a depth of 5 m in the high-relief spur and groove zone seaward to the deepest area explored by SCUBA diving, 46 m on the steeply inclined fore-reef slope."

Remarks.—Manning (1993b:128) listed four genera of pinnotherid crabs that were characterized by the presence of (1) simple dactyli on the walking legs and (2) a Mxp3 palp composed of only two segments: the American genera *Calyptraeotheres* Campos, 1990 and *Epulotheres* Manning, 1993(a) and the Indo-west Pacific genera *Ostracotheres* Milne Edwards, 1853 and *Xanthasia* White, 1846. In addition to being much smaller than species of any of these genera, *Nannotheres* differs from them as follows: (1) it lacks the sharp anterolateral

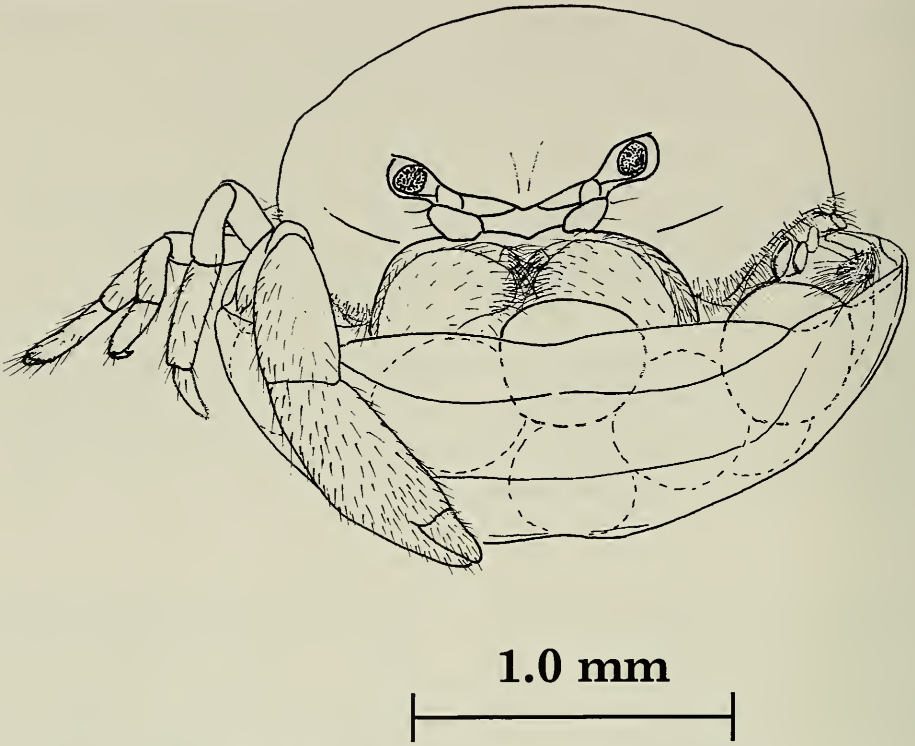

Fig. 1. *Nannotheres moorei,* new genus, new species. Ovigerous female holotype, USNM 277631, frontal view.

border and anterior longitudinal sulci of the dorsal surface of the carapace that are found in *Calyptraeotheres*; (2) it lacks the upturned lateral margins and prominent, median, mushroom-shaped tubercle found on the carapace of *Xanthasia*; (3) the Mxp3 is very different from that of *Ostracotheres,* in which the broad, spatulate propodus is much larger than the carpus; and (4) it has a 2-segmented palp on the Mxp3 in contrast to the 3-segmented palp of *Epulotheres,* which, as we will show below, was misinterpreted by Manning (1993a) in his original account of the genus.

Nannotheres moorei, new species
Figs. 1, 2, 3a

Material.—Belize, Lighthouse Reef [17°20'N, 87°32'W], The Blue Hole, depth 43 m, on a dead pteriid bivalve, *Malleus candeanus* (d'Orbigny), leg. Eberhard Gishler: 1 ovigerous ♀, cb about 1.5 mm (holotype, USNM 277631).

Description.—Adult female: size small, carapace width of ovigerous female about 1.5 mm. Carapace thin, membranous, apparently subcircular, regions indistinct; lateral surfaces almost vertical, lower extreme setose. Front depressed. Eyes very small, visible in dorsal view.

Mxp3 with ischium and merus indistinguishably fused, broadly ovate distally, mesial margin concave proximally, strongly convex and weakly tuberculate distally; palp articulated at about midlength of inner distal face of ischium-merus, 2-segmented, proximal longer, distalmost segment short, rounded, terminally setose. Exopod 2-segmented.

Chela (P1) with movable finger about as long as palm (measured dorsally), cutting edges lacking distinct teeth, cutting edge of fixed finger with low, long, convex, sharp superior flange. Palm height more than half dorsal length. Surfaces of palm overall sparsely setose, inner face with strong setae in lower half.

Walking legs (P2–P5) equal right and left, sparsely setose, P3 and P4 lacking swimming setae; relative lengths, P5 < P4 < P2 < P3; dactyli of walking legs subequal, simple, and similar; propodus of P5 shortest of all propodi. P2 with dactylus 0.7 times as long as propodus, latter 3.7 times longer than high, 1.2 times as long as carpus; merus 1.7 times as long as carpus. P3 with dactylus (missing from right P3 in Fig. 2*d*) 0.7 times as long as propodus, latter 3.6 times longer than high, 1.2 times as long as carpus; merus 1.7 times as long as carpus. P4 with dactylus 0.7 times as long as propodus, latter 2.8 times longer than high, 1.3 times as long as carpus; merus 1.8 times as long as carpus. P5 with dactylus 0.9 times as long as propodus, latter 2.6 times longer than high, 1.1 times as long as carpus; merus 1.3 times as long as carpus.

Abdomen extending well beyond bases of walking legs and buccal mass, lateral edge of abdomen folded inward.

Plp1 biramous, both branches 2-segmented; Plp2 biramous, exopod 2-segmented, extending around outside of egg mass; Plp3–4 uniramous, 2-segmented. Ova large, 17 in number, 0.35–0.5 mm in diameter.

Size.—Unique holotype, ovigerous female, carapace width about 1.5 mm.

Etymology.—Named for Donald R. Moore, Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Florida, whose keen eye spotted this minute crab on the edge of its host's shell after it had been brought on deck.

Remarks.—Schmitt et al. (1973:9) listed four nominal species of *Pinnotheres* that were associated with bivalve molluscs of the genus *Pinctada* Bolten, *P. margarita* Smith, 1869, from the eastern Pacific; *P. margaritiferae* Laurie, 1906, from Ceylon; *P. villosulus* Guérin-Méneville, 1831, from Indonesia; and *P. trichopus* Tesch, 1918, from Indonesia. In addition to being larger, all of these species have three-segmented palps on Mxp3, so they can be separated at once from *Nannotheres* on the structure of the Mxp3 alone. Campos (1989) transferred the American *P. margarita* Smith to his new genus *Tumidotheres.*

Pesta (1911) reported *Pinnotheres* sp. from a *Pinctada* taken in the Molucca Islands and remarked that the host had a nodular growth inside the shell that housed the crab. We could see no such feature in the host of our specimen from Belize. Barnard (1950) also recorded a *Pinnotheres* sp. from a *Pinctada.*

Examination of the specimens of *Malleus candeanus* from Belize studied by Waller & Macintyre (1982) yielded no other specimens.

Although a note accompanying the specimen suggested that it was found, dead, on the edge of the shell of its host, examination of the dried host revealed that the left chela of the crab remained attached to the mantle of the host. The crab seemed to have little internal tissue; the only visible muscles were associated with the egg-bearing pleopods.

Our first comparison of this little crab was with the type species of *Epulotheres* Manning, 1993(a), *E. angelae,* from the Caribbean Sea, as it, too, is small and was reported to have a two-segmented palp on Mxp3. Reexamination of the Mxp3 revealed that the original account was in error, as it has a three-segmented palp (Fig. 3*b*). It can be separated from *Nannotheres* on that feature alone. *Epulotheres* remains a valid genus, distinct from *Pinnotheres* s.s., for its Mxp3 has a very different shape from that of *Pinnotheres pisum* (Linnaeus, 1767), the type species of *Pinnotheres* Bosc, 1802. In *Nannotheres* the fused ischium-merus is much more oval, the inner margin lacking the angled projection found in the Mxp3 of *Pinnotheres*; the carpus and propodus of the Mxp3 are subequal in length and shaped very differently from those of *P. pisum*; and the palp is very short

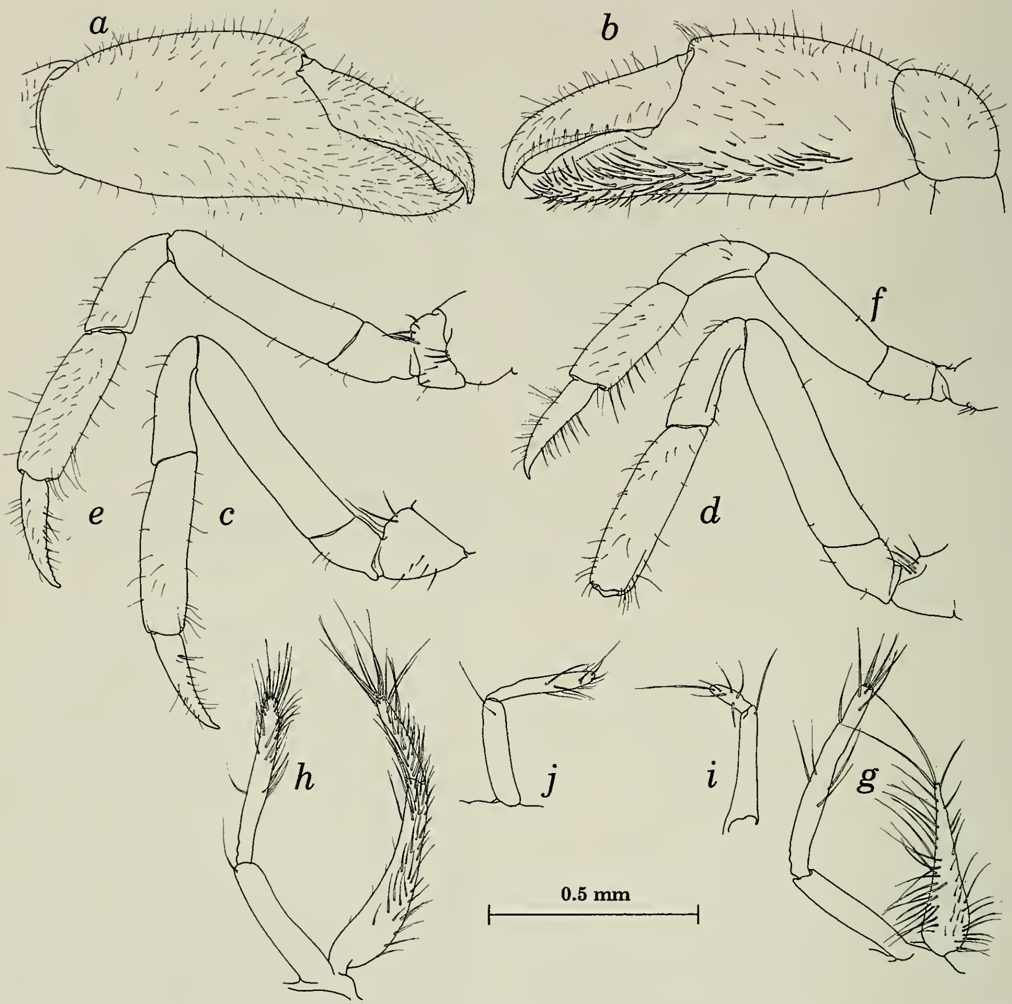

Fig. 2. *Nannotheres moorei*, new genus, new species. Ovigerous female holotype, USNM 277631. *a*, Right chela, outer face; *b*, Right chela, inner face; *c*, Right P2, anterior face; *d*, Right P3, anterior face (dactylus missing); *e*, Right P4, anterior face; *f*, Right P5, anterior face; *g*, Right Plp1, anterior face; *h*, Right Plp2, anterior face; *i*, Right Plp3, anterior face; *j*, Right Plp4, anterior face.

and inserted almost at the mid-point of the distal margin of the propodus in *N. moorei*, rather than being long and slender and inserted basally as in *P. pisum*.

We believe that this species may be the smallest known brachyuran crab. It is smaller than members of the pygmy pirimelid crab *Sirpus* Gordon, 1953(a), in which ovigerous females are as large as 4.5 to 7.0 mm long in *S. monodi* Gordon, 1953(b). Adults of S. *gordonae* Manning & Holthuis, 1981, are 2.5 to 3.1 mm long, and adults of the type species of *Sirpus, S. zariquieyi* Gordon, 1953(a), are 3.4 to 5.1 mm long (Manning & Holthuis 1981:71); ovigerous females are not known in these latter taxa. *Nannotheres moorei* also is smaller than all of the cryptochirid crabs mentioned by Kropp & Manning (1987) and Kropp (1989, 1990), which may be narrower but always are longer. Ovigerous females of the diminutive *Epulotheres angelae* Manning, 1993 are twice as wide, with carapace widths of 3.0 and 3.1 mm.

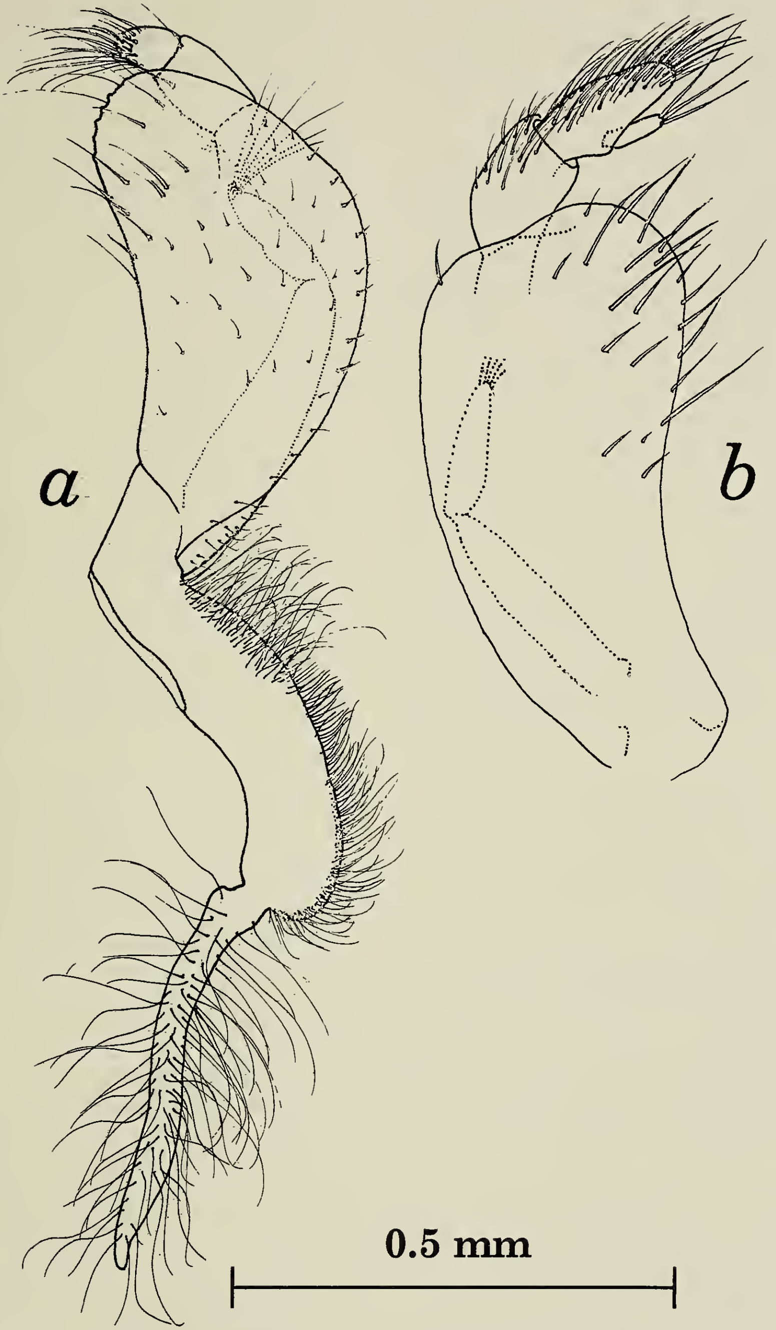

Fig. 3. Outer face of MXP3. *a, Nannotheres moorei,* new genus, new species, ovigerous female holotype, USNM 277631; b, *Epulotheres angelae* Manning, spent female holotype, USNM 256975.

Distribution.—Known only from the type locality, The Blue Hole, Lighthouse Reef, Belize, Caribbean Sea.

Acknowledgments

We thank our colleague Donald R. Moore for bringing this little crab to our attention. We thank our colleagues in the Department of Paleobiology at the National Museum of Natural History, Thomas R. Waller for identifying the host and Warren Blow for helping with the identification of the host, examining other specimens of *Malleus* from Belize, and for providing a copy of Waller & Macintyre (1982). This is contribution no. 392 from the Smithsonian Marine Station at Link Port, Fort Pierce, Florida. Support of that facility for studies on the systematics of pinnotherids is gratefully acknowledged. This is contribution no. 52 from the Laboratory for Crustacean Research, University of Southwestern Louisiana.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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New species of *Macrogynoplax* (Insecta: Plecoptera: Perlidae) from Peru and Guyana

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Abstract.—*Macrogynoplax truncata,* new species, and *M. yupanqui,* new species, are described from specimens collected in Peru, and *M. flinti,* new species, and *M. kanuku,* new species, are described from specimens collected in Guyana. Holotype males are designated for each species and a revised key is provided for adults of the nine species known for the genus.

Macrogynoplax currently includes five uncommon species, each apparently endemic to remote regions of eastern South America (Zwick 1973, Froehlich 1984, Stark & Zwick 1989). Two species (*M. neblina* Stark, *in* Stark & Zwick 1989:248 and *M. spangleri* Stark, *in* Stark & Zwick 1989:251) are known from Cerro de la Neblina in southern Venezuela and the others (*M. geijskesii* Zwick, *in* Stark & Zwick 1989:253, *M. guayanensis* Enderlein, 1909:403, and *M. veneranda* Froehlich, 1984:39) are known from a few specimens from Suriname, Guyana, or southeastern Brazil. In this study I report the occurence of two undescribed *Macrogynoplax* species in Peru and an additional undescribed pair in southern Guyana. Holotypes are deposited in the National Museum of Natural History (USNM).

Macrogynoplax yupanqui, new species
Figs. 1–4

Adult habitus.—Biocellate. White in alcohol, possibly green in life. Unpigmented lobes along inner margins of compound eyes.

Male.—Forewing length 12 mm. Paraprocts prominently spined on anteroapical margin (Fig. 2). Sternum 9 with a pair of basolateral knobs; hammer inflated, bulblike (Fig. 1). Aedeagal tube covered with an outer skirtlike membranous sheath armed with fine transparent spines; tube with an inner, partially exposed sclerite; posteromedian margin of sclerite notched, and sclerotized lateral margins convergent apically. Short, membanous, apical aedeagal section bilobed on ventromedian surface; apex sparsely clothed with fine transparent setae (Figs. 3–4).

Female.—Unknown.

Nymph.—Unknown.

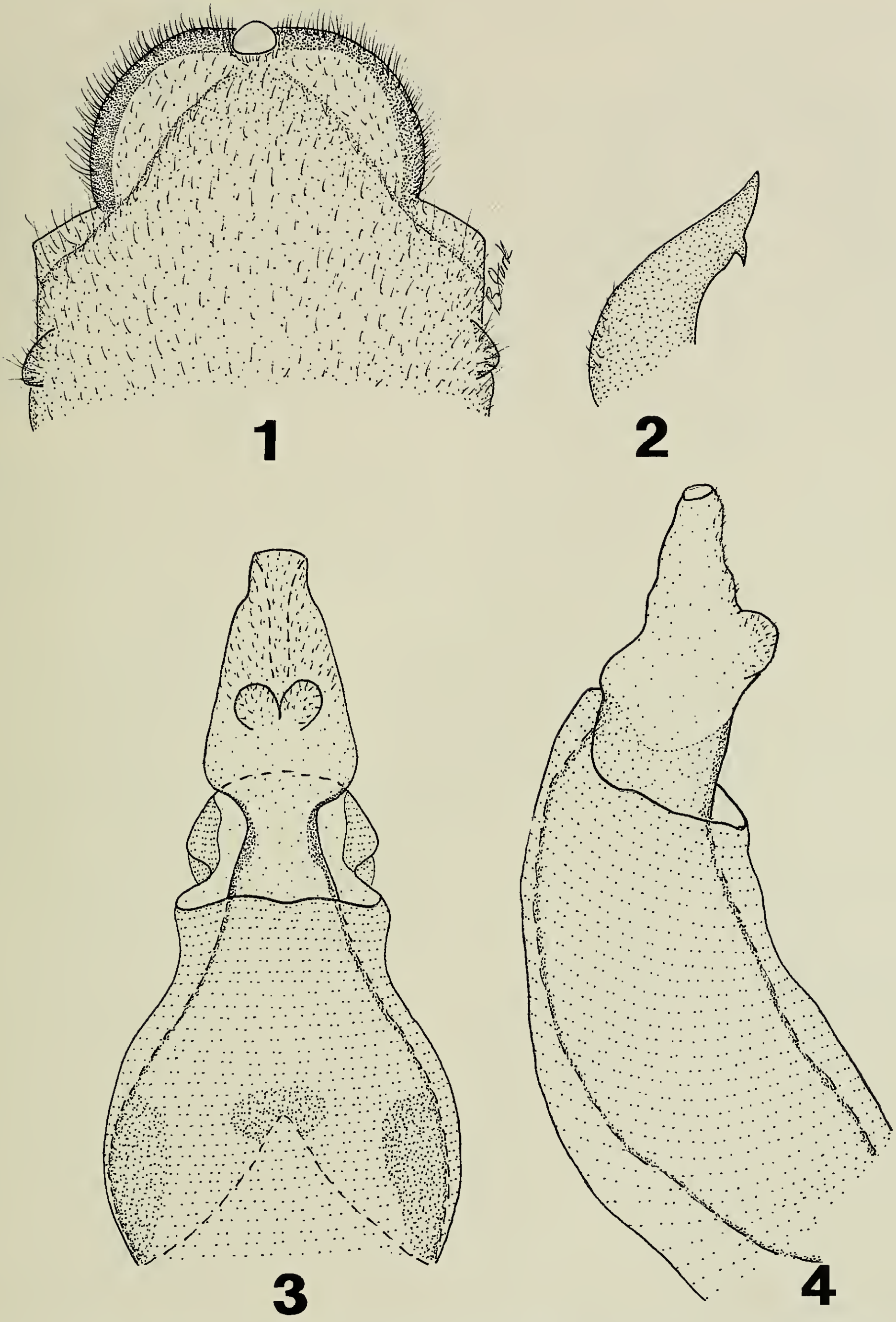
Etymology.—This species honors Tupa Inca, or Yupanqui, tenth ruler in the Inca dynasty.

Types.—Holotype ♂ from Rio Tambopata, 30 km SW Maldonado, 290 m, Madre de Dios, Peru, 21–25 Oct 1979, J. B. Heppner (USNM).

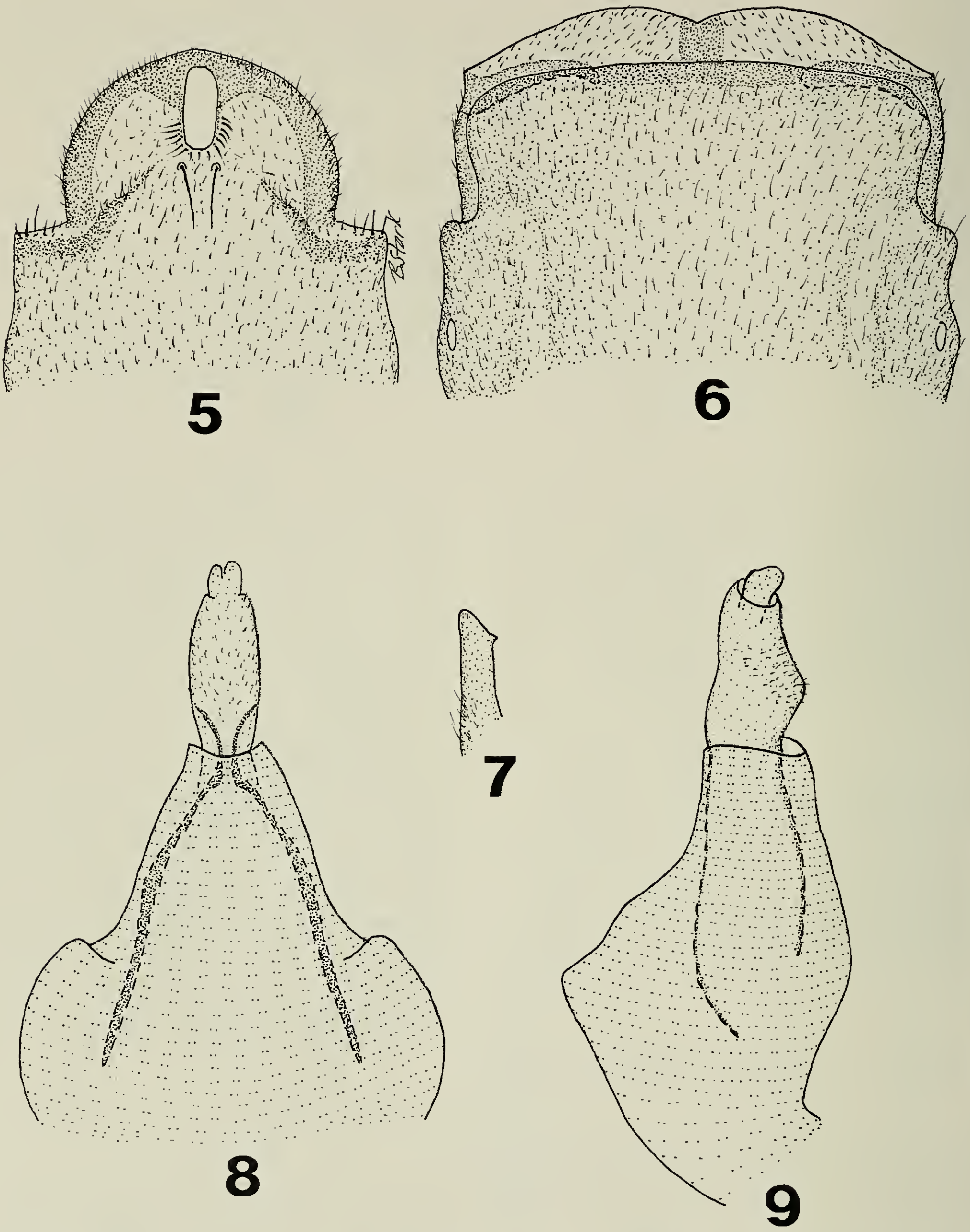
Macrogynoplax truncata, new species
Figs. 5–9

Adult habitus.—Biocellate. White in alcohol, possibly green in life. Unpigmented lobes along inner margins of compound eyes.

Male.—Forewing length 10 mm. Paraprocts small, anteroapical spine minute (Fig. 7). Hammer rectangular (Fig. 5). Aedeagal tube enclosed by an outer skirtlike membranous sheath armed with fine transparent spines; inner sclerite partially exposed apically; sclerotized lateral margins of sclerite convergent apically. Short, mem-



Figs. 1–4. *Macrogynoplax yupanqui* male genitalia. 1. Sternum 9; 2. Paraproct, lateral; 3. Aedeagal tube, ventral; 4. Aedeagal tube, lateral.



Figs. 5–9. *Macrogynoplax truncata* male and female genitalia. 5. Male sternum 9; 6. Female sterna 8 and 9; 7. Paraproct, lateral; 8. Aedeagal tube, ventral; 9. Aedeagal tube, lateral.

branous, apical aedeagal section sparsely clothed with fine transparent setae; apex finely divided into a pair of small membranous lobes (Figs. 8–9).

Female.—Forewing length 12 mm. Subgenital plate covers most of sternum 9; truncate posterior margin heavily sclerotized. Sternum 9 lateral bars short; median field with a narrow longitudinal sclerite (Fig. 6).

Nymph.—Unknown.

Etymology.—The species name refers to the truncate posterior margin of the female subgenital plate.

Types.—Holotype ♂ and paratype ♀ from Rio Nanay, 25 km SW Iquitos, 120 m, Callicebus Res. Station, Loreto, Peru, 10–17 Jan 1980, J. B. Heppner (USNM).

Macrogynoplax flinti, new species
Figs. 10–13

Adult habitus.—Biocellate. Pinned specimens white with slight green tint in wing veins; possibly green in life. Unpigmented lobe along inner margins of compound eyes.

Male.—Forewing length 9 mm. Paraprocts small, anteroapical spine minute. Hammer outline triangular; sternum 9 with a pair of basolateral knobs (Fig. 10). Aedeagal tube partially enclosed by a membranous sheath armed with fine transparent spines; tube armed with a prominent ventrobasal pair of hooks and an anteapical shelf like process; tube apex with a pair of small membranous lobes, sparsely clothed with fine setae, and a long slender process (Figs. 11–13).

Female.—Unknown.

Nymph.—Unknown.

Etymology.—The patronym honors O. S. Flint, Jr., collector of the type series, for his outstanding contributions to our knowledge of Neotropical aquatic entomology.

Types.—Holotype ♂ and paratype ♂ from Aramatani Creek, Dubulay Ranch, Guyana, 5°39.4′N, 57°55.5′W, 15–18 Apr 1995, O. S. Flint (USNM).

Habitat.—Aramatani Creek is a shallow stream about two meters in width flowing through an area of wet rain forest. The substrate is mixed sand and organic debris and the normally clear water develops a tea-colored stain from runoff following periods of heavy rainfall (O. S. Flint, pers. comm.).

Macrogynoplax kanuku, new species
Figs. 14–18

Adult habitus.—Biocellate. Pinned specimens white with slight green tint in wing veins; possibly green in life. Unpigmented lobes along inner margins of compound eyes.

Male.—Forewing length 9 mm. Paraprocts small, anteroapical spine minute. Hammer outline elongate oval, orientation vertical on upturned apex of sternum 9; basolateral knobs present on sternum 9 (Fig. 14). Aedeagal tube partially enclosed by a membranous sheath armed with fine transparent spines; tube armed with a prominent ventrobasal pair of hooks; distal section a simple, partially sclerotized cylinder with a pair of small apical lobes, sparsely clothed with fine setae (Figs. 16–18).

Female.—Forewing length 12 mm. Subgenital plate covers about half of sternum 9; posterior margin rounded and notched. Sternum 9 lateral bars narrowly separated on midline; median field with a slender pale sclerite (Fig. 15).

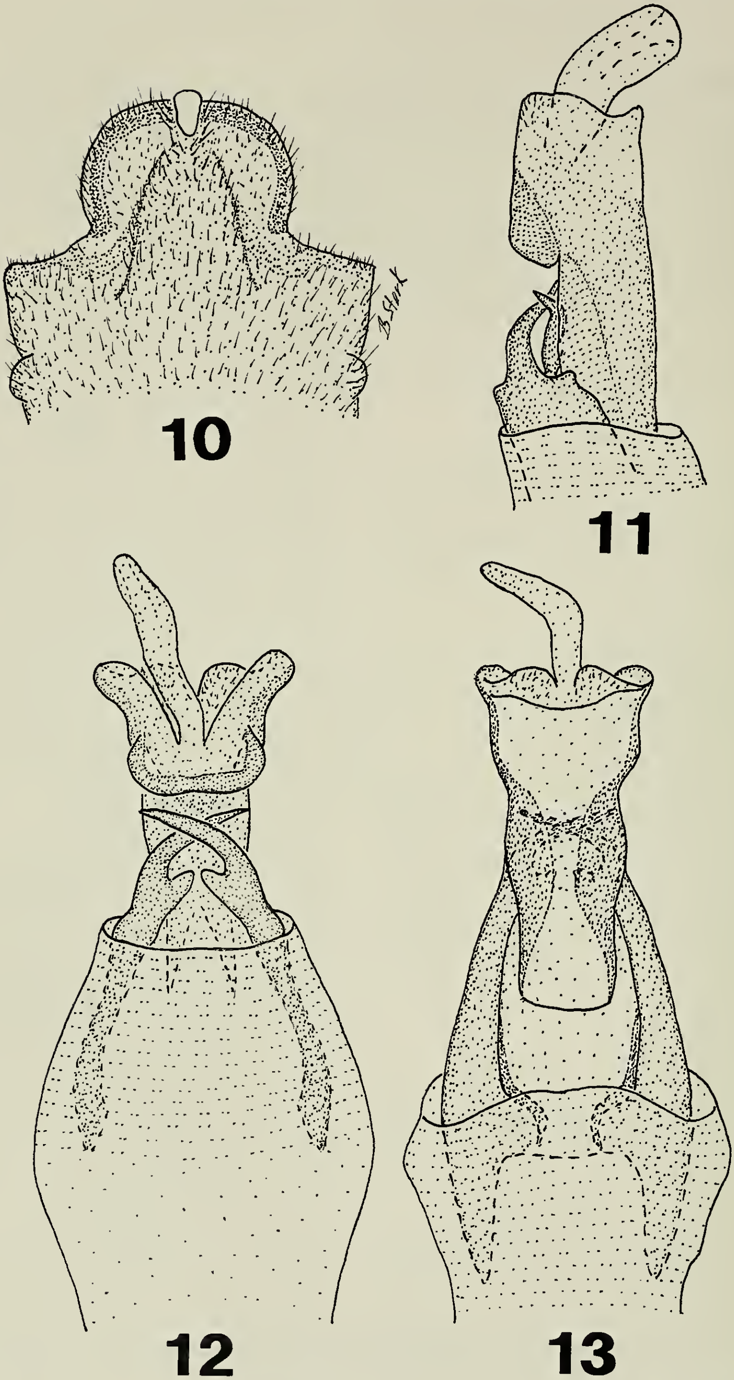
Nymph.—Unknown.

Etymology.—The species name is based on the Kanuku Mountains of southern Guyana.

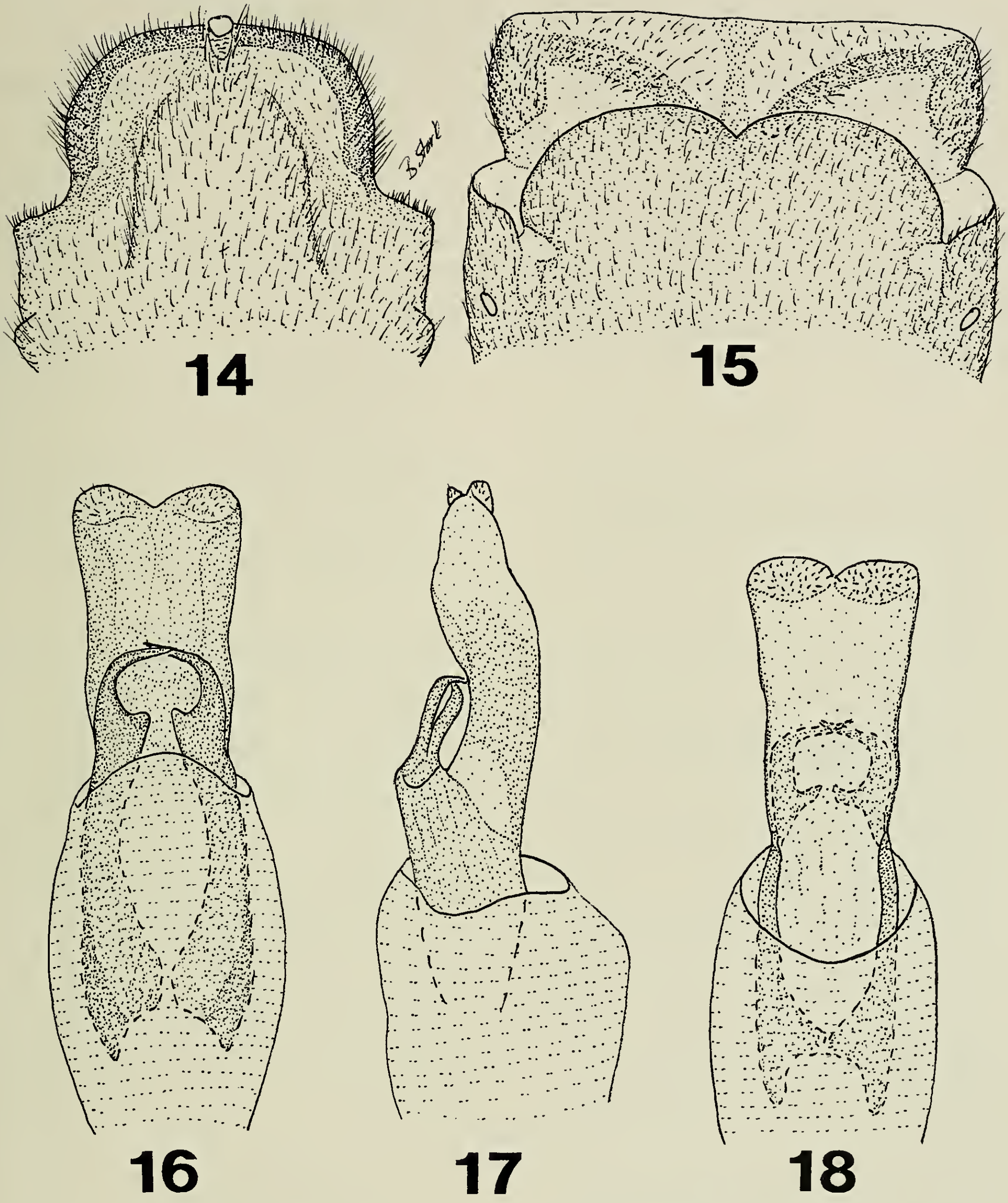
Types.—Holotype ♂ and paratype ♀ from Kumu River, Kanuku Mountains, Guyana, 3°15.9′N, 59°43.5′W, 28–30 Apr 1995, O. S. Flint (USNM).

Habitat.—Kumu River at the collecting site is 2–3 meters in width and tumbles down a heavily forested slope. Substrate varies from sand to boulders and there are numerous small springs, falls and plunge basins (O. S. Flint, pers. comm.).

Discussion.—Macrogynoplax truncata and *M. yupanqui* are similar to *M. spangleri* in aedeagal structure and in shape of the male 9th sternum. *M. truncata* males are easily distinguished from all known *Macrogynoplax* by hammer shape (Fig. 5) and by the apical aedeagal shape (Figs. 8–9). Females of *M. truncata* are the only known species with a truncate subgenital plate



Figs. 10–13. *Macrogynoplax flinti* male genitalia. 10. Sternum 9; 11. Aedeagal tube, lateral; 12. Aedeagal tube, ventral; 13. Aedeagal tube, dorsal.



Figs. 14–18. *Macrogynoplax kanuku* male and female genitalia. 14. Male sternum 9; 15. Female sterna 8 and 9; 16. Aedeagal tube, ventral; 17. Aedeagal tube, lateral; 18. Aedeagal tube, dorsal.

(Fig. 6). *Macrogynoplax yupanqui* males key to *M. spangleri* in Stark & Zwick (1989) but they are distinguished on the basis of the strong paraproct spine (Fig. 2) and by the paired ventroapical aedeagal lobes (Fig. 3). *Macrogynoplax flinti* and *M. kanuku* share prominent sclerotized aedeagal hooks with *M. geijskesii* (Figs. 12, 16), but these two species seem more closely related to each other than either is to *M. geijskesii*. *Macrogynoplax flinti* can be distinguished on the basis of the triangular hammer (Fig.

10) and the shelflike ventroapical aedeagal process (Fig. 12), but *M. kanuku* can probably be reliably separated from *M. geijskesii* only on the basis of the complexly lobed apical aedeagal section in the latter species. The subgenital plate of female *M. kanuku* is similar to that of *M. spangleri,* but perhaps is not as long, and the pale mesal sclerite of sternum 9 (Fig. 15), should distinguish females of these species. The following key to adult specimens is modified from Stark & Zwick (1989).

Males

1\. Large subterminal sclerotized hooks on venter of aedeagal tube (Figs. 12, 16) 2
– Sclerotized aedeagal hooks absent (Fig. 3) 4
2\. Hammer oriented vertically on upturned margin of sternum 9, outline oval (Fig. 14) 3
– Hammer oriented horizontally, apex of sternum 9 not upturned, outline triangular (Fig. 10) .... *flinti*
3\. Aedeagal apex a simple cylinder with a pair of distal, sparsely hirsute lobes (Figs. 14–18) .... *kanuku*
– Aedeagal apex complexly lobed .... *geijskesii*
4\. Hammer outline rectangular (Fig. 5) .... *truncata*
– Hammer outline circular (Fig. 1) .. 5
5\. Sternum 9 apical plate strongly constricted at base, sides distinctly convex 6
– Sternum 9 apical plate slightly or not at all constricted at base, sides parallel to slightly convex (Fig. 1) 7
6\. Aedeagal apex expanded laterally, sclerites almost joined proximal to apex .... *veneranda*
– Aedeagal apex gradually narrowed, sclerites separated except for apices which almost touch .... *neblina*
7\. Aedeagal apex with paired dorsal lobes (Fig. 3); paraproct spine curved downward (Fig. 2) ... *yupanqui*
– Aedeagal apex without dorsal lobes; paraproct spine straight (Fig. 7) .... *spangleri*

Females

(*M. geijskesii, M. flinti* and *M. yupanqui* unknown)

1\. Subgenital plate truncate (Fig. 6) .... *truncata*
– Subgenital plate notched or rounded 2
2\. Subgenital plate extending beyond posterior margin of sternum 9 .... *guyanensis*
– Subgenital plate not reaching beyond posterior margin of sternum 9 3
3\. Lateral bars of sternum 9 fused mesally under subgenital plate .... *neblina*
– Lateral bars of sternum 9 separated mesally 4
4\. Subgenital plate almost reaching posterior margin of sternum 9; lateral bars narrowly separated .... *spangleri*
– Subgenital plate reaching slightly beyond midpoint of sternum 9; lateral bars widely or narrowly separated 5
5\. Lateral bars of sternum 9 widely separated .... *veneranda*
Lateral bars of sternum 9 narrowly separated .... *kanuku*

Acknowledgments

I am grateful to N. Adams and O. S. Flint (National Museum of Natural History) for arranging the loan of material used in this study. O. S. Flint also provided field notes on the Guyana collecting sites.

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Australian beach flies (Diptera: Canacidae)

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Abstract.—The Australian fauna of beach flies (8 genera and 14 species), excluding Zaleinae, is reviewed, including description of seven new species as follows (type locality indicated in parentheses): *Nocticanace australina* (NSW: Lord Howe Island, Roach Island Beach), *Procanace mcalpinei* (NSW: Karuah), *Chaetocanace flavipes* (WA: West Kimberley, 4 km SSW of Cape Bertholet), *Chaetocanace koongarra* (WA: Koongarra, 15 km E of Mt. Cahill), *Chaetocanace longicauda* (NT: 35 km W Jabiru, South Alligator River area), *Dynomiella australica* (TAS: Squeaking Point near Port Sorell), and *Xanthocanace collessi* (WA: West Kimberley, 5 km SSW of Cape Bertholet). *Procanace* Hendel and *Dynomiella* Giordani Soika are reported for the first time from Australia. An undescribed genus and species, represented by a single female, is also reported.

The Australian fauna of the family Canacidae, more commonly known as beach or surf flies, has never been treated comprehensively. Only the subfamily Zaleinae, which is questionably a canacid, has been considered recently (McAlpine 1982, 1985). Although relatively few species occurring in Australia have been described, nine species in six genera (Mathis 1989a, Colless & McAlpine 1991), additional taxa have been discovered recently, and description of these, within the context of a faunal review, is the primary purpose of this paper.

Three of the nine described species are in the genus *Zalea* McAlpine. This enigmatic genus has been segregated as the subfamily Zaleinae (McAlpine 1982, 1985) but is perhaps better placed in the family Tethinidae (Mathis 1992, Freidberg 1995). *Zalea,* which was recently revised (McAlpine 1982, 1985), is not included here.

The new species described herein mostly represent recent discoveries but also clarify the status of an unidentified species of *Nocticanace* Malloch that was reported previously from Australia (Colless & McAlpine 1991). Two of the new species are representatives of *Procanace* Hendel and *Dynomiella* Giordani Soika, both genera previously unknown from Australia. The Australian species of *Dynomiella* is of particular interest, being the first record of this genus outside of Africa and representing a significant range extension. Four of the other six new species belong in genera previously known from Australia (*Chaetocanace* Hendel and *Xanthocanace* Hendel), and the remaining species, perhaps representing a new genus, is included in keys and discussions but is not described, being known from a single female.

The more inclusive purpose of this paper is to document comprehensively the Australian fauna (excluding the subfamily Zaleinae), including keys to genera and species known from the region. Illustrations, particularly of characters of the external male terminalia to aid in species identification, and locality data to understand better the distribution of the included taxa are also provided. This effort is intended to foster further interest in the natural history and phylogeny of the family, which is almost exclusively associated with maritime beaches in temperate and tropical regions of the world.

Methods and Materials

For each genus and species reviewed, a synonymy, the known distribution, including detailed information on the type locality, the depository of the primary types, specific locality data for Australia, the generalized distribution, a diagnosis, and a remarks section, as appropriate, are provided. In the synonymies, only literature that is pertinent to the Australasian Region or a taxon's nomenclatural history is cited. For new species, a more complete description is provided, in addition to characters included in diagnoses of appropriate species groups and genera. The species groups that are recognized for the genera *Nocticanace* and *Procanace* are not necessarily monophyletic assemblages and are used primarily to divide conveniently the genera into manageable units and to facilitate their identification. Their characterization and the species composition may change as a result of future revisionary and phylogenetic studies. The descriptive format for the new species follows Mathis & Wirth (1979) and Mathis (1982, 1988). More details concerning the morphology and higher classification of Canacidae are found in Mathis (1982) and Wirth (1987).

Two venational ratios are used in the descriptions. Costal vein ratio: The straight line distance between the apices of vein R_{2+3} and R_{4+5}/distance between the apices of veins R_1 and R_{2+3}. M vein ratio: The straight line distance along vein M between crossveins (dm-cu and r-m)/distance apicad of dm-cu.

Specimens, holotypes in particular, are housed in the following institutions (acronyms are used in the descriptive portion of this paper).

AM	Australian Museum, Sydney (Dr. David K. McAlpine).
ANIC	The Australian National Insect Collection, CSIRO, Division of Entomology, Canberra (Dr. Peter S. Cranston).
BMNH	The Natural History Museum (formerly the British Museum (Natural History)), London, England (Dr. Brian Pitkin).
UQIC	University of Queensland Insect Collection, Brisbane (Ms Margaret A. Schneider).
USNM	former United States National Museum, collections in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.
ZIL	Zoological Institute, University of Lund, Sweden (Dr. Roy Danielsson).

Family Canacidae Jones

Key to Australian Genera of Canacidae

1. Lateroclinate fronto-orbital setae 3; katepisternal seta usually present (lacking in the *grisescens* group of *Procanace*); lamella of ♀ terminalia bearing 2 moderately large setae, one apical the other subapical, each rather bluntly rounded (subfamily Nocticanacinae) 2

– Lateroclinate fronto-orbital setae either 4 or more, or 3 and with katepisternal seta lacking (subfamily Canacinae) 3

2. Intrafrontal setae absent, although anterior ⅓ of frons occasionally with scattered setulae ....*Procanace* Hendel

– One or 2 intrafrontal setae in addition to any other setulae .... *Nocticanace* Malloch

3. Lamella of ♀ reduced and lacking any large setae ....new genus

– Lamella of ♀ terminalia large with 1 large, apical seta, this usually acutely pointed 4

4. Anterior notopleural seta present; lateral scutellar setae usually 2 pairs 5

– Anterior notopleural seta absent; lateral scutellar setae 1 pair 7

5. Vein M with last section arcuate; mesofrons uniformly and densely setulose; 4–6 fronto-orbital setae; setae generally pale .... *Xanthocanace* Hendel

– Vein M with last section more or less straight, not distinctly arcuate; mesofrons with bare areas, not densely setulose; 4 fronto-orbital setae; setae generally dark colored .. 6

6. Arista bearing 2 rows of hairs, these extended from base to apex, 1 row dorsal, the other ventral; postocellar setae conspicuously smaller than ocellar setae and with proclinate and slightly divergent orientation (the *albiceps* group). .... *Isocanace* Mathis

– Arista with at least apical ⅓ bare; postocellar setae subequal in size and with similar orientation as ocellar setae ... *Dynomiella* Giordani Soika

7. Mesofrons well sclerotized, distinct from membranous-appearing parafrons; anteroclinate genal seta, large, black; upturned genal setae lacking; arista with 2 rows of setulae extended to apex; postpronotum setulose .... *Chaetocanace* Hendel

– Mesofrons and parafrons not distinct from each other except by color in some species, both appearing membranous although usually microtomentose; anteroclinate genal seta small, pale; upturned genal setae 2; arista with apical ⅓ to ½ bare, stylelike; postpronotum bare of setulae .... *Trichocanace* Wirth

Subfamily Nocticanacinae Mathis

Genus *Nocticanace* Malloch

Nocticanace Malloch, 1933:4. Type species: *N. peculiaris* Malloch, by original designation.—Mathis, 1989b:594 [key to species groups]; 1992:8–10 [world catalog].

Diagnosis.—Small to medium-sized beach flies, length 1.8 to 3.7 mm; general coloration brown to grayish black.

Head: Intrafrontal setae 1 pair; postocellar setae either absent or much reduced, less than ¼ length of ocellar setae; ocelli forming an isosceles triangle, distance between posterior ocelli greater than that between either posterior ocellus and the anterior ocellus. Lower facial margin sinuous; clypeus low, width subequal to length of antenna. Two large upturned genal setae; anteroclinate genal seta moderately well developed, at least ½ length of larger upturned genal setae. Palpus grayish black, bearing 1 to several long setae, each seta 2 to 3 times as long as greatest width of palpus.

Thorax: Anepisternum with scattered setulae; proepisternal seta absent; katepisternal seta present, well developed. Legs entirely grayish black; forefemur bearing 4–6 long, evenly spaced setae along posteroventral margin, length of setae at least equal to and usually greater than width of femur.

Discussion.—*Nocticanace,* now with 35 species (Mathis 1991), has more species than any other genus of the family. These have been divided into five species groups (Mathis 1989b, Mathis & Freidberg 1991), mostly to facilitate their identification. The new Australian species described below is part of the *pacifica* group, the largest group in the genus with 22 species. This genus probably occurs on mainland Australia in addition to Lord Howe Island.

The *pacifica* Group

Diagnosis.—General coloration dark, grayish brown to grayish black. Thorax: Acrostichal setulae absent; apical scutellar setae distinctly upturned; anterior notopleural seta absent; proepisternal seta(e) present; anepisternum with scattered setulae; katepisternal seta present. Legs entirely dark, grayish brown to black; forefemur with 4–6 long and evenly spaced setae along posteroventral margin, length greater

Figs. 1–2. External male terminalia of *Nocticanace australina*: 1, epandrium, cercus, and surstylus, lateral view; 2, surstylus, ventrolateral view. Scale = 0.1 mm.

than width of femur; midfemur of male without comblike row of setae; hindtibia lacking spinelike setae apically. Wing with length of apical section of vein CuA_1 long, about twice length of crossvein dm-cu; M vein ratio 0.45–0.5.

Nocticanace australina, new species
Figs. 1–2

Nocticanace species, Colless & McAlpine, 1991:779.

Diagnosis.—This species is distinguished from congeners, especially of the *pacifica* group, by its dark coloration (grayish brown to charcoal) and by the napiform shape of the surstylus in lateral view.

Description.—Small to moderately small beach flies, length 1.9 to 2.4 mm; generally dark colored, densely microtomentose, appearing dull, grayish brown to charcoal black.

Head: Frons grayish black. Antenna black. Face whitish gray to grayish black depending on angle of view; gena similar in color to face.

Thorax: Mesonotum brown to brownish black; pleural areas gray to charcoal gray. Wing lightly infuscate, faintly brownish black; costal vein ratio 0.17; M vein ratio 0.5. Legs uniformly and entirely grayish black.

Abdomen: External male terminalia: surstylus in lateral view (Figs. 1–2) napiform, anterior and posterior margin shallowly rounded, ventral margin produced to form a narrow ventromedial process that is curved anteroventrally; posterior margin of surstylus bearing fringe of long setulae, these oriented medially.

Type material.—The holotype male is labeled "[Australia. New South Wales:] Roach Isl. Beach[,] Lord Howe Isl[and].[,] 23 Feb 1988[,] H. J. de S. Disney[,] Rock pools/Austr. Mus. Collection." Paratypes are as follows: Australia. New South Wales: Lord Howe Island. Old Gulch, Dec 1972, Z. Liepa (1 ♂; ANIC); Roach Island Beach (rock pools), 23 Feb 1988, H. J. de S. Disney (7 ♂; AM, USNM); Salmon Beach, Dec 1972, Z. Liepa (1 ♀; ANIC). The holotype is double mounted (glued to a paper point), is in excellent condition, and is deposited in the ANIC.

Distribution.—Australasian: Eastern Australia (NSW).

Etymology.—The specific epithet, *australina,* refers to the continent where this species occurs.

Remarks.—Colless & McAlpine (1991) first listed this species, although then undescribed, from Australia.

Genus *Procanace* Hendel

Procanace Hendel, 1913:93. Type species: *Procanace grisescens* Hendel, by original designation.—Wirth, 1951:253–259 [revision].—Delfinado, 1970:527–531 [revision of species from New Guinea].—Delfinado & Wirth, 1977:392 [Oriental catalog].—Hardy & Delfinado, 1980: 388–406 [revision of Hawaiian species].—Mathis, 1989a:669–670 [Australasian/Oceanian catalog]; 1989b:603–607 [key to species groups]; 1992:10–12 [world catalog].

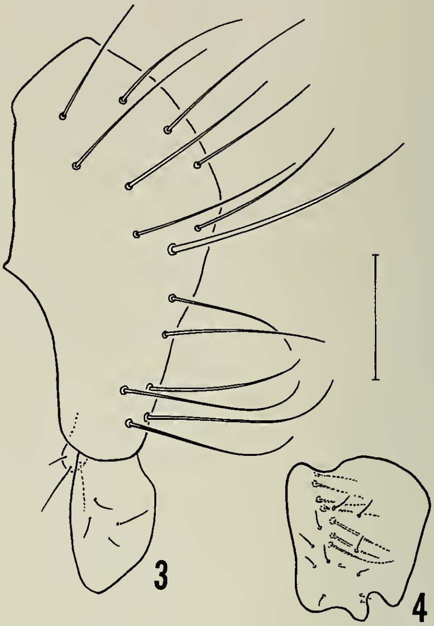
Diagnosis.—General coloration whitish gray, olivaceous, to blackish brown.

Head: Intrafrontal setae absent, but with a few setulae inserted anteriorly; fronto-orbital setae 3; ocelli forming equilateral or isosceles triangle, if isosceles, the greater distance is between posterior ocelli. Arista pubescent over entire length. Two large upturned genal setae; anteroclinate genal seta moderately well developed. Palpus not bearing long setae. Epistomal margin, in lateral view, more or less horizontal.

Thorax: Acrostichal setae, especially a prescutellar pair of large setae, usually lacking (setulae present in species of the *williamsi* group); scutellar disc lacking setae (1–2 pairs of scutellar disc setulae occur in *P. nakazatoi* Miyagi of the *williamsi* group); 2 pairs of marginal scutellar setae, apical pair not upturned; anterior and posterior notopleural setae present, length of both subequal; anepisternum with scattered setulae. Katepisternal setal usually present (lacking in species of the *grisescens* group). Hindtibia lacking spinelike setae apically.

Abdomen: Male genitalia as follows: epandrium in posterior view wider than high; cerci reduced, poorly sclerotized; surstylus with an anterior and a posterior lobe, the latter larger, sometimes markedly so and shape unique to species.

Discussion.—*Procanace,* now with 30 species, is the second largest genus in the family. Mathis (1989b) divided the genus into five species groups, largely to expedite identification of the various species. Some of the groups are monophyletic, but others may not be. The new Australian species is in the *fulva* group, which is diagnosed below.



Figs. 3–4. External male terminalia of *Procanace mcalpinei*: 3, epandrium, and surstylus, lateral view; 4, surstylus, posteroventral view. Scale = 0.1 mm.

The *fulva* Group

Diagnosis.—General coloration whitish olivaceous to brown. Head: Postocellar setae either absent or much reduced; ocelli forming equilateral triangle. Palpus yellow. Clypeus low, height ⅓ to ¼ eye height. Thorax: Acrostichal setulae absent; proepisternal seta(e) usually present; anepisternum with scattered setulae; katepisternal seta present. Femora and tibiae grayish, tarsi yellowish; forefemur lacking 4–6 long and evenly spaced setae along posteroventral margin, length greater than width of femur; midfemur of male bearing comblike sparse row of setae. Wing with length of apical section of vein CuA_1 short, subequal to or slightly longer than crossvein dm-cu; M vein ratio 0.75 to 0.8.

Remarks.—The *fulva* group, now with nine species, occurs along the western margin of the Pacific Ocean (eastern Palearctic, Oriental, and Australasian regions).

Procanace mcalpinei, new species
Figs. 3–4

Diagnosis.—This species is distinguished from congeners by the shape of the surstylus, which in lateral view is irregularly ovate. The posterior margin of the surstylus bears a median tooth and short emargination just dorsad of tooth.

Description.—Moderately small beach flies, length 2.0 mm; generally grayish brown to brown, generally dull, microtomentose.

Head: Mesofrons brown, similar to mesonotum; parafrons more blackish brown; postocellar setae reduced, about ½ length of ocellar setae, proclinate slightly divergent. Scape and pedicel grayish black; 1st flagellomere brownish yellow with faint blackish tinges. Face grayish white; gena low, about ⅓ eye height, concolorous with face anteriorly, yellowish along anteroventral margin of eye, becoming slightly grayer posteriorly.

Thorax: Mesonotum light brown to faintly olive brown, dull; pleural areas grayer. Wing lightly infumate, faintly brownish; costal vein ratio 0.18; M vein ratio 0.8. Legs brownish yellow; femora thinly invested with whitish microtomentum.

Abdomen: Dorsum concolorous with mesonotum. External male terminalia as follows: epandrium bearing numerous long setae; surstylus in lateral view (Fig. 3–4) irregularly ovate, median surface bearing dorsoventral row of stout setulae, posterior margin (Fig. 4) with short emargination at dorsal ¼ and an edentate projection medially.

Type material.—The holotype male is labeled "[AUSTRALIA.] Karuah, N.S.W. 23.xii.1968 [23 dec 1968] inlet: beach I. C. Yeo." The holotype is double mounted, is in good condition (right antenna missing, abdomen removed and dissected, structures in an attached microvial), and is deposited in UQIC.

Distribution.—This species is known only from the type locality.

Etymology.—The specific epithet, *mcalpinei,* is a genitive patronym to recognize and honor the contributions of David K. McAlpine to the study of acalyptrate Diptera, the Australian fauna in particular.

Subfamily Canacinae Jones

Tribe Dynomiellini Mathis

Genus *Chaetocanace* Hendel

Chaetocanace Hendel, 1914:98. Type species: *Canace biseta* Hendel, by original designation and monotypy.—Malloch, 1924:333 [generic key].—Curran, 1934:357 [generic key].—Wirth, 1951:265 [review].—Mathis, 1982:7–9 [review]; 1992:5 [world catalog].

Diagnosis.—Resembling *Isocanace* but differing from it and other genera by the following combination of characters.

Head: Mesofrons distinct from parafrons, shinier, less microtomentose, with 4–6 large, lateral, generally proclinate setae, middle area bare; postocellar setae subequal to ocellar setae and with same orientation; 4 pairs of large, lateroclinate fronto-orbital setae; arista plumose, length of branching rays nearly equal to twice basal aristal width; upturned genal setae lacking, anteroclinate genal seta 1, inserted near level of anterior margin of eye.

Thorax: Dorsocentral setae 4 (1 + 3), all subequal in size; acrostichal setae small (if at all evident), in 2 rows, lacking large pair of prescutellar setae; 1 pair of scutellar setae; anterior supra-alar seta lacking or much reduced in length; anterior notopleural seta lacking; anepisternal setae pale; katepisternal seta lacking; hindtibia with conspicuous, rather stout, apical seta anteroventrally; apical section of vein M straight.

Abdomen: Female genital lamellae very broad basally, basilateral margins rounded, narrowed abruptly near level of cleft, lamellae very narrow from level of cleft to apices, with only 1 large stout, acute, terminal seta at each apex. External male terminalia: surstylus a single ventral projection from ventral margin of epandrium, shape like an inverted T or more or less triangular, ventrally produced to an anterior and posterior angle.

Remarks.—There are now four Australian species of *Chaetocanace,* including three that are newly described. This more than doubles the known species in this genus and establishes Australia as the center for diversity for *Chaetocanace*. Only *C. biseta* apparently does not occur in Australia.

Key to Australian Species of *Chaetocanace*

1. Mesonotum and frons mostly brown to blackish brown, subshiny; surstylus shaped like an inverted T (Fig. 7), basal portion a gradually narrowed extension from the ventral margin of the epandrium, apical ⅓ projected anteriorly and posteriorly .... *C. koongarra*, new species
– Mesonotum and frons brown to gray, dull; surstylus shaped otherwise 2
2. Femora mostly yellow; mesonotum mostly gray or tannish gray; surstylus only gradually becoming wider ventrally, ventral margin shallowly emarginate (Fig. 6) .... *C. flavipes*, new species
– At least fore- and hind femora mostly gray; mesonotum mostly grayish brown to brown; surstylus becoming markedly wider ventrally, more or less triangular 3
3. Anteroventral process of surstylus shaped like a long foot (Fig. 8); posteroventral process distinctly pointed ....*C. longicauda*, new species
– Anteroventral process of surstylus not footlike 4
4. Surstylus with posterodorsal angle acutely pointed .....*C. biseta* (Hendel)
Surstylus with posterodorsal angle bluntly rounded ..*C. brincki* Delfinado

Chaetocanace brincki Delfinado
Fig. 5

Chaetocanace brincki Delfinado, 1975:221 [HT ♂ (ZIL); Sri Lanka. Northern Province: Mannar (16 km E), Nay Aru at Pallamadu; figs. of ♂ & ♀ terminalia].—Delfinado & Wirth, 1977:391 [Oriental catalog].—Mathis, 1982:9 [catalog, key]; 1989a:670 [Australasian/Oceanian catalog]; 1992:5 [world catalog].

Australian specimens examined.—New South Wales: North Cronulla, 12 Mar 1962, D. K. McAlpine (1 ♂; AM). Queensland: Cairns (bay shore, puddles), 19–25 Apr 1957, W. W. Wirth (25 ♂, 26 ♀; AM, ANIC, USNM). Eurimbula (mangroves), 28 Mar 1975, D. K. McAlpine (1 ♂; AM). Western Australia: Batten Point (30 km NE by E of Borroloola), 18 Apr–30 Oct 1975, 1976, D. H. Colless, M. S. Upton (4 ♀; ANIC).

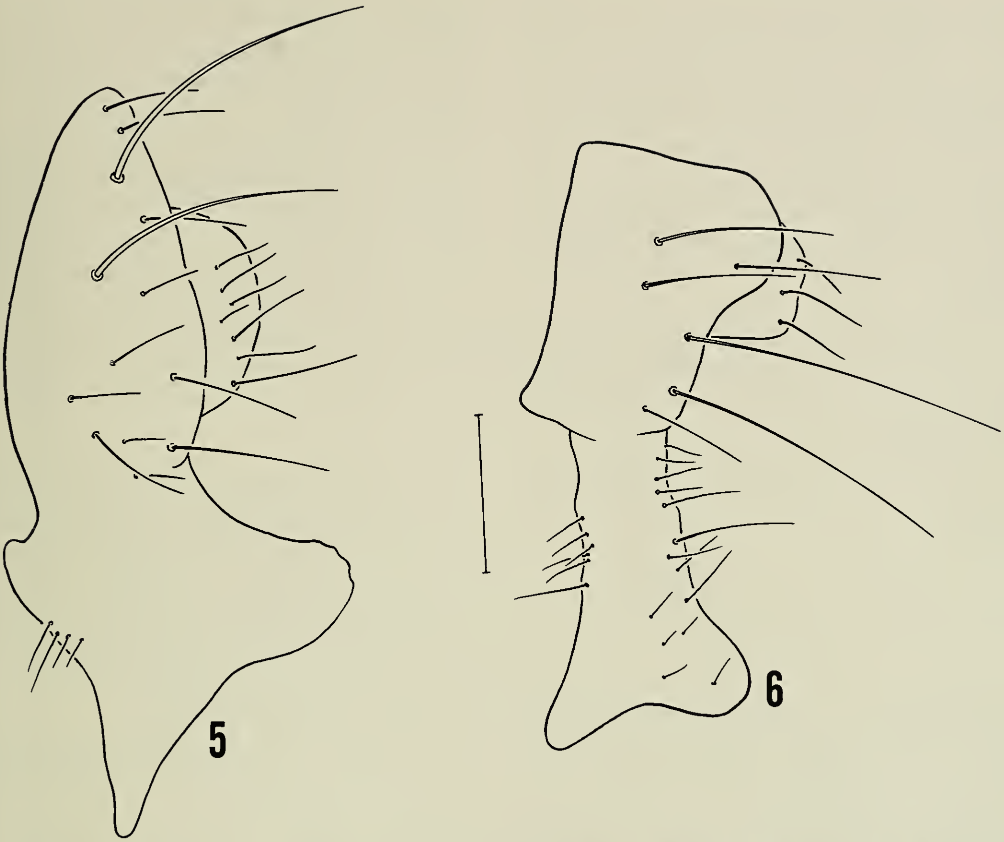
Distribution.—Australasian/Oceanian: Australia (NSW, QLD, WA). Oriental: Philippines (Luzon). Sri Lanka. Palearctic: Japan (Hokkaido, Honshu, Kyushu, Shikoku), Korea (Seoul).

Diagnosis.—Externally this species is very similar to *C. biseta* (Hendel), and many Australian specimens have been misidentified as the latter or as the new species described below. I can distinguish between *C. biseta* and this species only on the basis of characters of the male terminalia, especially the shape of the surstylus (Fig. 5), which is more or less triangular in lateral view, with the posterodorsal corner broadly produced and bluntly rounded. This species differs from *C. koongarra* in having the mesonotum lighter in color, mostly dull, brown to grayish brown, and only the apical tarsomere is brown.

Remarks.—This species was reported previously from Australia (Mathis 1992), but only from Queensland. It is now found to be more widespread, occurring southward to New South Wales and westward to Western Australia.

Chaetocanace flavipes, new species
Fig. 6

Diagnosis.—This species is distinguished from *C. brincki* primarily by the shape of the external male terminalia, spe-



Figs. 5–6. External male terminalia of *Chaetocanace* species: 5, epandrium, cercus, and surstylus of *C. brincki,* lateral view. 6, epandrium, cercus, and surstylus of *C. flavipes,* lateral view. Scale = 0.1 mm.

cifically the surstylus which in lateral view becomes very gradually wider ventrally to form short anterior and posterior processes.

Description.—Small to moderately small beach flies, body length 1.8 to 2.3 mm.

Head: Frons blackish brown and subshiny on anterior ⅔, portion posterior to anterior ocellus dark brown and less shiny. Antenna blackish brown; arista brown. Face and gena densely microtomentose, whitish to faintly bluish white.

Thorax: Mesonotum gray, especially laterally and anteriorly, to mostly grayish brown to brown with faint olivaceous coloration, dull; pleural areas generally whitish gray; anepisternum faintly bluish; katepisternum whitish gray. Acrostichal setae greatly reduced or lacking, not evident. Wing hyaline; costal vein ratio 0.28; M vein ratio 0.5. Legs yellow; femora lightly and sparsely invested with whitish microtomentum; apical tarsomere brown.

Abdomen: External male terminalia as follows: surstylus in lateral view (Fig. 6) gradually becoming wider ventrally, anteroventral and posteroventral angles produced into short processes, posterior process wider and more bluntly produced; ventral margin shallowly emarginate.

Type material.—The holotype male is labeled "PAPUA NEW GUINEA[,] Central Prov[ince]. Lea Lea[,] 6 Oct 1985, J. W. Ismay (saltpan margin)." Forty paratypes (16♂, 24♀; USNM) bear the same locality data as the holotype (dates vary from 23 Feb to 6 Oct 1985, 1986). Other paratypes are as follows: Australia. Western Australia: West Kimberley, Cape Bertholet (4 km

SSW; at light), 18 Apr 1977, D. H. Colless (1 ♂; ANIC). West Kimberley, Cape Bertholet (8 km S), 18–19 Apr 1977, D. H. Colless (1 ♂, 1 ♀; ANIC). Drysdale River (15.02°S, 126.55°E), 3–8 Aug 1975, I. R. B. Common, M. S. Upton (1 ♂, 2 ♀; ANIC). The holotype is in excellent condition, is double mounted (minute nadel in block of plastic), and is deposited in the USNM.

Distribution.—This species is known thus far from the type locality in Papua New Guinea (Central Province) and Western Australia.

Etymology.—The specific epithet, *flavipes,* refers to the yellow legs, especially the femora.

Chaetocanace koongarra, new species
Fig. 7

Diagnosis.—This species is distinguished from *C. brincki* primarily by the shape of the external male terminalia, specifically the surstylus which is narrowly produced on the basal ⅔, gradually tapered toward venter, thereafter on apical ⅓ rather abruptly produced anteriorly and posteriorly to form distinct processes, posterior process shorter and invested with long microtomentum.

Description.—Moderately small beach flies, body length 2.4 mm.

Head: Frons blackish brown and subshiny on anterior ⅔, portion posterior to anterior ocellus dark brown and less shiny. Antenna blackish brown; arista brown. Face and gena densely microtomentose, whitish to faintly bluish white.

Thorax: Mesonotum blackish brown to brown, subshiny, darker and shinier through dorsocentral tract of setae, similar to frons; anterior supra-alar seta present although greatly reduced, less than ½ length of posterior seta; pleural areas generally whitish gray; anepisternum faintly bluish; katepisternum whitish gray. Acrostichal setae greatly reduced or lacking, not evident. Wing hyaline; costal vein ratio 0.22; M vein ratio 0.63. Legs mostly yellow; femora lightly and sparsely invested with whitish to whitish gray microtomentum; apical 1–2 tarsomeres brown.

Abdomen: External male terminalia as follows: surstylus in lateral view (Fig. 7) narrowly produced basally, gradually tapered toward venter, thereafter rather abruptly produced anteriorly and posteriorly to rounded processes; posterior ventral process shorter and anterior process, bearing few setulae but invested with hairlike microtomentum; anterior ventral process bare.

Type material.—The holotype male is labeled "[AUSTRALIA.] Koongarra, 15km E of Mt. Cahill, N[orthern].T[erritory]. 6–9 March 1973[,] D. H. Colless/At light." The holotype is in good condition, is double mounted (minute nadel in block of polyporus), and is deposited in the ANIC.

Distribution.—This species is known only from the type locality.

Etymology.—The specific epithet, *koongarra,* is the name of the type locality and is a noun in apposition.

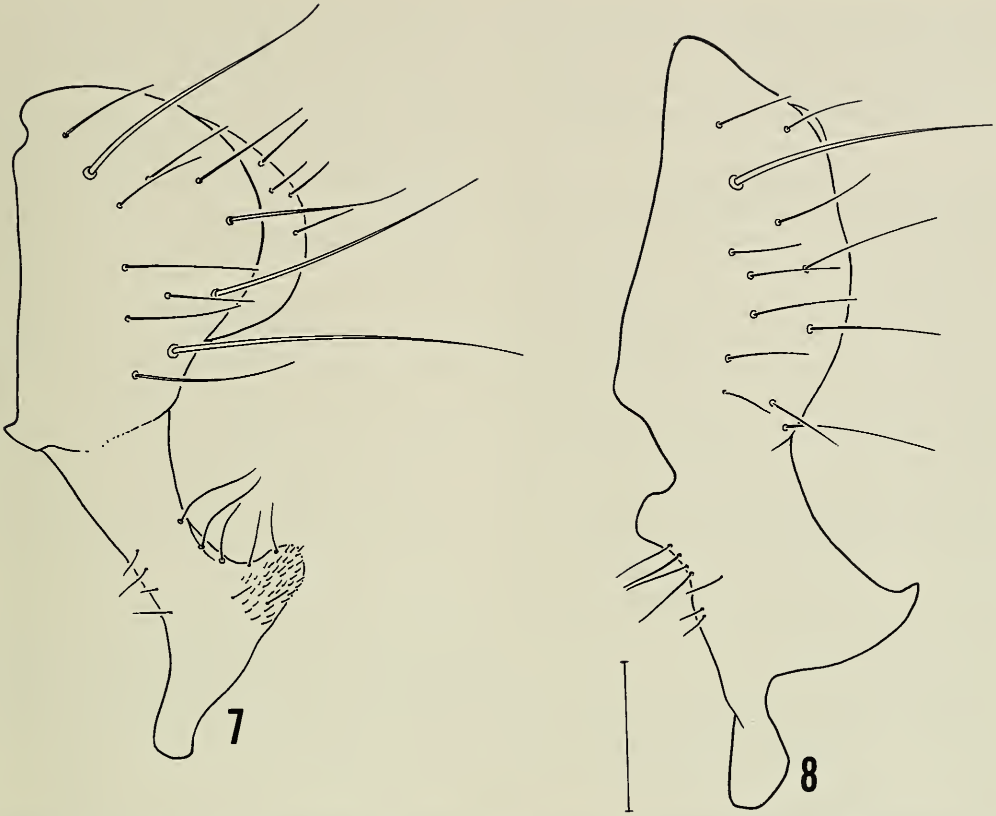
Chaetocanace longicauda, new species
Fig. 8

Diagnosis.—This species is distinguished from *C. brincki* primarily by the shape of the external male terminalia, specifically the surstylus which has the anteroventral process greatly produced, elongate, forming a footlike process; posteroventral process of surstylus distinctly pointed.

Description.—Moderately small beach flies, body length 2.1 to 2.6 mm.

Head: Frons grayish brown, dull. Antenna blackish brown; arista brown. Face and gena densely microtomentose, whitish to faintly bluish white.

Thorax: Mesonotum grayish brown, dull; pleural areas generally whitish gray; anepisternum faintly bluish; katepisternum whitish gray. Acrostichal setulae in 2 rows; anterior supra-alar seta lacking. Wing hyaline; costal vein ratio 0.2; M vein ratio 0.5.



Figs. 7–8. External male terminalia of *Chaetocanace* species: 7, epandrium, cercus, and surstylus of *C. koonqarra,* lateral view. 8, epandrium, cercus, and surstylus of *C. longicauda,* lateral view. Scale = 0.1 mm.

Legs with femora mostly gray, midfemora lighter gray; tibiae and tarsi yellow, apical 1–2 tarsomeres brown.

Abdomen: External male terminalia as follows: surstylus in lateral view (Fig. 8) more or less triangular, anteroventral process greatly produced, elongate, shaped like a foot, posteroventral angle distinctly pointed, ventral margin deeply sinuous.

Type material.—The holotype male is labeled "AUSTRALIA: N[orthern]. T[erritories].; S. Alligator River area, 35kmW Jabiru[,] blacklight, 9iv1980 [9 Apr 1980] GFHevel & JAFortin." The holotype is in fair condition (collected in alcohol, dried, then pointed, dorsum appearing "rubbed"), is double mounted (glued to a paper triangle), and is deposited in the ANIC. Fifteen paratypes (3 ♂, 12 ♀; ANIC, USNM) bear the same label data as the holotype. Other paratypes are as follows: Australia. Queensland: Cairns, 19 Apr 1957, W. W. Wirth (1 ♂; USNM).

Distribution.—This species is known thus far only from Northern Territory (the type locality) and Queensland, Australia.

Etymology.—The specific epithet, *longicauda,* is a noun in apposition, referring to the long, footlike posteroventral process of the surstylus.

Genus *Dynomiella* Giordani Soika

Dynomiella Giordani Soika, 1956:130. Type species: *Dynomiella arenicola* Giordani Soika (= *Canace stuckenbergi* Wirth, 1956), by original designation.—Mathis, 1982:9–11 [review]; 1992:5 [world catalog].

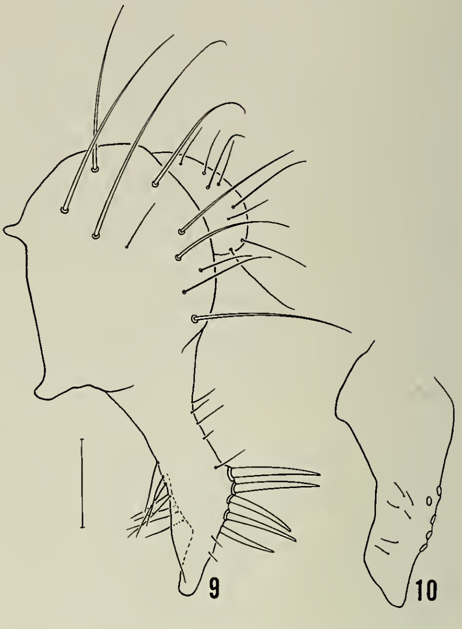
Canace, in part, of authors.—Wirth, 1956: 48–51 [revision, key]; 1960:390 [synonymy of *Dynomiella* with *Canace*].—Cogan, 1980:694 [Afrotropical catalog].

Diagnosis.—Resembling *Canacea* Cresson (Nearctic) but differing from it and other genera by the following combination of characters.

Head: Mesofrons similar to parafrons in vestiture but densely microtomentose, dull, frequently with coloration difference, usually mesofrons darker, brown, with 3–5 large, proclinate setae along lateral margins, midportion of mesofrons bare of setae; postocellar setae subequal to ocellar setae and with similar orientation; 4 large, lateroclinate, fronto-orbital setae; arista short, generally lacking setulae, apical ⅓ to ½ bare, stylelike; upturned genal setae 2; anteroclinate genal setae 1.

Thorax: Dorsocentral setae 4 (1 + 3), all subequal in size; acrostichal setae conspicuous, in 2–4 regular to irregular rows anteriorly, becoming more regular posteriorly, middle rows with setulae slightly larger and with large pair of prescutellar setae; lateral scutellar setae 2 pairs and with several setae dorsally; supra-alar seta 1, anterior seta usually lacking; 2 notopleural setae; color of pleural setulae variable but usually pale, setae black; postpronotum bare of setulae; 1–2 large, anepisternal setae; katepisternal seta lacking; forefemur armature variable, some species with row of stout, spinelike setae anteroventrally; hindtibia lacking apical seta anteroventrally; apical section of vein M straight.

Abdomen: Female genital lamellae variable, either only moderately broad basally, short, and with lamellar processes over three-fourths total length, each process gradually tapered to apex; or lamellae very broad basally, subtriangular, long, over one-third total length, with each lamellar process narrow, parallel sided; in both cases apex of each lamellar process bearing 1 large, stout, moderately acutely to acutely pointed seta; surstylus with slight, anteriorly curved process, slightly hooklike.



Figs. 9–10. External male terminalia of *Dynomiella australica*: 9, epandrium, cercus, and surstylus, lateral view; 10, surstylus, posteroventral view (large stilettolike setae along median margin not included). Scale = 0.1 mm.

Dynomiella australica, new species
Figs. 9–10

Diagnosis.—This species is similar to *D. glauca* (South African) but differs in having only 2 rows of acrostichal setulae; the scutellum broadly rounded posteriorly, bearing a single pair of scutellar setae (the apical pair) and sparse setulae on scutellar disc that are more concentrated laterally; and postpronotum bearing 2 large setae. Fore- and midfemora totally lacking prominent black setae along the posteroventral and anteroventral surfaces.

Description.—Moderately small to medium-sized beach flies, length 2.4 to 3.4 mm; generally microtomentose, generally gray but with some whitish gray to brownish gray areas, slightly darker dorsally.

Head: Triangular mesofrons (ocellar triangle or frontal vittae) well developed, usually more brown to bronze colored than gray to charcoal-gray parafrons, lateral margins straight not curved medially, anterior angle extended to anterior margin of frons, all of median area bare of setae or setulae, mesofrontal seta along lateral margins only; parafrons bearing sparse, randomly inserted setulae, 5–10, none especially well developed. Ocelli forming equilateral triangle.

Thorax: Acrostichal setulae large, in 2 regular rows, sometimes with 1–2 smaller setulae laterad of rows anteriorly; scutellum with posterior margin broadly rounded and short, not triangular; only apical scutellar setae well developed, lacking a basal pair; scutellar disc bearing sparse setulae, 5–7, these more concentrated laterally; postpronotum bearing 2 large setae, dorsal seta almost as large as posterior seta. Setulae of anepisternum and katepisternum fine, pale, pilelike, only 2 large setae toward posterior margin of anepisternum black, prominent. Wing hyaline with faintly brown hues; costal vein ratio 0.24; M vein ratio 0.6. Setae and setulae of legs pale, mostly white but some faintly yellowish white except for ventroapical, spinelike black setae of midtibia; forefemur lacking prominent setae along anteroventral surface; midfemur lacking row of prominent setae along posteroventral surface; tarsi yellow.

Abdomen: Generally gray; setulae on ventral surface of tergites white; tergites 1–2 with setulae on dorsum mostly white; setulae along posterior margin of 3rd tergites black; setulae on dorsum, especially along posterior margin, of tergites 4–7 and epandrium black. External male terminalia as follows: epandrium deeply and widely cleft posterodorsally; surstylus in lateral view (Figs. 8–9) narrow, 3× as long than wide, basal ⅔ projected directly ventrad from ventral margin of epandrium, thereafter angled anteroventrally, apical ⅓ much narrower, posterior margin along angle bearing 4–5 well-developed, stilettolike setae; anterior margin with moderately long, fine setulae; surstylus in posteroventral view (Fig. 9) narrow, becoming narrower toward apex, median margin mostly straight, bearing stilettolike setae, lateral margin sinuous, angulate inward at basal ⅓, thereafter shallowly incurved to apical ¼ which is recurved to apex.

Type material.—The holotype male is labeled "Squeaking Pt. nr Port Sorell, Tas[mania, Australia] 24.xi.1968 [24 Nov 1968] stony beach I. C. Yeo/U.Q.I.C. loan 724 [pale green on dorsum; number handwritten]/HOLOTYPE ♂ Dynomiella australica W.N.Mathis [red; gender and species name handwritten]." The holotype is double mounted (smaller pin in a long rectangular block of polyporus), is in good condition, and is deposited in UQIC. The allotype female and 23 other paratypes (11 ♂, 12 ♀; UQIC, USNM) bear the same label data as the holotype.

Distribution.—Australasian: Australia (TAS).

Etymology.—The specific epithet, *australica,* is an adjective and refers to the continent where this species occurs.

Genus *Isocanace* Mathis

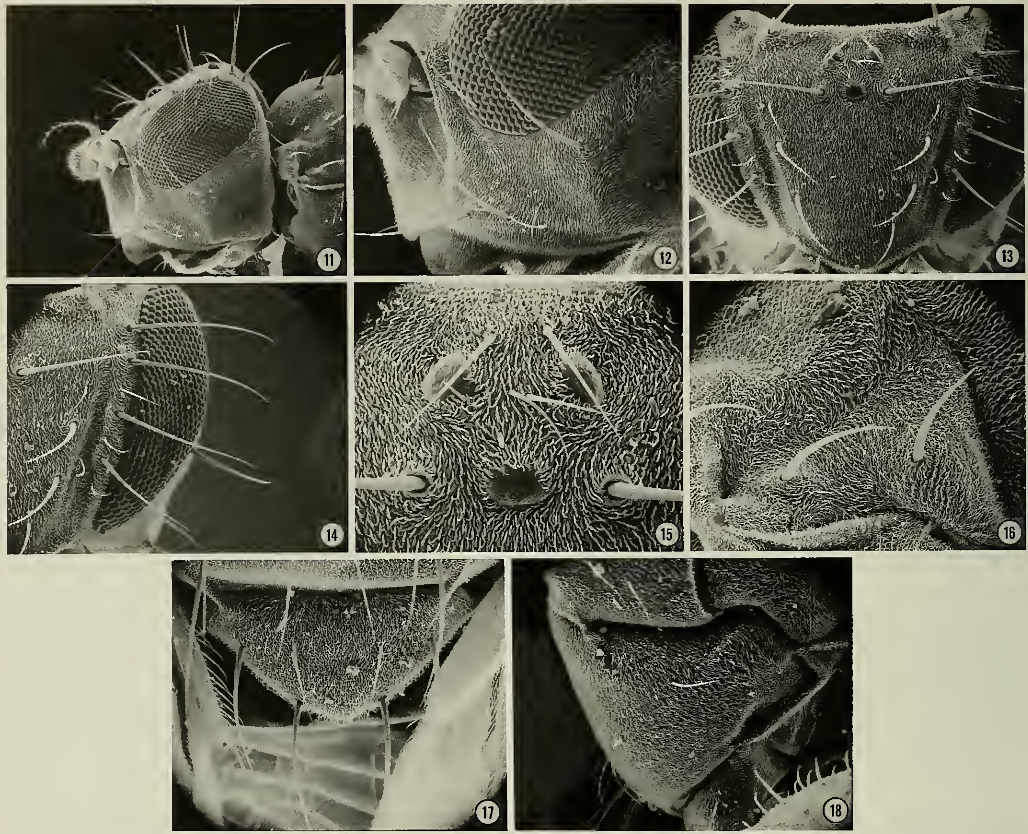
Isocanace Mathis, 1982:11. Type species: *Isocanace briani* Mathis, by original designation.—Mathis, 1992:5–6 [world catalog].

Canace, in part, of authors.—Mathis & Wirth, 1979:786.

Diagnosis.—Resembling *Chaetocanace* Hendel but differing from it and other genera by the following combination of characters.

Head: Mesofrons distinct from parafrons, shinier, less microtomentose, with 2–3 large, lateral, generally proclinate setae; postocellar setae smaller than ocellar setae and with more proclinate orientation; 4 pairs of large, lateroclinate, fronto-orbital setae; arista plumose, length of branched rays varying from approximately subequal to nearly twice basal aristal width; upturned genal setae 2–3; anteroclinate genal seta 1.

Thorax: Dorsocentral setae 4 (1 + 3); acrostichal setae evident, in 2 rows but lack-



Figs. 11–18. Scanning electron micrographs of *Isocanace albiceps*: 11, head, lateral view; 12, gena and setae, lateral view; 13, frons, dorsal view; 14, same, left side, dorsal view; 15, ocellar triangle, dorsal view; 16, Notopleuron and setae, lateral view; 17, Scutellum, dorsal view; 18, Katepisternum and setae, lateral view.

ing large pair of prescutellar acrostichal setae; 2 pairs of scutellar setae and frequently with some smaller setae inserted dorsally; with only 1 pair of supra-alar setae; 1–2 notopleural setae, if only 1, anterior seta lacking; color of pleural setae variable, pale yellow to black; postpronotum bare of setulae; katepisternal seta present or absent; 1 large anepisternal seta; hindtibia lacking apical seta anteroventrally; apical section of vein M straight.

Abdomen: Female genital lamellae very broad basally, basilateral margins rounded, narrowed rather abruptly at level of cleft, lamellae very narrow from level of cleft to apices, with only 1 large, stout, acute terminal seta at each apex; surstylus quite variable, generally slender and with apical curvature.

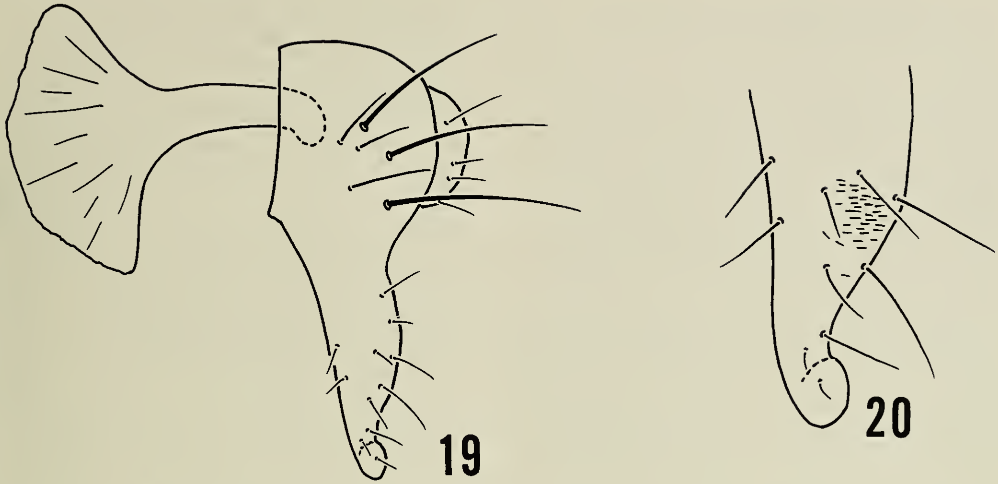
The *albiceps* Group

Diagnosis.—Similar to the *briani* group but differing as follows: Head: mesofrons bare in middle; upturned genal setae 2. Thorax: katepisternal seta lacking; number of acrostichal setae reduced, usually less than 10, and usually paired; anterior notopleural seta subequal to posterior seta.

Isocanace albiceps (Malloch)

Figs. 11–18

Canace albiceps Malloch, 1925:87 [HT ♀ (AM); Australia. New South Wales: Sydney].—Wirth, 1951:262 [review].



Figs. 19–20. External male terminalia of *Isocanace albiceps*: 19, epandrium, cercus, and surstylus, lateral view; 20, surstylus, lateral view. Scale = 0.1 mm.

Isocanace albiceps.—Mathis, 1982:18 [generic combination]; 1989a:670 [Australasian/Oceanian catalog]; 1992:6 [world catalog].—Colless & McAlpine, 1991: 779 [fig. of head].

Australian specimens examined.—New South Wales: Broulee, 17 Sep 1978, Z. Liepa (2 ♂, 3 ♀; ANIC). Careel Bay, 22 Mar–23 Oct 1956, 1962, D. K. McAlpine, W. W. Wirth (35 ♂, 56 ♀; AM, ANIC, USNM). Karuah (inlet, beach), 23 Dec 1968, I. C. Yeo (4 ♂, 9 ♀; UQIC). McCarrs Creek, 20 Sep 1956, W. W. Wirth (2 ♂; USNM). Merimbula (mangrove flat), 12 Feb 1963, D. K. McAlpine (1 ♀; AM). Mona Vale, 11 Nov 1956, W. W. Wirth (1 ♂; USNM). North Cronulla (mangroves), 29 Jan–22 Mar 1962, D. K. McAlpine (4 ♂, 3 ♀; AM). Putty Beach (near Terrigal), 25 Nov 1987, R. Blanche, B. Day, D. K. McAlpine (1 ♂; AM). Queensland: Deception Bay, 23 May 1966, Z. Liepa (1 ♂; ANIC). Tasmania. Squeaking Point, near Port Sorell (stony beach), 24 Nov 1968, I. C. Yeo (1 ♂, 8 ♀; UQIC).

Distribution.—Australasian: Eastern Australia (NSW, QLD, TAS).

Diagnosis.—Specimens of *I. albiceps* are similar to those of the *briani* group but are distinguished by: mesofrons bare in middle; postocellar seta short and with more proclinate orientation; arista with branching rays long, some nearly double basal aristal width; upcurved genal setae 2; anterior notopleural seta subequal in length to posterior seta; anepisternal setae pale; katepisternum lacking a large seta; surstylus (Figs. 19–20) comparatively wide in lateral view, narrowed subapically, but widened again apically and slightly bulbous, with slight median projected process, posterior margin of surstylus sinuous, anterior margin straight.

Genus *Trichocanace* Wirth

Trichocanace Wirth, 1951:252. Type species: *Trichocanace sinensis* Wirth, by original designation and monotypy; 1964:225–227 [revision; key].—Delfinado & Wirth, 1977:392 [Oriental catalog].—Mathis & Wirth, 1979:795 [diagnosis, discussion].—Mathis, 1982:20–22 [review]; 1992:6 [world catalog].

Diagnosis.—Resembling *Xanthocanace* Hendel and *Chaetocanace* Cresson but differing from them and other genera by the following combination of characters.

Head: Mesofrons and parafrons dull, membranouslike, with fine microtomentose vestiture, distinguished from each other by color and in one species by density of microtomentum, with larger setulae along lateral margins and a few smaller setulae on midportion, but with bare area anterior of median ocellus; postocellar setae subequal to ocellar setae and with same orientation, ocellar setae anterolaterad of ocellar triangle; 4 pairs of large, lateroclinate, fronto-orbital setae; arista with setulae basally, setulae not longer than aristal base, apical one-fourth or less bare, stylelike; upturned genal setae 2, posterior seta directly ventrad of midportion of eye, anterior seta aligned with anterior margin of eye; anteroclinate genal seta present, although small and pale.

Thorax: Dorsocentral setae 4 (1 + 3), anterior 2 smaller than posterior setae; acrostichal setulae small, pale, in 4–6 rows, lacking large, prescutellar pair of setae; scutellar setae 1 pair, large, with a few smaller, pale setulae dorsally; supra-alar seta 1, anterior seta lacking; anterior-notopleural seta lacking; anepisternal and katepisternal setae pale, numerous, mostly long and thin, pilose; katepisternal seta lacking; hindtibia without conspicuous, stout, apical seta anteroventrally; apical section of vein M rather straight, not arcuate.

Abdomen: Female genital lamellae broad basally, basal ⅓ to ½ more or less elliptical, with dorsal surface extended, apical ½ to ⅔ as 2 parallel-sided, narrow processes, each bearing 1 large, apical, acutely pointed, stout seta and several smaller setae; surstylus a simple ventral process from epandrium, variously shaped, but usually with apex slightly to obviously curved anteriorly.

Key to Australian Species of *Trichocanace*

1. Large black species, with heavy gray to pearl-gray microtomentum; dorsum of thorax subshiny; frons dull black laterally, with broad, median, pearl-gray stripe and gray, microtomentose, posterior margin; both sexes with conspicuous, anteroventral and posteroventral combs, each with 6–10 strong, black spinelike setae on distal half of forefemur .... *T. atra* Wirth
– Dull gray species; frons not black striped; forefemur with only anteroventral comb or combs lacking 2
2. Large species, wing length 3.5 mm; forefemur lacking combs .... *T. sinensis* Wirth
– Small species, wing length 2.4 mm; forefemur with inconspicuous, anteroventral comb of 6–8 brownish, slender, sharp spinelike setae on distal half .... *T. marksae* Wirth

Trichocanace atra Wirth
Fig. 21

Trichocanace atra Wirth, 1964:227 [HT ♂ (USNM, 67135); Australia. Queensland: Cairns; fig. of ♂ terminalia].—Delfinado & Wirth, 1977:392 [Oriental catalog].—Mathis 1982:21 [catalog, key]; 1989a: 670 [Australasian/Oceanian catalog]; 1992:6 [world catalog].

Australian specimens examined.—Northern Territory: Howard Crossing, 12 May 1955, L. D. Crawford (1 ♀; ANIC). Queensland: Bowen (12 mi SE), 6 May 1955, K. R. Norris, Common (1 ♀; ANIC, allotype). Dunwich, North Stradbroke Island, 20–21 Apr 1965, G. Monteith (5 ♀; CNC). Emu Park (NE Rockhampton), 7 May 1970, Z. Liepa (1 ♂; ANIC). Mt. Tozer (11 km ENE, 12°43′S, 143°18′E), 11–16 Jul 1986, D. H. Colless (1 ♂; ANIC). Southport, 6 May 1971, B. H. Kay (1 ♂, 1 ♀; UQIC). Western Australia: Martin's Well (1 km S), West Kimberley, 26 Apr 1977, D. H. Colless (1 ♂; ANIC).

Distribution.—Australasian: Australia (NT, QLD, WA). Oriental: Philippines (Mindanao), Thailand (Cholburi).

Diagnosis.—This is the most distinctive

21

Fig. 21. External male terminalia of *Trichocanace atra*: 21, epandrium and surstylus, lateral view. Scale = 0.1 mm.

species of the genus and is easily distinguished from congeners by the following characters: large size (wing length 3.3 mm or larger), generally mostly black color with dense gray to pearly gray microtomentum; dorsum of thorax subshiny; frons dull black laterally, with broad, median, pearl-gray stripe and gray, microtomentose, posterior margin; forefemur of both males and females bearing anteroventral and posteroventral comblike rows of 6–10 well-developed setae along distal half.

Trichocanace marksae Wirth
Figs. 22–31

Trichocanace marksae Wirth, 1964:226 [HT ♂ (USNM, 67134); Australia. Queensland: Cairns (bayshore); fig. of ♂ terminalia].—Mathis, 1982:21 [catalog, key]; 1989a:670 [Australasian/Oceanian catalog]; 1992:6 [world catalog].

Australian specimens examined.—Queensland: Cairns (bay shore), 25 Apr–21 Dec 1957, 1976, G. F. Hevel, W. W. Wirth (6 ♂, 22 ♀; ANIC, USNM).

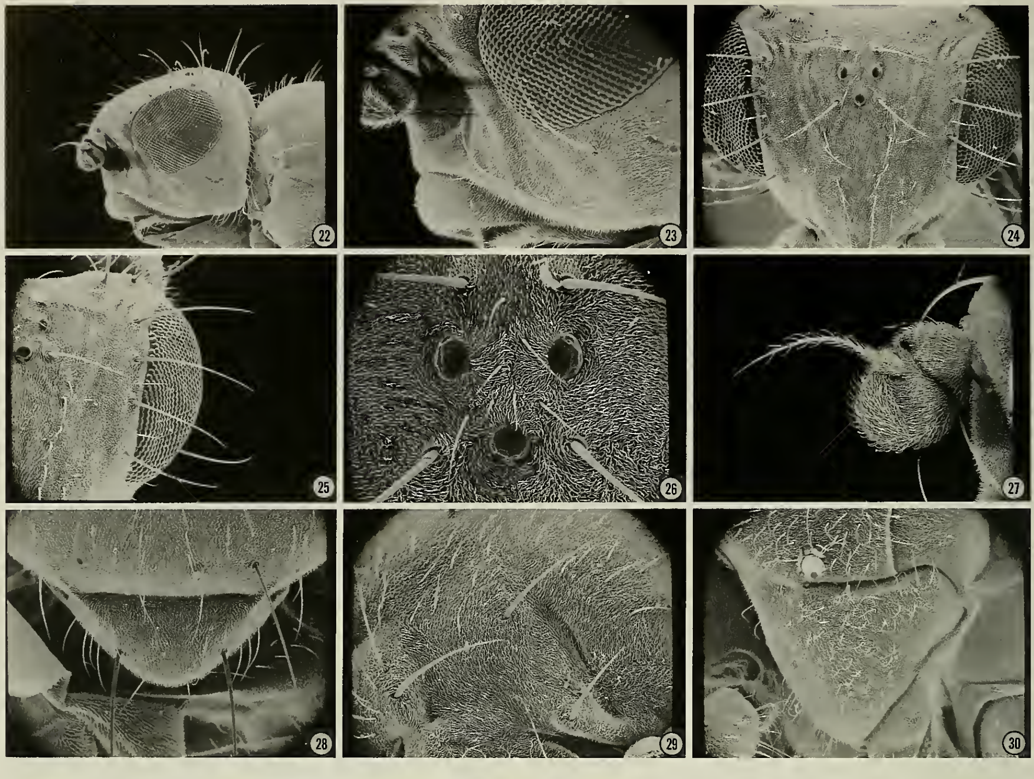
Distribution.—Australasian: Eastern Australia (QLD).

Diagnosis.—This species is the smallest of the genus (wing length 2.5 mm or smaller) and is otherwise distinguished as follows: generally dull gray; frons not striped; and forefemur bearing only anteroventral, comblike row of 6–8 brownish, slender, sharp setae. External male terminalia as follows: Epandrium in lateral view (Fig. 31) with anterior margin shallowly sinuous, posterior margin gently curved, acutely narrowed dorsally; surstylus in lateral view (Fig. 31) narrow, length more than twice width, anterior margin more or less straight, bearing patch of 4–6 moderately long setulae near middle, posterior margin rounded, ventral margin pointed anteroventrally.

Trichocanace sinensis Wirth

Trichocanace sinensis Wirth, 1951:253 [HT ♂ (BMNH); China. Fukien Province: Foochow (= Minhow); fig. of head, wing, ♂ terminalia]; 1964:225 [review].—Delfinado & Wirth, 1977:392 [Oriental catalog].—Mathis & Wirth, 1979:795 [review].—Mathis, 1982:22 [catalog, key]; 1989a:670 [Australasian/Oceanian catalog]; 1992:6 [world catalog].

Australian specimens examined.—Queensland: Cairns (bay shore), 19 Apr–18–21 Dec 1957, 1976, G. F. Hevel, W. W. Wirth (2 ♂, 2 ♀; ANIC, USNM). Cardwell,



Figs. 22–30. Scanning electron micrographs of *Trichocanace marksae*: 22, head, lateral view; 23, gena and setae, lateral view; 24, frons, dorsal view; 25, same, left side, dorsal view; 26, ocellar triangle, dorsal view; 27, antenna, lateral view; 28, scutellum, dorsal view; 29, notopleuron and setae, lateral view; 30, katepisternum and setae, lateral view.

8 Dec 1962, K. R. Norris (9 ♂, 5 ♀; ANIC).

Distribution.—Afrotropical: Madagascar (sub-Ouest). Australasian: Eastern Australia (QLD). Oriental: China (Fukien Province), Malaysia (Negri Sembilan), Thailand (Bangkok).

Diagnosis.—This species is large (wing length 3.5 mm), similar to *T. atra,* but differs as follows: generally dull gray; frons not bearing black stripes; and forefemur lacking comblike rows of stout setae.

Genus *Xanthocanace* Hendel

Xanthocanace Hendel, 1914:98. Type species: *Canace ranula* Loew, by original designation.—Malloch, 1924:334 [discussion, generic key].—Cresson, 1936: 270 [synonymy, discussion].—Curran, 1934:357 [generic key].—Wirth, 1951: 249 [review, key].—Miyagi, 1963:123 [review, key].—Delfinado & Wirth, 1977:393 [Oriental catalog].—Mathis, 1982:22–25 [review]; 1989a:670 [Australasian/Oceanian catalog]; 1992:6–7 [world catalog].

Dinomyia Becker, 1926:107. Type species: *Canace ranula* Loew, by monotypy, preoccupied, Martynov, 1909, and Dyar, 1919.—Cresson, 1936:270 [synonymy with *Xanthocanace*].

Myioblax Enderlein, 1935:235. Type species: *Canace ranula* Loew, by monotypy.—Cresson, 1936:270 [synonymy with *Xanthocanace*].

Diagnosis.—Resembling *Trichocanace* Wirth but differing from it and other genera by the following combination of characters.

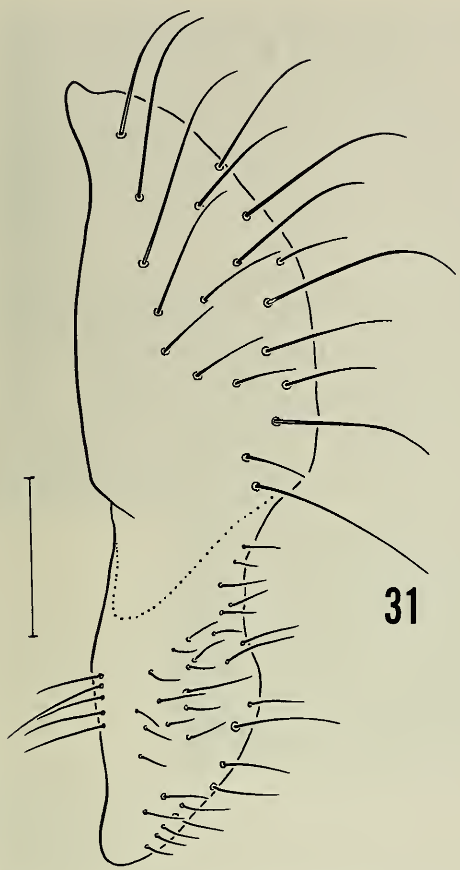


Fig. 31. External male terminalia of *Trichocanace marksae*: 31, epandrium and surstylus, lateral view. Scale = 0.1 mm.

Head: Mesofrons distinct from parafrons, frequently shiny with metallic reflections, with numerous, uniformly scattered, pale setulae but lacking larger setae along lateral margins, anterior margin extended anteriorly beyond level of antennal bases; postocellar setae subequal to ocellar setae, with slightly more divergent orientation; 5–6 pairs of large to moderately sized, pale, lateroclinate, fronto-orbital setae, anterior 1–2 with slight to nearly complete proclinate orientation; arista with apical ⅓ to ½ bare, lacking branching rays, stylelike; upturned genal setae lacking, anteroclinate genal setae 1–3, inserted along anteroventral margin of gena.

Thorax: Dorsocentral setae variable, usually only posterior 1–2 setae conspicuously larger than surrounding setae, but some specimens with up to 6 large setae, some presutural, but posterior ones larger; acrostichal setulae in 4 to several rows, these more evident anteriorly, lacking large pair of prescutellar setae; 2 pairs of scutellar setae, pale, numerous dorsal setae; 1–2, supra-alar setae present, anterior one usually lacking; anterior notopleural seta present; anepisternal setulae pale; katepisternal seta lacking; hindtibia without conspicuous, apical seta anteroventrally; apical section of vein M arcuate.

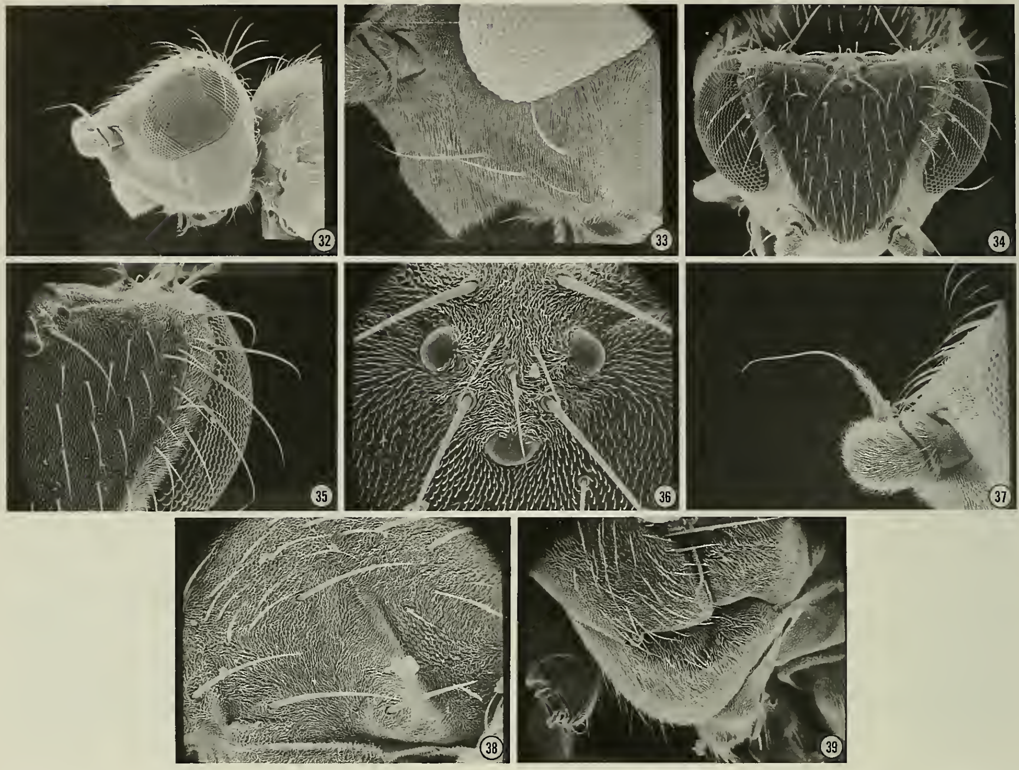
Abdomen: Female genital lamellae moderately wide basally, not narrowed abruptly near level of cleft, bearing only 1 large, stout, acute terminal seta at each apex; surstylus a simple ventral projection from epandrium, tapered gradually, apex acute to blunt.

Key to Australian species of *Xanthocanace*

1. Mesofrons of male thinly microtomentose, somewhat dull, but with some subshiny, metallic luster; mesofrons of female entirely silvery gray microtomentose, dull . . . . *X. collessi*, new species
– Mesofrons of male mostly shiny, very thinly microtomentose; mesofrons of female mostly dull, microtomentose, with some brownish coloration medially, lateral margins gray . . . . *X. nigrifrons* Malloch

Xanthocanace nigrifrons Malloch
Figs. 32–40

Xanthocanace nigrifrons Malloch, 1924: 334 [HT ♂ (AM); Australia. New South Wales: Woy Woy; figs. of head].—Wirth, 1951:250 [review].—Miyagi, 1963:125–126 [distribution, key].—Griffiths, 1972: 256 [discussion of ♂ terminalia].—Mathis, 1982:24 [catalog, key]; 1989a:670



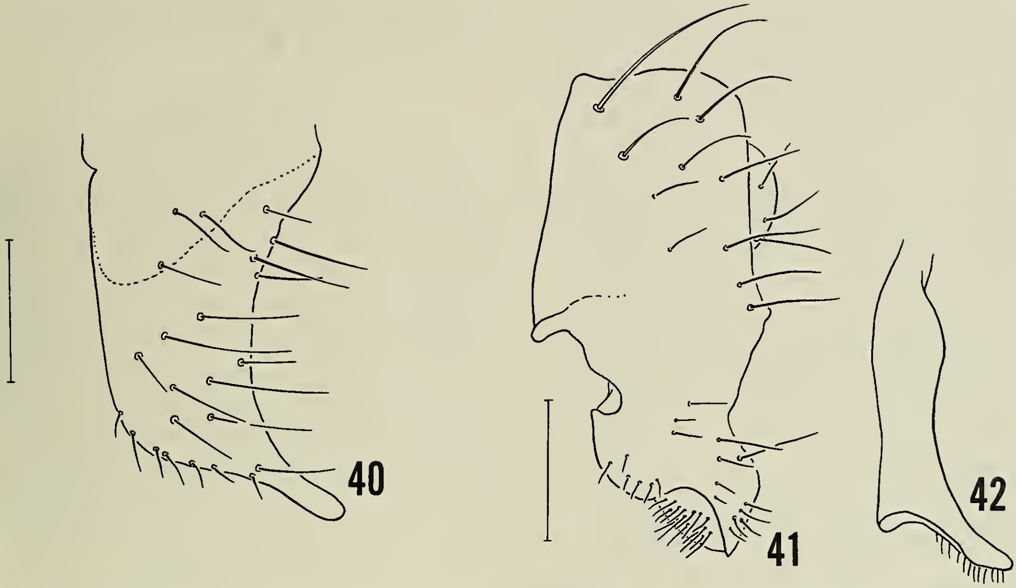
Figs. 32–39. Scanning electron micrographs of *Xanthocanace nigrifrons*: 32, head, lateral view; 33, gena and setae, lateral view; 34, frons, dorsal view; 35, Same, left side, dorsal view; 36, ocellar triangle, dorsal view; 37, antenna, lateral view; 38, notopleuron and setae, lateral view; 39, katepisternum and setae, lateral view.

[Australasian/Oceanian catalog]; 1992:7 [world catalog].

Australian specimens examined.—New South Wales: Angourie, 26 Jan 1980, B. J. Day, D. K. McAlpine (2 ♀; AM). Narrabeen Lagoon (tidal flat), 12 Oct–5 Dec 1956, W. W. Wirth (48 ♂, 49 ♀; ANIC, USNM). Queensland: MacKay Harbour (on sand of beach, high tide mark), MacKay, 25 Jul 1987, R. Jones (1 ♂; UQIC). Miriam Vale District, Eurimbula (sandy pool on beach), 28 Mar 1975, D. K. McAlpine (4 ♂, 12 ♀; AM, USNM). Tasmania: Squeaking Point near Port Sorell (stony beach), 24 Nov 1968, I. C. Yeo (18 ♂, 16 ♀; UQIC). Western Australia: Cape Bertholet (4 km SSE), West Kimberley, 19 Apr 1977, D. H. Colless (1 ♂; ANIC).

Distribution.—Australasian: Australia (NSW, QLD, TAS, WA).

Diagnosis.—This species is distinguished from congeners by the following combination of characters: length over 2.5 mm; mesofrons of male very thinly microtomentose, subshiny, bluish black; mesofrons of female almost entirely microtomentose, dull; midfemur of male lacking posteroventral comb of 5–10 small, black setae on distal half; femora with at least apical half yellow. External male terminalia as follows: surstylus in lateral view (Fig. 40) bearing short and moderately long setulae, shape narrow, twice as long as wide, basal ⅔ a gradually narrowing straight process from ventral epandrial margin, thereafter curved abruptly posteroventrally as a much narrower, digitiform process, apex bluntly rounded.



Figs. 40–42. External male terminalia of *Xanthocanace* species: 40, surstylus of *X. nigrifrons,* lateral view. 41, epandrium, cercus, and surstylus of *X. collessi,* lateral view; 42, surstylus of *X. collessi,* posterior view (setae and setulae not included). Scale = 0.1 mm.

Remarks.—I examined a single female as part of this study from Victoria (Mallacoota Inlet, SE Genoa, 4 Aug 1973, Z. Liepa (ANIC)) that is very similar to and may be conspecific with this species. This female is darker in coloration, particularly on the mesonotum, and the mesofrons also has darker hues with slightly more metallic luster shining through the microtomentum. Additional specimens, especially males, will be needed to resolve the status of this population.

Xanthocanace collessi, new species
Figs. 41–42

Diagnosis.—This species is similar to *X. sabroskyi* Mathis & Freidberg and especially *X. zeylanica* Delfinado and is distinguished from either and other congeners by the following combination of characters: Mesofrons of male thinly microtomentose, with some subshiny, metallic luster; mesofrons of female entirely microtomentose silvery gray, dull; femora mostly whitish gray except for yellow apices; tibiae yellow.

Description.—Moderately small to medium-sized beach flies, length 2.2 to 3.3 mm: body mostly silvery white to slightly metallic bluish to whitish gray, darker dorsally with some subshiny areas with metallic luster.

Head: Mesofrons of male thinly microtomentose, somewhat dull, partially subshiny with some metallic gray to silvery gray luster; mesofrons of female entirely silvery gray microtomentose, dull; mesofrontal setulae abundant, conspicuous. Face, gena, and clypeus concolorous, silvery white, densely microtomentose.

Thorax: Mesonotum silvery gray, frequently with some faint bluish coloration, slightly subshiny, with weak metallic luster; pleural areas lighter, becoming almost completely white. Wing faintly milky white; costal vein ratio 0.28; M vein ratio 0.52. Legs: midfemur of male lacking row of 5–10 closely set black setae along apical half of posteroventral surface; femora mostly whitish gray to gray, except for yellow apices; tibiae yellow to whitish yellow.

Abdomen: Dorsum concolorous with mesonotum. Male preabdomen as follows: sternite 3 generally rectangular with rounded corners, slightly narrower anteriorly than posteriorly; sternite 4 nearly as wide as long, anterior margin narrower than posterior margin, posterior margin shallowly and narrowly notched medially; sternite 5 broadly V-shaped with arms angled posteriorly, posterior margin fused with more lightly sclerotized 6th sternite. External male terminalia as follows: epandrium with a deep, narrow, posteromedian cleft dorsally, not bearing long black setae with posterior orientation; surstylus in lateral view (Fig. 41) nearly as wide as long, anteroventral margin rounded, posteroventral margin produced ventrally to a pointed projection, posterior margin shallowly sinuous; surstylus in posterior view (Fig. 42) very narrow, apical ¼ as a slender slipper, with apex oriented posteromedially, ventral margin bearing fringe of short setulae.

Type material.—The holotype male is labeled "[AUSTRALIA] 5 km SSW of Cape Bertholet WA West Kimberley 21 Apr 1977 D. H. Colless/At light/HOLOTYPE ♂ Xanthocanace collessi W. N. Mathis [red; gender and species name handwritten]." The holotype is double mounted (smaller pin in a block of polyporus), is in good condition, and is deposited in ANIC. The female allotype and three other paratypes (♀; ANIC) bear the same label data as the holotype. Other paratypes are as follows: Western Australia: Cape Bertholet (8 km S), West Kimberley, 17 Apr 1977, D. H. Colless (2 ♂, 28 ♀; ANIC, USNM). Cape Bertholet (3 km S), West Kimberley, 20 Apr 1977, D. H. Colless (2 ♀; ANIC). Cape Bertholet (4 km SSW), West Kimberley, 18 Apr 1977, D. H. Colless (2 ♀; ANIC).

Distribution.—Australasian: Australia (WA).

Etymology.—The specific epithet, *collessi,* is a genitive patronym to recognize the many contributions of Donald H. Colless to the study of Diptera, the Australian fauna in particular. He also collected all specimens of the type series.

New Genus

Diagnosis.—Resembling *Trichocanace* Hendel and *Chaetocanace* Cresson but differing from them and other genera by the following combination of characters.

Head: Mesofrons and parafrons dull, membranelike, with dense microtomentose vestiture, distinguished from each other by color and density of microtomentum, with larger setulae along lateral margins and a few smaller setulae on midportion, but with bare area anterior of median ocellus; postocellar setae subequal to ocellar setae and with same orientation, ocellar setae inserted anterolaterad of ocellar triangle; 3 large, lateroclinate, fronto-orbital setae; arista with basal segment bare, apical segments bearing tiny hairs; genal setae 3, anteroclinate and slightly upturned apically, aligned horizontally.

Thorax: Dorsocentral setae 6 (2 + 4), anterior seta smaller than posterior setae, 5th seta inserted slightly mediad to alignment of anterior setae, posterior seta inserted slightly lateral of alignment; acrostichal setulae lacking anteriorly but with a prescutellar pair of setae; lateral scutellar setae 2; scutellar disc with a few setulae, 3–5; supra-alar setae 1 large and 1–2 smaller setae anteriad; notopleural setae 2, both well developed; anepisternum with 2 larger setae along posterior margin, 2–3 smaller setae below and a few setulae medially; katepisternal seta lacking. Apical section of vein M rather straight, very shallowly sinuous, not arcuate. Hindtibia without a conspicuous, stout, apical seta anteroventrally.

Abdomen: Female genital lamellae reduced and lacking prominent setae apically and subapically.

New Species of New Genus

Australian specimens examined.—South Australia: Coward Springs (5 km NW), near Lake Eyre, 22 Sep 1972, Z. Liepa (1 ♀; ANIC).

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Marine fossil shark (Chondrichthyes) from nonmarine Eocene sediments, northeastern Kazakhstan

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Abstract.—A single tooth of the sand tiger shark, *Carcharias* sp., was collected from the upper Eocene Kusto svita in the Zaysan basin of northeastern Kazakhstan. The Kusto svita is nonmarine lacustrine strata with an extensive nonmarine biota of plants (especially charophytes) and terrestrial vertebrates (especially mammals). The shark tooth was apparently carried to the site by a predator/scavenger from the then-nearest seaway, more than 500 km to the northwest.

The Zaysan basin of northeastern Kazakhstan (Fig. 1) has an Upper Cretaceous-Miocene sedimentary fill dominated by freshwater shales, siltstones and fine sandstones deposited in and around ancient Lake Zaysan (Borisov 1963, Verzilin et al. 1980). The middle Eocene-middle Miocene strata here produce rich fossil assemblages of freshwater and terrestrial plants (charophytes and angiosperm leaves), invertebrates (ostracods, gastropods, unionid bivalves) and vertebrates (amiid and teleost fishes, salamanders, turtles, crocodylians, birds and mammals). We were thus surprised to find a single tooth of a marine selachian at a late Eocene site in the Zaysan basin. Here we document this fossil and suggest a probable mechanism for its transport from the marine to nonmarine environment.

Occurrence

During the summer of 1993, the fossil selachian tooth, KAN (Institute of Zoology, Kazakh Academy of Sciences, Almaty) 35 (12) 1660, was collected from screenwashed sediment at our locality K12 (UTM 387305E, 5260046N, zone 45), which is on the eastern bank of the Sarybulak River, downstream from the well known Eocene mammal locality called Sunduk (Russell & Zhai 1987, fig. 84). Locality K12 is in the Kusto svita in a bed of silty and sandy mudstone that is pale olive with dark yellowish orange limonitic mottling. This bed is 8 m below the top of the Kusto svita, which is approximately 50 m thick in this area.

Locality K12 produced an extensive vertebrate fossil assemblage now under study that includes an amiid fish, a trionychid turtle, a crocodylian, cylindrodontid and cricetid rodents, the hyaenodontid creodont *Hyaenodon,* and the anthracothere *Elomeryx.* Adjacent strata produce numerous charophytes (Kyansep-Romashkina 1980). Fossil mammals indicate the Kusto svita is of late Eocene age (Ergilian land-mammal "age" of Russell & Zhai 1987).

Description and Identification

KAN 35 (12) 1660 (Fig. 2). A single-cusped tooth missing much of root, which is heavily abraded. Crown tall (total length at least 21.9 mm), narrow, sharply pointed blade. Crown with distinctly sigmoidal outline in anterior view. Two cutting edges of

Fig. 1. Map of Kazakhstan showing location of Zaysan basin in the northeastern part of the country.

crown forming sharp, nearly parallel carinae extending almost to root. No lateral cusplets preserved, but crown base is missing where these would have been, if present at all. Crown enamel lingually smooth to very weakly striated longitudinally. Impossible to determine if root had transverse groove. Lingual face of root smooth and convex. Root not massive, but full extent cannot be determined.

This tooth is identical in form to the second upper anterior teeth of several kinds of lamniform sharks. Of the lamniform sharks with elongate anterior teeth, only the species of *Odontaspis, Carcharias* and *Isurus* have second upper anterior teeth that resemble KAN 35 (12) 1660. Unlike KAN 35 (12) 1660, the second upper anterior teeth of *Odontaspis* have cutting edges extending only down about one-half to two-thirds the distance from the apex of the crown. However, the lack of the entire root, so that the presence of lateral cusplets and a transverse groove cannot be established, make it possible that this tooth could be that of a mako, *Isurus,* though the presence of faint stria-

Fig. 2. Photograph of KAN 35 (12) 1660, incomplete tooth of *Carcharias* sp. from the Kusto svita in the Zaysan basin of northeastern Kazakhstan; A, labial; B, lingual; C, anterior. Approximately ×2; scale in mm.

tions on the lingual surface of the crown is characteristic of *Carcharias,* not *Isurus.* Closest resemblance of KAN 35 (12) 1660 is to anterior teeth of the sand tiger shark *Carcharias* (see Applegate 1965), to which we assign it as *Carcharias* sp.

Discussion

The species of *Carcharias* are marine sharks with a temporal range extending back to the beginning of the Late Cretaceous (Cenomanian) (Cappetta 1987, Welton & Farish 1993). The freshwater origin and fossil biota of the Kusto svita at site K12 excludes the possibility of the *Carcharias* tooth representing an animal that lived at the site, so it is not autochthonous to the deposit. Its allochthonous origin could not be as a fossil reworked from older sediments, simply because no such marine strata are present in or around the Zaysan basin (Borisov 1963). The youngest marine strata in this part of Kazakhstan are of Permian age, much older than the first known occurrence of *Carcharias.*

It seems most likely that this allochthonous shark tooth was brought to the site by a biological agent. During the late Eocene, the nearest marine water was the western Siberian seaway, with its eastern shoreline to the northwest of Semipalitinsk, about 500 km to the northwest of locality K12 (Tsekhovsky 1987, fig. 42). Sand tiger sharks are nearshore marine sharks that would have inhabited the shallow waters along the margin of such a seaway. Indeed, fossils of *Carcharias* and other lamniform sharks are known from Eocene-Oligocene strata in central and western Kazakhstan (Glikman 1964).

We propose that from this seaway a predator/scavenger—a crocodyle, bird or mammal—somehow carried the tooth to the site (probably by consumption), where it became fossilized out of context. At present no other explanation fits the data. The isolated nature of the tooth, the close association of this marine shark fossil with freshwater fossils and the lack of a sedimentary source from which it could have been reworked, make transport by a biological agent, probably predator/scavenger, the only reasonable explanation. To our knowledge, this is the first case in the fossil record of a probable predator/scavenger transport of a shark tooth from a marine environment to a nonmarine setting.

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Pholidichthys anguis, a new species of pholidichthyid fish from Northern Territory and Western Australia

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Abstract.—*Pholidichthys anguis* is only the second species known in the family Pholidichthyidae. It differs from *P. leucotaenia* in having 87–98 dorsal-fin rays (vs. 66–79), 70–81 anal-fin rays (vs. 49–62), 90–101 total vertebrae (vs. 71–79), a more slender body, and a shorter head and maxillary. In addition, the color pattern of juveniles (~50–103 mm SL) differ in having the depth of the slender dark stripe on midside at vertical from anal-fin origin about 1 mm, usually much less (vs. depth 2.5–3.3 mm). Study of whole specimens and skeletal preparations of *P. anguis* indicates that the species exhibits the same familial specializations as *P. leucotaenia.* The two species are distributed allopatrically. We hypothesize that the common ancestor of the two species of *Pholidichthys* had a Tethyan distribution exclusive of Australia-New Guinea (ANG). When ANG collided with SE Asia, the ancestor invaded ANG. During a subsequent interglacial period, ecological factors contributed to the isolation of the Australian portion of the ancestral population from the New Guinea portion, and permitted divergence of the isolates.

Pholidichthys and its only included species, *P. leucotaenia,* sole representative of the Pholidichthyidae, were described by Bleeker (1856) from Boeroe (= Buru), Indonesia. A purported second species, *P. anguilliformis,* was described by Lockington (1882) from the Gulf of California. The holotype of *P. anguilliformis* has not been seen since its description, but characters given for the species (especially its all spinous dorsal fin) and its type locality, probably indicate that it is not congeneric or confamilial with *Pholidichthys* Bleeker. Larson (*in* Trnski et al. 1989) indicated that an undescribed species of *Pholidichthys* (whose description is the main purpose of the present paper) also exists in the Indo-Pacific. Her report was based on specimens brought to her attention by prawn researchers of the Northern Territory Fisheries Division, Darwin. We know of no other described or undescribed taxa that are referable to the Pholidichthyidae.

In the last major study of *Pholidichthys,* Springer & Freihofer (1976) reviewed the literature on *P. leucotaenia* and described aspects of its osteology, neurology, and ontogenetic color-pattern changes. They also remarked on its behavior in aquaria, plotted its geographic distribution, and discussed its possible familial interrelationships.

Materials and Methods

Specimens of the new species are listed in the description. All but one specimen, an adult female, 245 mm SL, which we designate holotype, are small juveniles (most less than 70 mm SL, none between 103 mm and 245 mm) obtained from trawl hauls. Most of the specimens are curled and twisted and do not permit accurate SL measurements to be made. We arbitrarily selected a few specimens in good condition on which to take measurements (Table 1, Fig. 6). Nevertheless a cursory examination of many specimens convinces us that the main proportional differences we stress will hold when more specimens in good condition become available for measurement.

Comparative material of *Pholidichthys leucotaenia* is that listed by Springer & Freihofer (1976:2) and more recent material or records as follows: New Caledonia (Burgess & Axelrod 1975:fig. 65, photograph; see discussion in Springer 1982:71); Solomon Islands: Marau Island (Burgess & Axelrod (1975:fig. 64, photograph). Indonesia: Flores (Kuiter 1992:4, fig. E, and J. E. Randall, pers. comm.), Saparua (USNM 210334), Tulangbesi Islands (J. E. Randall, photograph, pers, comm.); Philippines: Tawi Tawi (USNM 122340, 150828, 151178), Jolo (USNM 122339), Apo (USNM 289924), Luzon (questionable record based on aquarium dealer reports). Papua New Guinea: Madang and vicinity (AMS I.34712.007, USNM 258321), d'Entrecasteaux Islands (J. E. Randall, photograph, pers. comm.). Singapore (ZMUC P.75457, obtained from an aquarium dealer).

Dorsal-, anal-, and caudal-fin rays, vertebrae, pleural, and epineural counts were made from radiographs (and from the 3 cleared-and-stained specimens). Many more specimens were radiographed than is indicated by the numbers of specimens reported in Table 2, but because of poor ossification or fineness of structure, we were unable to obtain all counts for all specimens, and for some we were unable to make any counts. Specimens were cleared with trypsin and counterstained with alizarin and alcian blue. Dorsal- and anal-fin ray counts include all elements (last two rays counted as two—last ray not split to base). Precaudal vertebrae are those anterior vertebrae lacking a hemal spine. Measurements were made with dial calipers and recorded to three significant figures. Standard length (SL) was taken from the midtip of the upper lip to the midbase of the caudal fin; head length (HL), from the midtip of the upper lip to the posteriormost edge of the operculum; snout length, from the midtip of the upper lip to the anteriormost edge of the orbit; upper jaw length, from the midtip of the upper lip to the posteriormost edge of the maxilla; predorsal length, from the midtip of the upper lip to the anterior base of the first dorsal-fin ray; orbital diameter is the greatest horizontal diameter; postorbital head length was taken from the posteriormost edge of the orbit to the posteriormost edge of the operculum; body depth was measured vertically at the anal-fin origin; mid-lateral dark stripe depth was measured where the stripe crossed a vertical from the anus; caudal-fin length is the length of the longest caudal-fin ray. Regression formulae and plotted curves are the products of a computer software program, PSI-Plot, version 3 (Poly Software International, P.O. Box 526368, Salt Lake City, UT 84152). Institutional abbreviations are those given by Leviton et al. (1985).

Pholidichthys anguis, new species
Figs. 1–3

Holotype.—NTM S.11799-001, mature female, 245 mm TL, WSW of Angurugu, Groote Eylandt, Northern Territory, Australia (14°05′S, 136°15′E), 19 m, 30 June 1984, Northern Territory Fisheries.

Paratypes.—130 specimens (~50–103 mm SL): AMS I.36375-001 (3), ANSP 173800 (3), BMNH 1995.8.14.1–3 (3), BPBM 36786 (3), CAS 82409 (3), MNHN 1995-0896-0898 (3), NTM S.13530-003 (26), QM I.30118 (3), ROM 69314 (3), USNM 337859 (9) and WAM P.31012-001 (3), all with same data: Arafura Sea, Northern Territory, North Goulburn Island (10°23′49″S, 135°43′53″E), depth 53 m, 23 Sept 1992. NTM S.13529-001 (49) and USNM 337860 (15, including 3 cleared and stained), Arafura Sea, Northern Territory, W of Cape Wessel (10°57.2′S, 136°06.2′E), depth 42–43 m, 22 Sept 1992. NTM S-13039-001 (3), Arafura Sea, Northern Territory, N of Melville Island (10°38′S, 130°52′E), 17 June 1989. NTM S-13339-002 (1), Timor Sea, Western Australia, Joseph Bonaparte Gulf (13°07′S, 128°56′E), depth 70 m, 23 Nov 1990.

Diagnosis.—A species of *Pholidichthys* with: 87–98 dorsal-fin rays; 70–81 anal-fin rays; 90–101 total vertebrae; depth of slender, dark stripe on midside of juveniles (up to at least 103 mm SL) 1.0 mm or less at vertical from anal-fin origin.

Description (Tables 1–2).—Dorsal fin 87–98, all rays segmented, all but a few of the most anterior and posterior rays branched (unable to determine condition in holotype), anteriormost ray not supernumerary, last ray not split to base, stay (Johnson 1984:caption of table 120) present. Supraneurals or predorsal bones absent.

Anal fin 70–81 (Table 2), all rays segmented, all but a few of the most anterior and posterior rays branched (unable to determine condition in holotype), anteriormost ray apparently supernumerary (anteriormost pterygiophore appears to be fusion of two pterygiophores), last ray not split to base, stay present; 7–10, usually 8 or 9, pterygiophores anterior to first hemal spine.

Vertebrae 23–28 + 64–75 = 90–101 (Table 2); posteriormost pleural rib articulating with next- to posteriormost or posteriormost precaudal centrum; epineurals 18–22.

Pectoral-fin rays 14 or 15 (14 in 16 of 17 specimens checked), dorsal- and ventralmost two rays simple, others branched.

Pelvic-fin small, rays I,2 or I,3; spine greatly reduced, visible only in osteological preparations; third (innermost) segmented ray greatly reduced when present, usually visible only in osteological preparations; segmented rays all simple; basipterygia abutting posteriorly, widely separated anteriorly; rays supported by an almost spherical cartilaginous process at ventroposterior end of basipterygium.

Caudal-fin rays 10, all simple, 5 rays above and 5 below diastema, parhypural and hypurals fused into single plate, no procurrent rays, no epurals.

Gillrakers on first arch (epibranchial-angle-hypobranchial; left side/right side): 5-1-8/5-1-8 (holotype); 5-1-9/5-1-8, 5-1-9/5-1-9, 6-1-9/6-1-10 (three cleared-and-stained specimens, left & right sides).

One nostril (anterior) each side; number and distribution of sensory pores as in *P. leucotaenia* (Springer & Freihofer 1976: figs. 12 and 14), except that interorbital commissural pore (Springer & Freihofer 1976:fig. 12) varying from present and obvious to absent.

Teeth: In general, all teeth are moderately laterally compressed canines with slightly recurved tips. In juveniles, ~80 mm SL, upper teeth on each side of each jaw arranged in 3 linear rows; most posterior row with smallest teeth, consisting of about 10 teeth, of which anteriormost 2 are overlapped externally by posteriormost 1 or 2 teeth of next row anterior, which consists of about 8 slightly larger teeth, of which anteriormost 2 or 3 are overlapped externally by posteriormost 2 or 3 teeth of next row anterior, which consists of about 6 teeth, which are initially larger but decrease in size and become misaligned anteriorly; external to small, misaligned teeth of previous row are largest 4 teeth. Anterior, largest teeth of upper jaw larger than those of lower jaw. In the holotype, the tooth rows have been disrupted and there appears to be 1 row of teeth posteriorly grading into 3 irregular rows anteriorly, with the outermost anterior teeth the largest.

Measurements of certain body characters are given in Table 1, and four of these characters are plotted (Fig. 6) against SL with their best fitted regression curve (usually a power curve) for comparison with the same characters in *P. leucotaenia.*

Color pattern (Figs. 1–3): All but 1 of the available specimens are juveniles of about 25 to 103 mm SL. The color pattern of the juveniles is fairly consistent, but the dark markings we describe vary from faintly to darkly dusky, and may be interrupted. We

Table 1.—Measurements in millimeters (and as percent SL) for certain characters of the species of *Pholidichthys.*

	P. anguis						
SL	69.1[1]	76.7[1]	77.3[2]	86.0[1]	87.4[2]	103[2]	245[3]
Head length	11.7 (16.9)	12.1 (15.8)	12.1 (15.7)	13.5 (15.7)	13.6 (15.6)	14.6 (14.2)	22.2 (9.1)
Snout length	2.2 (3.2)	2.4 (3.1)	2.4 (3.1)	2.8 (3.3)	2.8 (3.2)	3.0 (2.9)	4.5 (1.8)
Orbital diameter	3.1 (4.5)	2.5 (3.3)	3.2 (4.1)	3.0 (3.5)	3.4 (3.9)	3.2 (3.1)	3.4 (1.4)
Postorbital HL	6.9 (10.0)	7.6 (9.9)	7.1 (9.2)	8.2 (9.5)	8.6 (9.8)	9.0 (8.7)	15.2 (6.2)
Upper jaw length	4.3 (6.2)	4.1 (5.3)	4.3 (5.6)	4.6 (5.4)	4.7 (5.4)	5.3 (5.1)	7.6 (3.1)
Predorsal length	11.9 (17.2)	12.5 (16.3)	12.4 (16.1)	13.4 (15.6)	13.1 (15.0)	14.2 (13.7)	25.1 (10.2)
Body depth	4.7 (6.8)	5.0 (6.5)	5.5 (7.1)	5.9 (6.9)	6.0 (6.9)	6.3 (6.1)	10.3 (4.2)
Caudal-fin length	5.1 (7.4)	5.1 (6.6)	5.2 (6.7)	5.6 (6.5)	5.5 (6.3)	7.0 (6.8)	14.5 (5.9)
Mid-lateral dark stripe depth	0.6 (0.9)	0.7 (0.9)	0.5 (0.6)	0.9 (1.0)	1.0 (1.1)	0.9 (0.9)	NA

	P. leucotaenia						
SL	49.7[4]	52.1[5]	66.2[4]	77.6[5]	79.4[5]	80.2[6]	83.3[6]
Head length	10.0 (20.1)	11.6 (22.3)	13.0 (21.2)	15.1 (19.5)	15.4 (19.4)	16.6 (20.7)	16.4 (19.7)
Snout length	2.2 (4.4)	2.5 (4.8)	2.4 (3.9)	3.2 (4.1)	3.4 (4.3)	3.4 (4.2)	3.5 (4.2)
Orbital diameter	2.5 (5.0)	3.0 (5.8)	2.8 (4.6)	3.0 (3.9)	3.2 (4.0)	3.2 (4.0)	3.1 (3.7)
Postorbital HL	6.8 (13.7)	7.0 (13.5)	8.2 (20.8)	9.4 (12.1)	10.1 (12.7)	10.2 (12.7)	10.6 (12.7)
Upper jaw length	3.2 (6.4)	3.8 (7.3)	4.2 (6.8)	5.2 (6.7)	5.0 (6.3)	5.3 (6.6)	5.2 (6.2)
Predorsal length	11.8 (23.8)	10.7 (20.5)	13.4 (21.9)	14.7 (18.9)	15.3 (19.3)	15.8 (19.7)	15.5 (18.6)
Body depth	5.2 (10.4)	4.6 (8.8)	6.3 (9.5)	6.7 (8.6)	7.1 (8.9)	8.8 (11.0)	9.3 (11.2)
Caudal-fin length	4.2 (8.4)	4.4 (8.4)	4.3 (7.0)	—	—	5.7 (7.1)	6.9 (8.3)
Mid-lateral dark stripe depth	3.0 (6.0)	2.5 (4.8)	3.3 (5.4)	3.3 (4.3)	2.8 (3.6)	2.7 (3.4)	2.7 (3.2)

	P. leucotaenia					
SL	97.5[7]	102[8]	115[9]	224[10]	225[10]	337[11]
Head length	17.3 (17.8)	18.9 (18.5)	20.3 (17.6)	30.5 (13.6)	28.7 (12.8)	41.8 (12.4)
Snout length	3.5 (3.6)	3.6 (3.5)	4.0 (3.5)	6.3 (2.8)	6.5 (2.9)	7.8 (2.3)
Orbital diameter	3.5 (3.6)	3.5 (3.4)	3.6 (3.1)	5.2 (2.3)	4.6 (2.0)	5.2 (1.5)
Postorbital HL	10.8 (11.1)	12.0 (11.8)	13.3 (11.6)	20.5 (9.2)	19.2 (8.5)	31.0 (9.2)
Upper jaw length	6.0 (6.2)	6.0 (5.9)	6.6 (5.7)	10.9 (4.9)	10.6 (4.7)	14.1 (4.2)
Predorsal length	17.2 (17.6)	18.2 (17.8)	18.7 (16.3)	30.1 (13.4)	27.8 (12.4)	42.7 (12.7)
Body depth	8.5 (8.7)	7.6 (7.4)	8.9 (7.7)	19.4 (8.7)	18.1 (8.0)	20.7 (6.1)
Caudal-fin length	6.5 (6.7)	7.7 (7.5)	8.9 (7.7)	14.2 (6.3)	14.4 (6.4)	—
Mid-lateral dark stripe depth	3.3 (3.4)	2.8 (2.7)	3.1 (2.7)	NA	NA	NA

[1]USNM 337860, [2]NTM S.13039-001, [3]Holotype, NTM S.11779-001; [4]AMS I.34480-001, [5]USNM 289924, [6]USNM 215258, [7]AMS I.34712-007, [8]USNM 122340, [9]USNM 150828, [10]CAS 32048, [11]USNM 212163.

describe the dark markings in their most pronounced and complete form. Tip of chin with dark smudge, another on snout above upper lip continuing ventrally below eye and posteriorly from mid-postorbital margin as broad, dark stripe; stripe constricting at upper posterior margin of operculum and continuing as dark, slender midlateral stripe, which decreases in depth (depth at no point much greater than 1 mm, usually less) as it proceeds posteriorly to base of caudal fin, where it is briefly interrupted, beginning again, slightly intensified, on caudal fin, and extending, diffusely, for variable distance, up to the end of the fin. Slender, dark stripe dorsally on head, originating at postorbital margin, continuing posteriorly just ventral to dorsal-fin base, tapering and becoming fainter posteriorly until it vanishes, usually on or before reaching posterior third of body. No other prominent markings on head, body, or fins.

Female adult (holotype, 245 mm SL). Head overall dusky with darker, diffuse

Table 2.—Frequency distributions for certain meristic characters of the species of *Pholidichthys* (localities arranged west to east). "x" denotes count recorded by Kailola (1973:11), but not encountered during our study. ? denotes a specimen with a count equal to or slightly greater than indicated by the column heading.

	Dorsal-fin rays																											
Species	66	67	68	69	70	71	72	73	74	75	76	77	78	79	...	86	87	88	89	90	91	92	93	94	95	96	97	98
P. anguis																												
J. Bonaparte Gulf																		1										
N Melville Id																									2	–	–	1
N. Goulburn Id																1[1]	–	–	–	3	1	1	2	1	1			
Cape Wessel																				6	4	5	6	6	–	1	–	1
Groote Eylandt																	1											
P.leucotaenia	x	x	x	x	x	x	3	3	1	1	8	4	1	1														

	Anal-fin rays																										
Species	49	50	51	52	53	54	55	56	57	58	59	60	61	62	...	70	71	72	73	74	75	76	77	78	79	80	81
P. anguis																											
J. Bonaparte Gulf																?											
N Melville Id																								1	1	1	
N Goulburn Id																	1[1]	3	–	1	3	2	1	1	?		
Cape Wessel																		2	3	2	7	4	5	2	–	–	1
Groote Eylandt																			1								
P. leucotaenia	x	x	x	x	x	2	1	–	4	4	3	1	6	1													

	Total vertebrae																					
Species	71	72	73	74	75	76	77	78	79	...	90	91	92	93	94	95	96	97	98	99	100	101
P. anguis																						
J. Bonaparte Gulf											1											
N. Melville Id																1	–	1	1			
N Goulburn Id															2	3	2	3	1	–	?	
Cape Wessel													1	8	9	3	7	3	1	–	1	1
Groote Eylandt												1										
P. leucotaenia	1	–	2	4	3	2	5	6	1													

	Precaudal vertebrae							Caudal vertebrae																					
Species	22	23	24	25	26	27	28	48	49	50	51	52	53	54	55	56	...	64	65	66	67	68	69	70	71	72	73	74	75
P. anguis																													
J. Bonaparte Gulf					1													1											
N. Melville Id		1	1																									1	1
N. Goulburn Id				2	8	5															1	2	2	4	1	2	–	–	?
Cape Wessel				13	19	3	2													1	7	8	8	6	2	2	1		
Groote Eylandt			1																		1								
P. leucotaenia	2	4	9	11	1			2	1	7	2	3	5	3	1	1													

[1] Specimen has caudal vertebral fusions, which may have affected number of fin rays; caudal and total vertebral counts for this specimen not included in table.

dusky blotch posterior to orbit; blotch interrupted at preopercular margin, becoming much less distinct on opercle, continuing on body as moderately large, indistinct series of ovoid to elongate ovoid dusky areas, which become unrecognizable at about body midlength. Three horizontal pairs of dusky ovoid spots on abdomen (anteriorly, at midlength, posteriorly) continuing as series of about 20 diffuse, dusky spots on body below midlevel, spots ending on posterior half of body. Series of diffuse ovoid spots on dorsal body contour, beginning over posterior quarter of abdomen, continuing to caudal-fin.

Dorsal and anal fins variably dusky, with

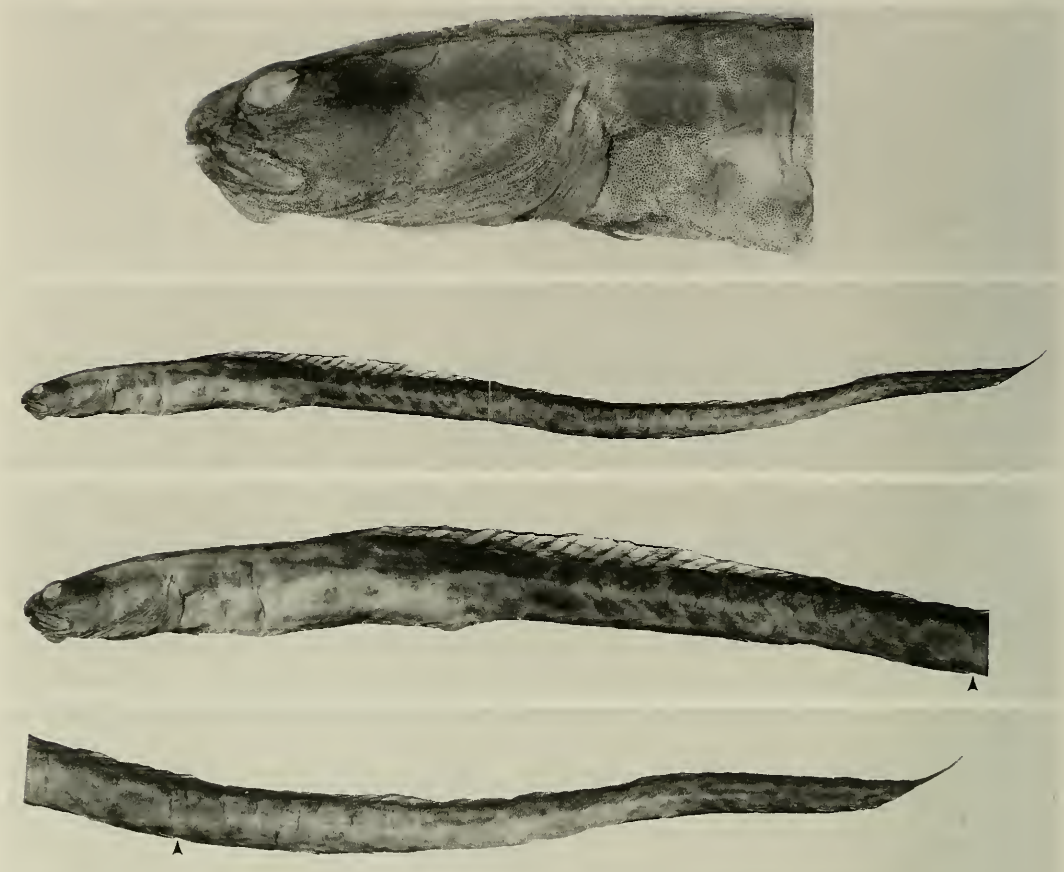

Fig. 1. Holotype of *Pholidichthys anguis,* NTM S.11799-001, female 245, mm SL, WSW of Groote Eylandt, Gulf of Carpentaria, Northern Territory, Australia. Bulge under lower jaw appears to be an abnormality. Full-length view is produced from two photographs pieced together. Arrows in lower two figures indicate same position in each photograph. (Photographs by T. B. Griswold)

distal edge of each darker; both fins becoming much darker near posterior end, where they join darkly dusky caudal fin. Pectoral and pelvic fins pale dusky. A color photograph taken of the fresh specimen shows the spots on the body to be brownish; background color tan. Large yellow eggs are visible through the transparent abdomen.

Remarks.—The holotype has an apparently abnormal padlike swelling on the chin, possibly caused by a parasite. As seen through the body wall of the holotype (Fig. 2), the maximum diameter of the eggs appears to be approximately 2 mm.

All specimens of *P. anguis* have come from benthic trawl samples from a mud substrate, which may include sand, shell, sponges, and rocky reef and coral patches. None have been found associated with coral reefs, as with *P. leucotaenia.*

Comparisons.—Study of whole specimens and skeletal preparations of *P. anguis* indicates that the species exhibits the same familial specializations as *P. leucotaenia* (e.g., presence of a septal bone, fused 5th ceratobranchials, single nostril, no spinous fin rays, lack of scales, etc; see Springer & Freihofer 1976). *Pholidichthys anguis* differs from *P. leucotaenia* in having 87–98 dorsal-fin rays (vs. 66–79), 70–81 anal-fin

Fig. 2. Holotype of *Pholidichthys anguis,* NTM S.11799–001, from color photograph taken when specimen was freshly collected; note eggs visible through transparent abdominal skin. (Photograph by A. Baker)

rays (vs. 49–62), 90–101 total vertebrae (vs. 71–79), a more slender body, shorter head, predorsal, and upper jaw lengths, lesser body depth (Fig. 6), and in the color pattern of juveniles, ~50–103 mm SL (depth of slender dark stripe on midside at vertical from anal-fin origin up to about 1 mm, usually much less, as opposed to depth 2.5–3.3 mm in *P. leucotaenia*; Table 1; also compare Figs. 3 and 4). The adult color pattern, apparently, is also different from that of *P. leucotaenia* (Fig. 5), although appearing somewhat similar to that of the preadult (Figure 5, middle). Only one adult of *P. anguis* is known, and it is conceivable that the pattern is as variable as that of *P. leucotaenia.* Interestingly, adults of *P. leucotaenia* are known only from aquarium raised juveniles, and none have been seen in the wild or collected.

Etymology.—The specific name is from the Latin *anguis,* meaning "snake," refers to the elongate form of the species, and is here used as a noun in apposition.

Distribution and Historical Biogeography

Pholidichthys anguis is known only from the coastal waters of Northern Territory between 128°56′ and 136°15′E in depths of 19–70 m (Fig. 7). Its distribution is allopatric to that of *P. leucotaenia,* which is known from habitats close to or among corals, from the southern Philippines south to Flores, Indonesia, and east and south to New Caledonia. We question two other locality records. Specimens indicated as originating from Calatagan, Batangas [Province], Luzon, Philippines (CAS 32048, 76415), were provided by aquarium importers, as seems to be the case with a specimen purportedly from Batangas (BMNH 1982.8.3.4). A Batangas locality appears to be reasonable, but should be verified by better documented new collections. To explain the current distributions of these two species, we propose the following scenario:

Wilson & Allen (1987:64) concluded that "the pan-tropical Tethyan fauna and its successor, the modern Indo-West Pacific

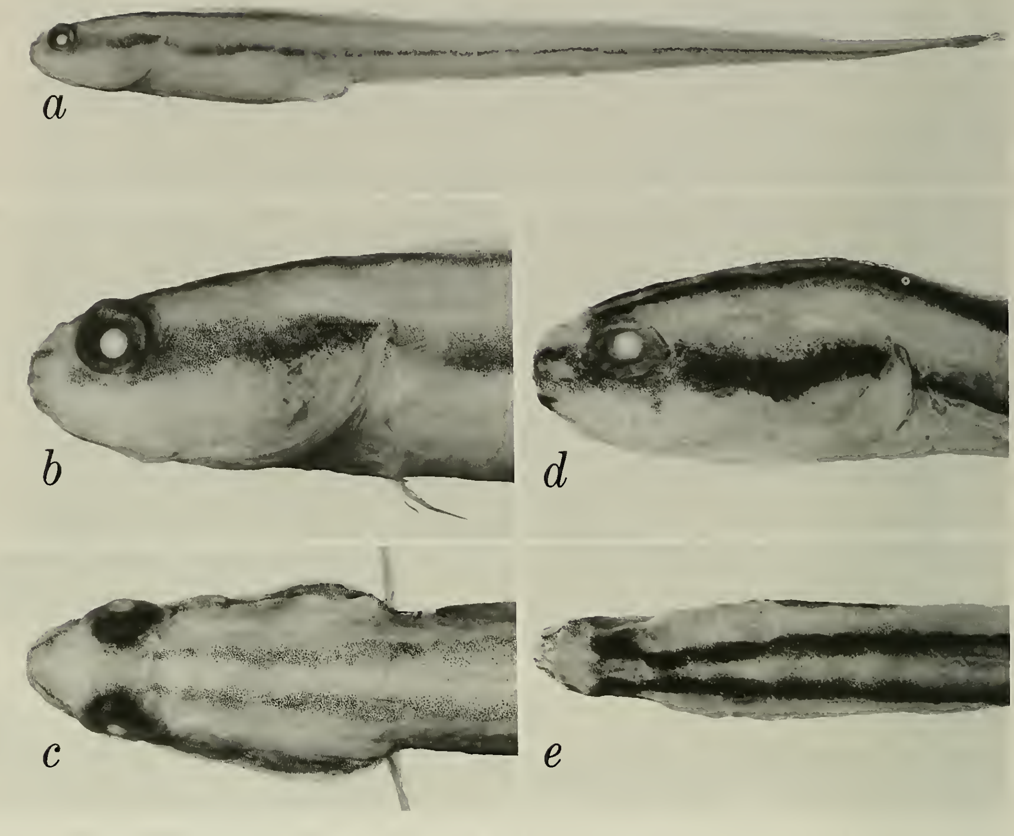

Fig. 3. *Pholidichthys anguis,* juveniles, Northern Territory, Australia. *a–c,* NTM 13039-001, 87.8 mm SL, N of Melville Island, Arafura Sea, dusky markings relatively typical, *c* shows dorsal surface of head and anteriormost portion of body; *d–e,* NTM S.13339-002, ca. 85, mm SL, Joseph Bonaparte Gulf, dusky markings unusually intense, *e* shows dorsal surface of head and anteriormost portion of body. (Photographs by T. B. Griswold)

fauna, have dominated the northern coast of Australia since the beginning of the Tertiary [ca. 65 m.y.a.].'' We believe their conclusion reasonable and hypothesize that the distribution of the common ancestor of the two species of *Pholidichthys* originated as part of the Tethyan fauna and occupied an area that excluded Australia-New Guinea. The ancestral distribution was possibly limited to the coastal areas of southeastern Asia (Malaya, Indonesia, Philippines) until, perhaps, as recently as mid-Miocene (ca. 16 m.y.a.), when southeast Asia and northern Australia-New Guinea were still separated by an expanse of deep, open sea. This expanse of sea acted as a barrier to dispersal between the two areas, particularly for shallow-dwelling marine organisms such as *Pholidichthys,* which lacks a planktonic stage (Trnski et al. 1989, Wirtz 1991). After Australia-New Guinea collided with the islands (Banda Arc) off southeast Asia (ca. 15 m.y.a.; Audley-Charles 1981, 1987, Burrett et al. 1991), the spacing of existing and newly formed islands may have permitted shallow-dwelling organisms to disperse between the colliding entities. If so, the common ancestor of the two extant *Pholidichthys* species was then able to disperse first to northern Australia-New Guinea and then into the New Britain-New Ireland-Solomon volcanic islands

Fig. 4. *Pholidichthys leucotaenia* juveniles (ca. 60 mm SL) photographed in aquarium (R. B. Hansen).

chain. This chain originated along a mid-Pacific plate ridge during late Eocene–early Oligocene and was gradually displaced westward to converge with New Guinea during the past half million years (Kroenke 1984, Yan & Kroenke 1993). After reaching the Solomons, *Pholidichthys* presumably dispersed south along the contiguous New Hebrides island chain (from which few fish collections have been made and *Pholidichthys* is as yet unreported) to close-by New Caledonia, and presumably

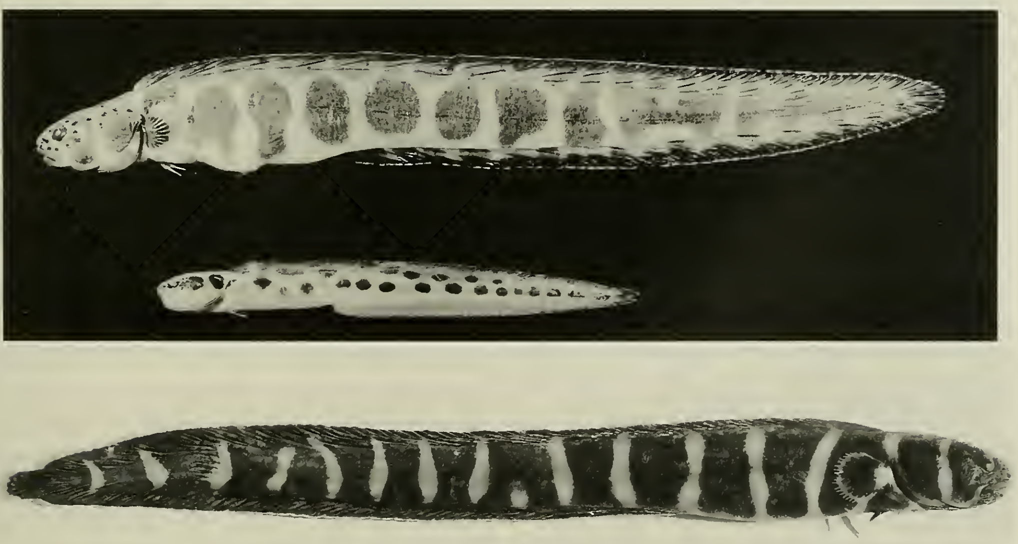

Fig. 5. *Pholidichthys leucotaenia,* aquarium specimens. Upper, adult, 205 mm SL, and middle, preadult, 108 mm, purportedly originating from Philippines (from Springer & Freihofer 1976: fig. 23); bottom, ZMUC P.75457, adult, ca. 175 mm SL, obtained from dealer in Singapore (G. Brovad, photographer).

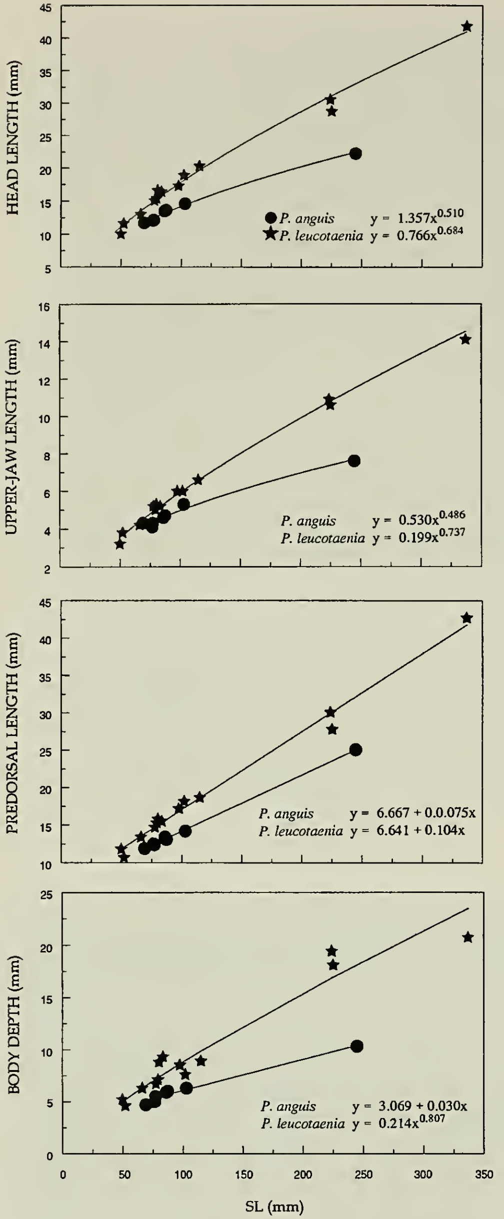

Fig. 6. Scatter plots, best-fit curves, and regression formulae for certain mensurable characters in *Pholidichthys* species based on data listed in Table 1.

the Loyalty Islands, with which the New Hebrides is colliding.

The apparent absence of *Pholidichthys* from the Queensland coast and adjacent Great Barrier Reef, where one might expect it to occur, appears puzzling at first, but many marine forms appear to have been unable to reach these areas from New Guinea, and vice-versa (a few didactic examples: the blenniid fishes *Ecsenius namiyei, E. sellifer, E. taeniatus, E. trilineatus* all occur in easternmost New Guinea, but are absent from the GBR; *E. mandibularis, E. australianus, E. stictus* all occur at the northern Queensland end of the GBR, but are absent from New Guinea—Springer (1988)). Coral reefs extend around the southeast tip of New Guinea and continue westward along its southern coast to about Port Moresby on the eastern side of the Gulf of Papua. The distribution of *P. leucotaenia* (Fig. 7) follows this reefal distribution. A large number of rivers drain into the western Gulf of Papua, which decreases salinity and increases turbidity in this portion of the Gulf, thus, creating a barrier to westward dispersal of many marine forms that have reached the eastern portion of the Gulf. The most apparent (shortest) dispersal route to the Great Barrier Reef from New Guinea would be down the islands and reefs that extend north from the Cape York Peninsula. This route would be blocked to the north, however, by the riverine barrier in the western portion of the Gulf of Papua, which we believe explains the absence of *Pholidichthys* and many other apparently stenohaline forms from the Great Barrier Reef and Queensland. *Pholidichthys* is present in the western Gulf of Carpenteria, where small coral reefs are also present, but not in the eastern Gulf, where no reefs are present. Heavy river drainage and sediment deposition in the eastern Gulf of Carpentaria probably also prevents the eastward dispersal of reef obligates, such as *Pholidichthys,* around the coast of the Gulf of Carpentaria to eastern Queensland and the Great Barrier Reef (Wells 1957:pl. 9, charts the world distribution of coral reefs).

The possibility of *Pholidichthys*' reaching Australia across the Arafura and Timor seas by dispersing along the southwestern coast of New Guinea and/or southeastern Indonesian island chain (Lesser Sunda to

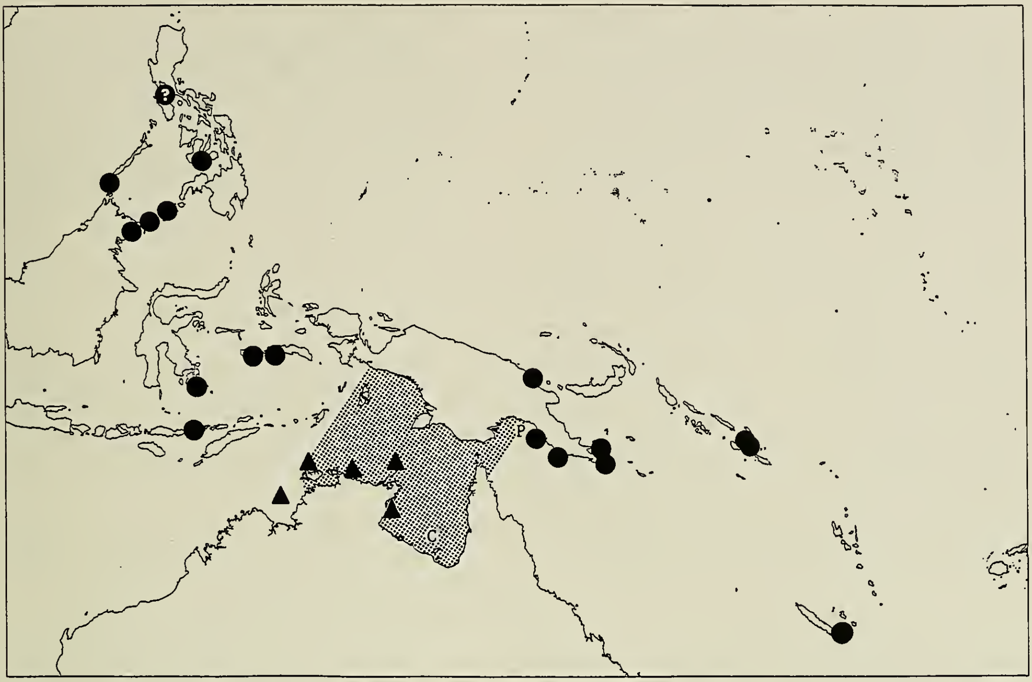

Fig. 7. Distribution of the species of *Pholidichthys.* Solid dots—*P. leucotaenia*; triangles—*P. anguis*; C = Gulf of Carpentaria; P = Gulf of Papua; shaded area represents emergent land joining northern Australia and New Guinea during most recent glacial sea-level low, ca. 18,000 B.P. (other emergent land areas not shown).

Aru islands) would also present problems under present-day land-sea distributions. The southwestern coast of New Guinea bears numerous rivers draining into the Arafura sea and, consequently, the obligate coral-reef stepping stones are absent in the area. The present-day, relatively wide, coral-reefless expanse of the Timor and Arafura seas and the deep ocean paralleling and separating the southeastern islands from Australia are barrier enough to prevent the dispersal of forms such as *Pholidichthys.* Similarly, the barrier maintains the present-day allopatry of the two *Pholidichthys* species.

During periods of Pleistocene glaciation (latest about 18,000 B.P.), the seaway passage (Torres Strait) between central Northern Territory and southern New Guinea was closed by a broad landbridge that extended between Northern Territory and much of southern New Guinea (Myers 1989:fig. 8, Springer & Williams 1990:fig. 7). The closure of the passage probably would not have altered river flow into the western Gulf of Papua, but the emergent land would have eliminated ancestral *Pholidichthys* in the region from the Gulf of Carpentaria to somewhat west of Melville Island, ca. 130°E. The present occurrence of *Pholidichthys* (*P. anguis*) in this relatively recently re-inundated area is the result of recent dispersal into Australian coastal habitats to the west. (Springer & Williams 1994: 128, attribute east-west differences in the morphology of the blenniid *Istiblennius meleagris,* which is restricted to the northern coast of Australia, to the barrier created by formerly emergent land in the Gulf of Carpetaria-Melville Island region). We suggest that reef habitats formed along the western side of the Pleistocene landbridge that permitted dispersal of the ancestral species of *Pholidichthys* to northwestern Australia. As sea level rose and created modern conditions, the Australian and southeast

Asian populations became isolated and diverged. We are uncertain how, or if it is necessary, to accommodate for river runoff from the emergent west side of the landbridge. Changes in the positions of river mouths on the west side would have been more radical than changes on the east side because of the greater area affected. Although we have chosen to base the final scene of our scenario on Pleistocene events of the past 18,000 years, a similar scenario could be developed for any of the earlier interglacials of the Quarternary. If only a small sample of the common ancestor reached Northern Territory and became isolated, rapid evolution (divergence) might be expected, as well as the current, apparently highly limited distribution of *P. anguis.*

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A new species of *Eleutherodactylus* from Honduras related to *Eleutherodactylus bransfordii* (Anura: Leptodactylidae)

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Abstract.—A new species of *Eleutherodactylus* is described from northeastern Honduras. It is a member of the *E. rhodopis* group, differing from its closest congeners *E. stejnegerianus* of Pacific slope of Costa Rica and western Panama, by having definite toe webbing and a larger thenar tubercle, and *E. bransfordii* of Nicaragua to Panama, in lacking nuptial thumb pads in males and having a smaller thenar tubercle.

A few years ago, the senior author (Savage 1981) referred a single specimen (LACM 45200) of small frog from northeastern Honduras to *Eleutherodactylus bransfordii* (sensu Savage & Emerson 1970) of Nicaragua, Costa Rica and Panama. Subsequently, in 1986 and 1992–1994, examples of frogs of this general morph were collected by L. D. Wilson, J. R. McCranie and M. Espinal. Examination of these animals, plus a recently collected specimen in the Florida Museum of Natural History, showed several differences from typical *E. bransfordii* and led us to re-evaluate the placement of the LACM specimen as well. Further study convinced us that the Honduran material was conspecific but represented an undescribed species distinct from *E. bransfordii.*

Methods

All measurements are in millimeters and were made with dial calipers with the aid of a dissecting microscope. Abbreviations used are: SVL (standard length), HL (head length; tip of snout to angle of jaw), HW (head width; greatest width), SL (snout length; anterior border of eye to nostril), TL (tibia length; one end of tibia to other, including covering tissues), FL (foot length; distance from posteriormost portion of inner metatarsal tubercle to tip of fourth toe), TPL (tympanum length), EL (eye length), DW (third finger disc width). Snout outline and profile terminology follows Heyer et al. (1990), finger and toe disc, disc pad and subarticular tubercle shape terminology follows Savage (1987), and color codes used for some of the color notes in life follow Smithe (1975). Museum acronyms follow Leviton et al. (1985).

Eleutherodactylus lauraster, new species
Figs. 1–2

Holotype.—USNM 344826, adult male, from above the Quebrada El Piñol (15°07′N, 86°43′W), Parque Nacional La Muralla, Departamento de Olancho, Honduras, elevation 1200 m, collected 21 July 1993 by Mario Espinal and James R. McCranie. Original field number LDW 9997.

Paratypes.—Honduras: Olancho: USNM 344827–28, adult females, from the type locality, 1180–1200 m; ROM 18095–96, adult males, 18097–98, adult females, from near the Río Seco, in the Sierra de Agalta, NNW of Catacamas, 990–1000 m; UF

Fig. 1. Adult female paratype of *Eleutherodactylus lauraster* (USNM 344830), SVL 19.7 mm.

90217, adult female, from the Sierra de Agalta, ca. 9 km N Santa María del Real, 1200 m; LACM 45200, adult female, from ca. 0.5 km SE San José del Río Tinto, 330 m; Gracias A Dios: USNM 344829–30, adult females, from the confluence of Quebrada Waskista and Río Wampú, 85 m.

Diagnosis.—A small species belonging to the *Eleutherodactylus rhodopis* group (Savage 1987), characterized by tiny males and slightly larger females that is distinguished from its close allies, *Eleutherodactylus bransfordii* and *E. stejnegerianus* by having finger I definitely shorter than II and definite basal webbing between the toes. From the former, it further differs in having the thenar tubercle definitely smaller than the palmar tubercle and in lacking nuptial thumb pads in adult males (thenar and palmar tubercles about the same size and nuptial pads present in adult male *E. bransfordii*). Although *E. lauraster* and *E. stejnegerianus* lack male nuptial pads, the latter species has even smaller thenar tubercles than the Honduran form, being equal to or smaller than the basal subarticular tubercle on fingers II–III.

Summary of characteristics.—Snout nearly rounded to rounded in dorsal aspect, rounded in profile; top of head flat; canthus rounded, distinct; loreal region concave; nostrils directed laterally, situated at a point about two-thirds distance between anterior border of eye and tip of snout; supratympanic fold distinct, narrowly obscuring upper edge of tympanum, tympanum otherwise prominent; narrow discs on fingers III–IV, with slightly pointed disc covers and swollen to cuspidate pads; no nuptial thumb pads; relative length of fingers I < II < IV < III; heels smooth to rugose, lacking tubercles; subarticular tubercles of hands and feet ovoid, projecting, usually obtuse in profile; six accessory palmar and numerous plantar tubercles; thenar tubercle definitely smaller than palmar tubercle, also somewhat narrower and raised, larger than basal subarticular tubercles under fingers II–III; palmar tubercle ovoid; discs on all toes, those on toes III–IV with slightly pointed

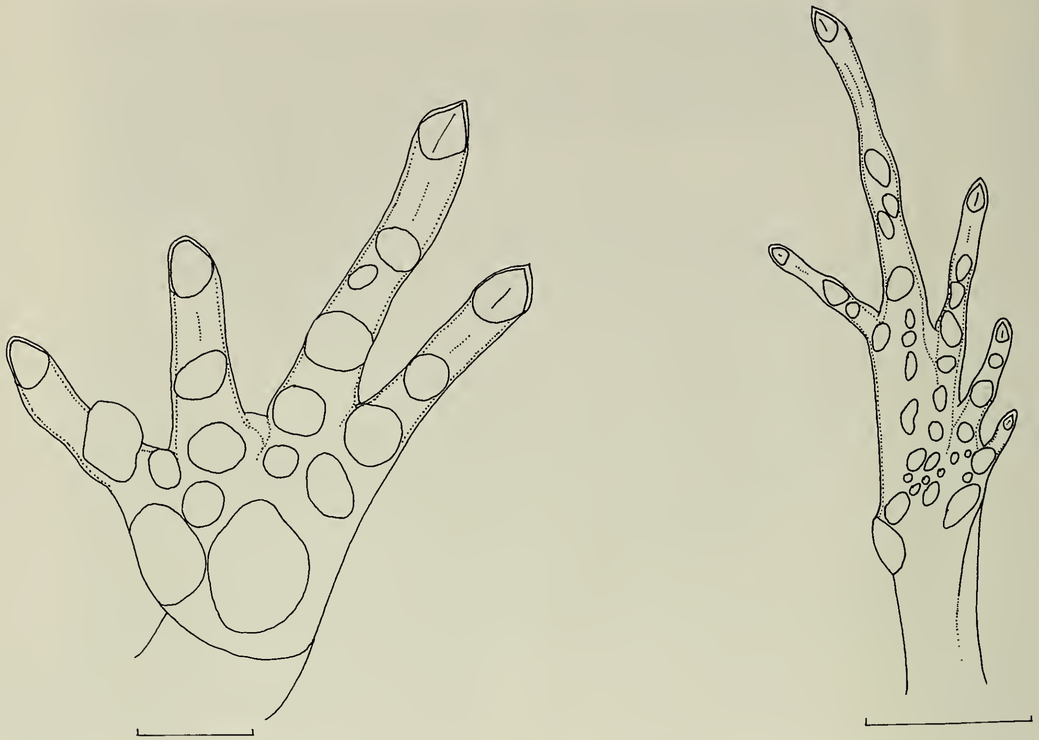

Fig. 2. *Eleutherodactylus lauraster.* Left: hand of adult female paratype (USNM 344828), scale = 1 mm; right: foot of adult male holotype (USNM 344826), scale = 3 mm.

disc covers and swollen to cuspidate pads; inner metatarsal tubercle elliptical in outline, projecting in profile; outer metatarsal tubercle rounded, projecting; relative length of toes I < II < V < III < IV; basal webbing between toes; inner tarsal fold weak; skin on dorsal surface of body smooth to tuberculate (tubercles and/or rugosity usually more obvious posteriorly), that of upper eyelids rugose and tuberculate, that of belly and ventral surfaces of thighs coarsely areolate; a distinct small inguinal gland present; prevomerine tooth patches on elevated, somewhat triangular ridges between and behind choanae, each ridge separated by distance equal to or greater than size of either patch; vocal slits and sac absent.

Coloration in life.—An adult female, USNM 344827, was recorded as follows: dorsal surfaces of head and body Dark Drab (color 119B) with Hair Brown (119A) markings: dorsal surfaces of limbs Army Brown (219B) with Sepia (219) crossbands; Sepia stripe extending from nostrils to eyes and continuing posteriorly from eyes to above point of insertion of forelimbs; posterior surfaces of thighs mottled pale brown and yellowish cream; ventral surfaces of head and body pale yellow with minute white flecks; ventral surfaces of thighs and groin pale yellow; iris copper with dark reticulations. Another adult female (USNM 344828) was recorded as follows: dorsal surfaces of head and body Cinnamon-Drab (219C) with Sepia (219) markings; dorsal surfaces of limbs Vinaceous Pink (221C) with Sepia crossbands; iris gold with indistinct gold reticulations; rest same as that recorded for USNM 344827. A third adult female (USNM 344830) was recorded as follows: dorsal surfaces of head and body Mahogany Red (132B) with a slightly darker middorsal hourglass-shaped figure and interocular bar; dorsal surfaces of limbs slightly paler than dorsum with dark Mahogany Red crossbands; posterior surfaces of thighs pale brown; all ventral surfaces and groin region flesh-colored; iris pale gold with black reticulations.

Color in preservative.—Dorsal surface of body pale to dark brown with small, scattered darker brown spots or blotches present dorsally and dorsolaterally in all but darkest specimens; dorsal surfaces of limbs pale to medium-brown with darker brown crossbands; a distinct, dark brown facial and supratympanic stripe usually present; ventral surfaces of head and body pale cream-colored, with numerous, although usually widely separated, brown punctations present on chin and throat, a few brown punctations may also be present on chest region and laterally on belly; ventral surfaces of thighs pale cream-colored, lightly to heavily punctated with brown; posterior surfaces of thighs brown, although less densely punctated pale areas usually present.

Measurements and proportions of holotype.—SVL 17.9; HL 7.9; HL/SVL 0.441; HW 5.8; HW/SVL 0.324; SL 1.7; EL 2.2; SL/EL 0.773; TL 10.1; TL/SVL 0.564; FL 9.1; FL/SVL 0.508; TPL 2.0; TPL/EL 0.909; DW 0.2; DW/TPL 0.100.

Measurements and proportions of paratypes.—(Females following and separated from males by a comma; means in parentheses) SVL 16.8–17.2 (17.0), 14.6–22.3 (18.5); HL/SVL 0.413–0.417 (0.415), 0.383–0.438 (0.411); HW/SVL 0.351–0.355 (0.353), 0.312–0.350 (0.331); SL/EL 0.720–0.870 (0.795), 0.650–0.909 (0.780); TL/SVL 0.558–0.583 (0.571), 0.503–0.578 (0.541); FL/SVL 0.517–0.530 (0.524), 0.431–0.544 (0.488); TPL/EL 0.800–0.826 (0.813), 0.500–0.682 (0.591); DW/TPL 0.100–0.105 (0.103), 0.091–0.188 (0.140).

Etymology.—The specific name proposed is a noun in apposition to honor our colleague Larry David Wilson. It derives from the Latin *laurus* = laurel, the source of the name Lawrence, and the diminutive suffix - *aster,* in allusion to his first name and his stature as herpetologist laureate for Honduras.

Natural history notes.—*Eleutherodactylus lauraster* is known from between 85–1200 m in the Lowland Moist Forest and Premontane Wet Forest formations of Holdridge (1967). Specimens were collected on the forest floor, while active both during the day and at night. Two adult females with ovarian eggs (ROM 18098, USNM 344830) were collected 12 August and 28 July, respectively.

Referred specimen.—Honduras: Gracias A. Dios: USNM 344831, juvenile, from the confluence of Quebrada Waskista and Río Wampú, 85 m.

Discussion

Eleutherodactylus lauraster is assigned to the *Eleutherodactylus rhodopis* group (*sensu* Savage 1987). The characterization of the group as published by Savage (1987) now requires some modification. Firstly, a lapsus led to a statement implying that the members of this group have "an inner tarsal tubercle or two" (Savage 1987:49). The correct verbage is "an inner tarsal tubercle or two may be present," as this feature only occurs in *Eleutherodactylus rhodopis.* Secondly, a weak inner tarsal fold is found in *E. bransfordii, E. lauraster, E. podiciferus* and *E. stejnegerianus.* Finally, the absence of toe webbing may no longer be used to define the group, since *E. lauraster* has basal webs on the toes and weak webs are sometimes present in some lower Central American forms. The remaining characters used by Savage (1987) to define the group remain valid, with the exception of the *mandibularis* muscle condition (see below).

Lynch (1993) concluded that the *depressor mandibularis* muscle condition found in this group was misinterpreted by Savage (1987). Lynch (1993) generally rejected the systematic significance of differences in the characters of the *depressor mandibularis* utilized by Savage (1987) as modified from Starrett (1968). This is not the place to respond to Lynch's arguments, which will be addressed elsewhere. However, he did confirm that examples of the five species of the *E. rhodopis* group that he examined share the DFSQdAT (as pointed out by Starrett, 1968, contra Savage 1987). This feature is unique among *Eleutherodactylus* belonging to the Middle American clade (sensu Lynch 1986) or "subgenus *Craugaster.*"

All other members of the *Craugaster* clade diagnosed by the synapomorphy of having only the *externus superficialis adductor mandibularis* (e) present, have dfsq, DFsqat, or DFSQAT conditions of the *adductor.* The jaw muscle formula for the *E. rhodopis* group is corrected to DFSQdAT + e and is diagnostic. Lynch (1993) reported this formula for *Eleutherodactylus bransfordii, E. hobartsmithi, E. mexicanus, E. pygmaeus,* and *E. rhodopis.* We add *E. lauraster, E. podiciferus,* and *E. stejnegerianus* to that list. We predict that the remaining species of the *E. rhodopis* group (*E. jota, E. saltator,* and *E. sartori*) also have the same jaw muscle configuration.

The status of populations placed in *Eleutherodactylus bransfordii* Cope (1886) by Savage & Emerson (1970) are in a state of flux. Miyamoto (1983) pointed out that in Costa Rica, Pacific slope samples differ significantly in allozyme features from Atlantic versant frogs and revived the name *Eleutherodactylus stejnegerianus* Cope (1893) for them. Morphological features have now been determined to distinguish between these forms as well (see diagnosis of *Eleutherodactylus lauraster* and the key below).

Eleutherodactylus bransfordii and *E. stejnegerianus* are essentially allopatric but overlap geographically at a few sites along low passes near the continental divide in northern Costa Rica. In addition, Miyamoto's (1983) allozyme evidence indicated that a third cryptic species occurred with *E. stejnegerianus* at some Costa Rican localities. The status of this form and its relations to the other recognized species continue under investigation.

Eleutherodactylus lauraster is somewhat intermediate in characters between *E. bransfordii* and *E. stejnegerianus* but differs from both in having a short thumb. It most closely resembles the latter species in having a reduced thenar tubercle and in lacking nuptial pads in adult males. However, neither of these features is conclusive evidence of close relationship. Because ongoing work on the karyology of this group by S. H. Chen gives promise of resolving the phylogeny of the cluster of *bransfordii*-like species, any conclusions based on the few morphological features separating the recognized forms remain premature.

The recognition of *Eleutherodacylus lauraster* brings the number of species referred to the *E. rhodopis* group to eleven. The following key may be used to identify the included taxa.

Key to the Frogs of the *Eleutherodactylus Rhodopis* Group

1a. No inner tarsal tubercles 2
1b. One or two distinct inner tarsal tubercles (Atlantic slope: San Luis Potosí, Mexico, to western Honduras; Pacific slope: Oaxaca, Mexico, to El Salvador) .... *E. rhodopis*
2a. A thenar and 1 palmar tubercle; nuptial pads and/or vocal slits present or not in adult males ... 3
2b. A thenar and 2 palmar tubercles that may be partially fused; no nuptial pads or vocal slits in adult males 9
3a. No inner tarsal fold; no vomerine teeth; no nuptial pads or vocal slits in adult males 4
3b. A definite inner tarsal fold; vomerine teeth present 5
4a. A row of tubercles along outer edge of tarsus (Central Mexico from Colima to Guerrero, and the state of Mexico) ... *E. hobartsmithi*
4b. No row of tubercles on outer edge of tarsus (Atlantic slope: tropical

Mexico; Pacific slope: Jalisco, Mexico, to Guatemala) .... *E. pygmaeus*

5a. No enlarged calcar on heel; no ulnar or outer tarsal folds 6

5b. An enlarged triangular calcar on heel; ulnar and outer tarsal folds present (western Panama) ... *E. jota*

6a. Heel smooth to granulate; tubercles on underside of hand projecting 7

6b. One to 3 enlarged heel tubercles; tubercles on undersides of hands low and rounded; no nuptial pads but vocal slits present in adult males (uplands of Costa Rica and western Panama) .....*E. podiciferus*

7a. Thenar and palmar tubercles about same size, larger than subarticular tubercles on fingers II–III; nuptial pads present but no vocal slits in adult males (Atlantic slope from Nicaragua to central Panama) ....*E. bransfordii*

7b. Thenar tubercle much smaller than palmar tubercle, no nuptial pads or vocal slits in adult males 8

8a. Definite basal toe webbing present; finger I definitely shorter than finger II; thenar tubercle larger than basal subarticular tubercle under finger III (Atlantic slope of eastern Honduras) ......*E. lauraster*

8b. No toe webbing or slight webs present basally only between toes II–IV; fingers I and II equal; thenar tubercle equal to basal subarticular tubercle under finger III (Pacific slope from Costa Rica to western Panama) ..*E. stejnegerianus*

9a. Inner metatarsal tubercle much larger than outer 10

9b. Metatarsal tubercles subequal in size (Pacific slope of Chiapas, Mexico) ....*E. sartori*

10a. Outer edge of tarsus with row of small tubercles (uplands of southern Mexico, west of Isthmus of Tehuantepec) .... *E. mexicanus*

10b. Outer edge of tarsus smooth (uplands of Guerrero and western Oaxaca, Mexico) ....*E. saltator*

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Hybrid wood warblers, *Dendroica striata* × *Dendroica castanea* (Aves: Fringillidae: Tribe Parulini) and the diagnostic predictability of avian hybrid phenotypes

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Abstract.—The plumage pattern and color and external morphology of hybrid wood warblers (*Dendroica striata* × *Dendroica castanea*) are described. This hybrid combination constitutes the only known case of hybridization between two broadly sympatric species of the genus *Dendroica* (Fringillidae; Tribe Parulini), that is represented by both male and female specimens in definitive alternate plumage. The plumage of the hybrids exhibited a mosaic of character states that varied in the degree of intermediacy between those of the parental species. External measurements of the hybrids fell within the cumulative ranges of characters of the postulated parental species. I hypothesize that the diagnostic predictability of hybrid phenotypes decreases as an inverse function of genetic relatedness of the hybridizing species.

Plumage color patterns are remarkably diverse among the 24 species of *Dendroica* (Aves: Fringillidae; Tribe Parulini) of North America and the Caribbean (taxonomy of Sibley & Monroe 1990), in contrast to the similarity of their body plans and trophic appendages. Several pairs of species thought to have recently diverged (Mengel 1964, Mayr & Short 1970, Bermingham et al. 1992) exhibit striking differences in male definitive plumage, suggesting that plumage pattern may evolve rapidly in response to sexual selection. Our understanding of the inheritance patterns of plumage color in *Dendroica* has been limited to evidence gleaned from hybridization at contact zones between parapatric taxa (e.g., *Dendroica occidentalis* × *Dendroica townsendi*; see Rohwer 1994) and rare instances of intergeneric hybridization (e.g., Parkes 1978, Graves 1993a).

Brodkorb's (1934) description of the hybrid, *Dendroica striata* (Blackpoll Warbler) × *Dendroica castanea* (Bay-breasted Warbler), was the first report of hybridization between broadly sympatric species of *Dendroica.* This specimen (University of Michigan Museum of Zoology [UMMZ] No. 53692) represents one of the few known intrageneric *Dendroica* hybrids represented by a male in definitive alternate plumage. Because male *D. striata* and *D. castanea* differ dramatically in plumage pattern and color, this specimen assumes unusual significance for the investigation of phenotypic inheritance in avian hybrids.

Recently, the existence of a female hybrid (UMMZ 216628) and an additional male hybrid (San Bernardino County Museum, uncataloged) identified as *D. striata* × *D. castanea,* was brought to my attention, respectively, by Janet Hinshaw and Kenneth Parkes. Here I perform a hybrid diagnosis on all three specimens based on plumage color and pattern and external morphology, following Graves (1990).

Materials and Methods

The male specimen reported by Brodkorb (1934) was collected on 19 May 1920,

Fig. 1. Lateral view (from top) of males: *Dendroica castanea*; hybrids, *D. striata* × *D. castanea* (UMMZ 53692 and SBCM); and *D. striata* (bottom).

by Norman A. Wood at Warren Dunes, Berrien County, Michigan (Figs. 1–4). The female specimen was collected on 25 May 1970 at Long Point, Ontario, by Joseph G. Strauch (Figs. 5–7). The second male specimen was collected by Lawrence Sansone, III, along the Rio Grande south of Brownsville, Cameron County, Texas, on 9 June 1969. For the purposes of the hybrid diagnosis, I considered all wood warblers that regularly breed north of the Mexican border as potential parental species ($n = 53$).

The first two specimens have broadly tapered rectrices indicating that they were adults in their second year or older (ASY in banding terminology) (Pyle et al. 1987). Plumage, especially the rectrices, of the Texas specimen is moderately worn. Thus, I am uncertain of the bird's age (SY or ASY). Because the specimens appeared to be in definitive plumage, I compared them to large series of definitive-plumaged specimens in the collections of the National Museum of Natural History, Smithsonian Institution.

For comparative purposes I measured the size of three species: *D. striata, D. castanea,* and *D. pinus.* Data for *D. pinus* were omitted from Table 1, after analyses showed that it was not involved in the parentage of the hybrids. Measurements of wing chord, tail length (from point of insertion of central rectrices to tip of longest rectrix), tarsus length, and bill length (from anterior edge of nostril), were made with digital calipers to the nearest 0.1 mm.

I evaluated the color of selected areas of plumage with a Color Mate Colorimeter (Milton Roy), employing a 9.4 mm aperture. The data in Table 2 were compiled from the averages of three independent measurements (specimen removed from ap-

Fig. 2. Dorsal view (from top) of males: *Dendroica castanea*; hybrids, *D. striata* × *D. castanea* (UMMZ 53692 and SBCM), and *D. striata* (bottom).

erture between trials) per specimen for each plumage area.

Colorimetric characters were described in terms of opponent-color coordinates (*L, a, b*) (Hunter & Harold 1987). This system is based on the hypothesis that signals from the cone receptors in the human eye are coded by the brain as light-dark (*L*), red-green (*a*), and yellow-blue (*b*). The rationale is that a color cannot be red and green or yellow and blue at the same time. Therefore, "redness" and "greenness" can be expressed as a single value *a,* which is positive if the color is red and negative if the color is green. Likewise, "yellowness" or "blueness" is expressed by *b* for yellows and $-b$ for blues. The third coordinate *L,* ranging from 0 to 100, describes the "lightness" of color; low values are dark, high values are light. In other words, the more light is reflected from the plumage the higher the *L* value will be.

Difference among character means of presumed parental species were evaluated with two sample t-tests (Wilkinson 1989). Significance of probability values was adjusted for the number of simultaneous tests of morphology (Table 1; $P = 0.05/8 = 0.006$) and plumage color (Table 2; $P = 0.05/12 = 0.004$).

Hybrid diagnoses followed a two-step procedure. First, the presumed parental species of each hybrid were hypothesized through the visual comparison of plumage pattern and color. These hypotheses were then examined with quantitative analyses of

Fig. 3. Ventral view (from top) of males: *Dendroica castanea*; hybrids, *D. striata* × *D. castanea* (UMMZ 53692 and SBCM); and *D. striata* (bottom).

colorimetric and morphometric data. Concordance of results was interpreted as strong support for the presumed parentage of the hybrid (Graves 1990, 1993a; Graves & Zusi 1990).

I used principal components analysis (PCA) on $\log_{10}$ transformed variables to reduce the dimensionality of data and to facilitate the analysis of morphology in two dimensions. Unrotated principal components were extracted from covariance matrices (Wilkinson 1989). Because the external measurements of *D. striata* and *D. castanea* overlap (Table 1), both species and sexes were pooled for PCA. Separate PCA for each sex were performed on $\log_{10}$ transformed colorimetric variables of back plumage (Tables 3, 4). Bivariate plots of factor scores from PCA analyses that included both back and crown color were less informative because significant differences in crown color of the parental species of both sexes polarized the distribution of factor scores.

Results

Plumage Characters

Males.—I concur with Brodkorb's (1934) identification but his brief, one-paragraph description of the Michigan specimen did not address alternate hypotheses or the external morphology of the parental species (p. 243):

> "It is similar to *D. striata,* but differs from the latter species in the following particulars: malar region and chin black, with only the anterior half of the interramal region and a spot one or two millimeters in length at the end of the rami

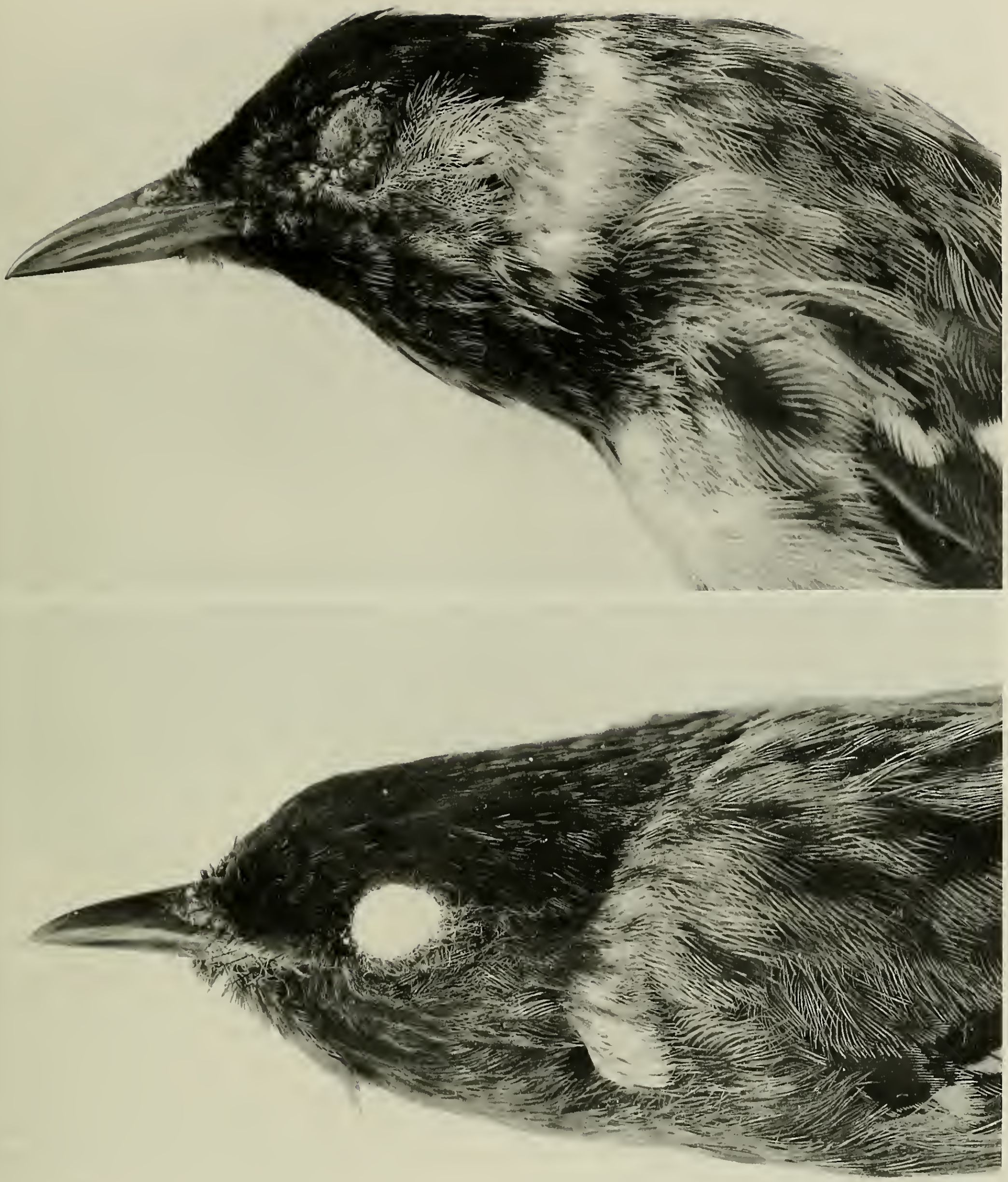

Fig. 4. Lateral view of male hybrids, *Dendroica striata* × *D. castanea:* UMMZ 53692 (top) and SBCM (bottom).

white; black streaks on the sides of throat coalescent, leaving a white line in the center of the throat only one to two mm. broad; chin, malar region, sides of neck, sides and flanks more or less marked with bay; suborbital, auricular, and postauricular regions, as well as breast, pale cream buff; the abdomen, sides, flanks, and under tail-coverts also somewhat suffused with this color."

Fig. 5. Lateral view of female *Dendroica castanea* (top), hybrid, *D. striata* × *D. castanea* (UMMZ 216628), and *D. striata* (bottom).

Hybrid wood warblers can be notoriously difficult to identify (Short & Robbins 1967, Graves 1988). In this case, however, identification was expedited by the distinctive characters of the Michigan specimen: (1) black crown (Fig. 1); and (2) mixture of black and chestnut in the malar region (Fig. 2). The black crown of the hybrid, which extends ventrally to the lower margin of the eye, is shared with *Dendroica striata* and the morphologically distinctive *Setophaga ruticilla.* The latter species can be conclusively excluded as a parental species for several reasons, most notably because the rectrices and remiges of the hybrid lack orange or yellow spots, even as traces. Therefore, by default, *D. striata* was one of the parental species. Determination of the other parental species was also relatively simple. Chestnut and black feathers on upper throat and malar regions of the hybrid could have been contributed only by *Dendroica castanea.*

Although the plumage of the Texas specimen differs in detail from the Michigan male, its diagnostic characters are the same (Appendix 1). In sum, plumage characters of these male hybrids can only be accounted for by two species, *D. striata* and *D. castanea.* Other pairs of warbler species lack the range of pattern elements and plumage colors exhibited by the hybrids.

Female.—Plumage characters of the hybrid that were critical to its identification can be categorized as color or pattern elements, although these are not mutually ex-

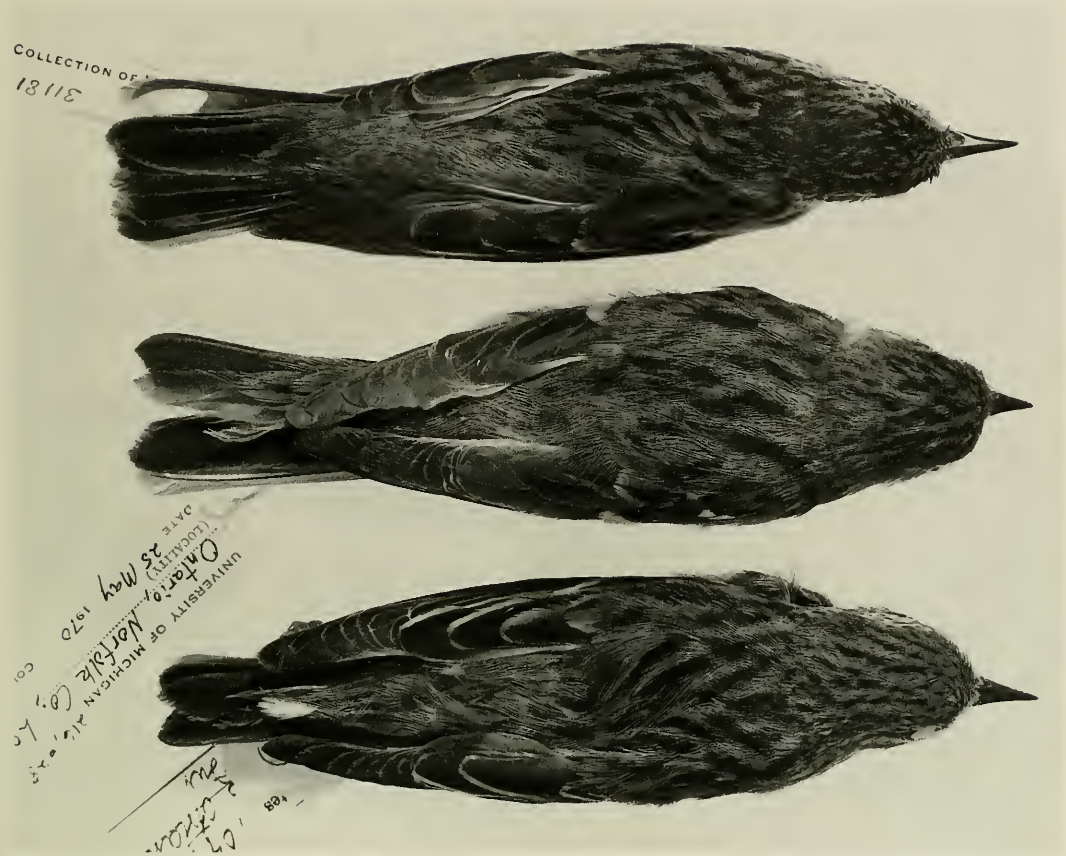

Fig. 6. Dorsal view of female *Dendroica castanea* (top), hybrid, *D. striata* × *D. castanea* (UMMZ 216628), and *D. striata* (bottom).

clusive. Prominent pattern elements include: (1) streaked crown, mantle, and scapulars; (2) poorly defined superciliary; (3) a well-defined neck patch; (4) muted streaks on the flanks and sides of breast; and (5) contrasting tips of the middle and greater wing coverts that form wing bars. Important color elements include: (1) olive crown and olive-gray mantle with blackish-brown shaft streaks; (2) buffy neck patch; (3) buff throat, upper breast, and flanks; and (4) pale chestnut markings on flanks.

Of the $\binom{53}{2}$ = 1378 possible pairwise combinations of wood warbler species in the geographic species pool, the number that could have produced each of the aforementioned hybrid characters was substantial. For example, 1027 pairs of species could have produced a hybrid with contrasting wing bars because one or both of the species possessed them. Of the many possible color and pattern characters present in the hybrid, only one—the buffy post-auricular neck patch—is restricted to a single species. Although females of several other species of *Dendroica* have a tendency to show a faint post-auricular patch in basic plumage, only *D. castanea* has a well-developed buff patch in definitive alternate plumage. Other characters of the hybrid, which are shared with *D. castanea* and two other species, are a buff throat and breast (shared with *Helmitheros vermivorus*) and chestnut markings on the flanks (also shared with *Dendroica pensylvanica*). Hybridization between the latter two species,

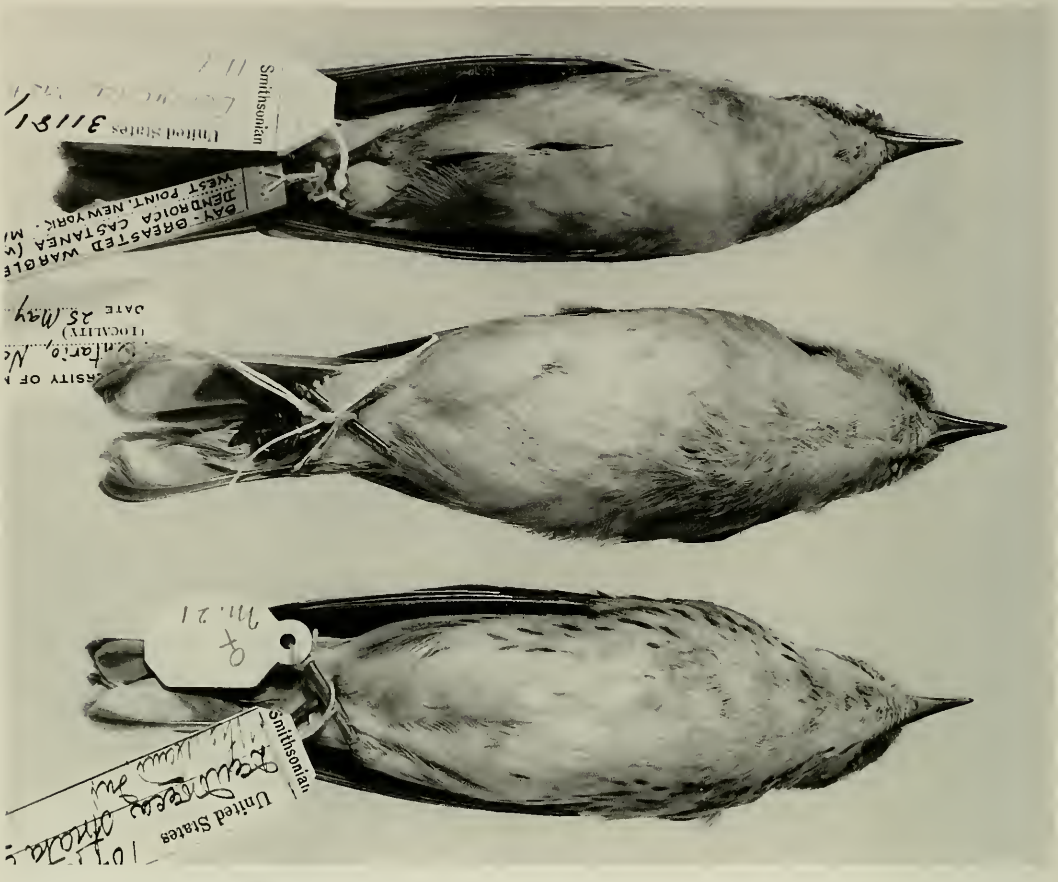

Fig. 7. Ventral view of female *Dendroica castanea* (top), hybrid, *D. striata* × *D. castanea* (UMMZ 216628), and *D. striata* (bottom).

Table 1.—Ranges and means (± one standard deviation) of measurements of definitive-plumaged males and females collected in May and June of *Dendroica castanea, D. striata,* and their putative hybrids (University of Michigan Museum of Zoology, No. 53692, ♂; No. 216628, ♀; San Bernardino County Museum (SBCM), ♂). An asterisk indicates that character means of *D. striata* and *D. castanea* differed at $P = 0.006$ (= 0.05/8).

	striata		*castanea*		Hybrids		
					UMMZ		SBCM
Character	♂♂ (n = 12)	♀♀ (n = 12)	♂♂ (n = 12)	♀♀ (n = 12)	♂	♀	♂
Wing chord	71.0 − 76.8 73.9 ± 1.9	68.6 − 70.7 70.7 ± 1.4	71.0 − 75.9 73.2 ± 1.5	68.0 − 72.1 70.6 ± 1.1	71.3	68.8	70.1
Tail	47.6 − 55.2 51.3 ± 2.0	47.4 − 50.9 *49.8 ± 1.0	51.0 − 55.6 52.5 ± 1.4	48.7 − 52.3 51.0 ± 1.0	50.3	49.5	50.1
Tarsus	18.1 − 19.9 *18.9 ± 0.6	17.5 − 18.7 18.1 ± 0.4	16.5 − 19.1 17.8 ± 0.8	16.8 − 18.2 17.6 ± 0.5	17.5	18.5	18.2
Bill	7.7 − 8.8 8.1 ± 0.3	7.6 − 8.5 8.0 ± 0.3	7.3 − 8.7 8.1 ± 0.4	7.4 − 8.4 7.9 ± 0.3	7.7	7.7	8.3

Table 2.—Spectrophotometric measurements of back and crown color of male and female *Dendroica striata, D. castanea,* and their hybrids. Asterisks indicate character means of *D. striata* and *D. castanea* are significantly different at $P = 0.004$ (= 0.05/12).

	Males		Hybrid	
	striata (n = 12)	*castanea* (n = 12)	(UMMZ)	(SBCM)
Back				
Lightness (L)	26.5 − 32.9 29.2 ± 2.1	28.8 − 37.0 31.3 ± 2.5	29.4	33.6
Red (a)	0.3 − 1.2 0.8 ± 0.3	0.8 − 3.0 1.4 ± 0.6	1.5	1.4
Yellow (b)	4.7 − 11.1 7.2 ± 1.8	7.1 − 13.1 8.8 ± 1.6	7.9	8.5
Crown				
Lightness (L)	13.0 − 16.9 *14.4 ± 1.4	20.0 − 25.0 22.5 ± 1.6	16.9	14.4
Red (a)	0.2 − 0.9 *0.6 ± 0.2	8.7 − 14.5 12.2 ± 1.8	1.5	2.4
Yellow (b)	0.2 − 2.1 *1.1 ± 0.5	9.5 − 16.6 13.6 ± 2.0	2.4	4.5

	Females		
	striata (n = 12)	*castanea* (n = 12)	Hybrid (UMMZ)
Back			
Lightness (L)	28.5 − 33.7 31.6 ± 1.7	29.9 − 34.3 32.6 ± 1.3	33.8
Red (a)	0.8 − 2.6 1.6 ± 0.6	0.7 − 1.5 1.2 ± 0.2	1.4
Yellow (b)	9.1 − 14.8 *12.4 ± 1.9	7.5 − 11.6 9.1 ± 1.1	9.0
Crown			
Lightness (L)	24.5 − 34.1 28.9 ± 3.1	24.3 − 32.4 28.0 ± 2.8	29.8
Red (a)	0.5 − 2.5 *1.4 ± 0.6	1.0 − 12.9 8.0 ± 3.8	1.4
Yellow (b)	10.0 − 18.3 13.5 ± 2.3	11.8 − 18.1 14.7 ± 2.0	12.6

Table 3.—Factor loadings for the first two principal components from an analysis of back color in male *Dendroica striata, D. castanea,* and the male hybrids (UMMZ 53692 and SBCM).

Variable	Principal component axes	
	I	II
Lightness (L)	0.007	0.021
Red (a)	0.193	−0.025
Yellow (b)	0.076	0.062
Variance explained	88.4%	10.0%

Table 4.—Factor loadings for the first two principal components from an analysis of back color in female *Dendroica striata, D. castanea,* and the female hybrid (UMMZ 216628).

Variable	Principal component axes	
	I	II
Lightness (L)	0.004	0.002
Red (a)	0.137	0.026
Yellow (b)	0.049	−0.073
Percent variance explained	76.4%	21.9%

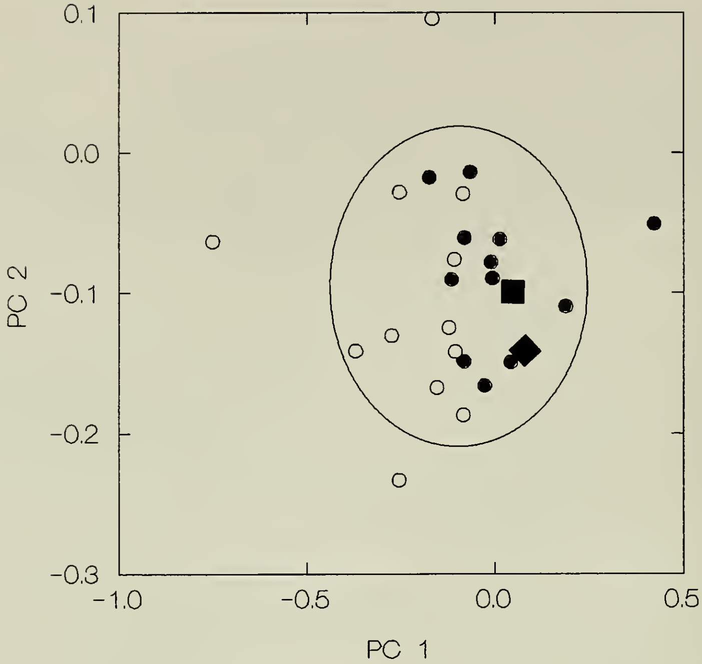

Fig. 8. Bivariate plots of factor scores from a principal components analysis of back color (see Table 3) for male *Dendroica striata* (empty circles), *D. castanea* (filled circles), and *D. striata* × *D. castanea* hybrids (Michigan hybrid = diamond; Texas hybrid = square). The curved line in this and other plots represents the 95% confidence ellipse.

however, could not have produced the other characters present in the hybrid. Thus, *D. castanea* is clearly indicated as one of the parental species.

The olive crown and muted flank streaks of the hybrid could not have been contributed by *D. castanea* and must be characters of the other parent. Among female wood warblers in definitive alternate plumage, the only species possessing both yellow or olive crowns and lateral ventral streakings are *D. striata* and *D. pinus.* The eye ring, chin, throat, breast, and upper belly of *D. pinus* vary from dull to bright yellow, and its dorsal plumage is heavily saturated with yellow. The hybrid has little yellow in the underparts especially the breast, exhibiting about the same amount of yellow as expressed in series of *D. striata,* but considerably less than that of the dullest, definitive-plumaged *D. pinus.* This suggests that *D. pinus* is highly unlikely to have been a parental species. Thus, by the process of elimination, the second parental species was *D. striata.*

In sum, the plumage pattern and color of the female hybrid can be accounted for by the two most probable parental species, *Dendroica striata* and *D. castanea* (Appendix 2). Other *pairs* of species lack the diversity of plumage color and pattern elements exhibited by the hybrid.

Colorimetric Variation

Univariate comparisons.—Male *D. striata* are significantly darker than *D. castanea* on the back and crown, while the back and crown of *D. castanea* are both redder and yellower than those of *D. striata* (Table 2). As Brodkorb (1934) implied in his description, the crown of the Michigan hybrid is similar in general appearance to that of *D. striata* (see Appendix 1). Several of the

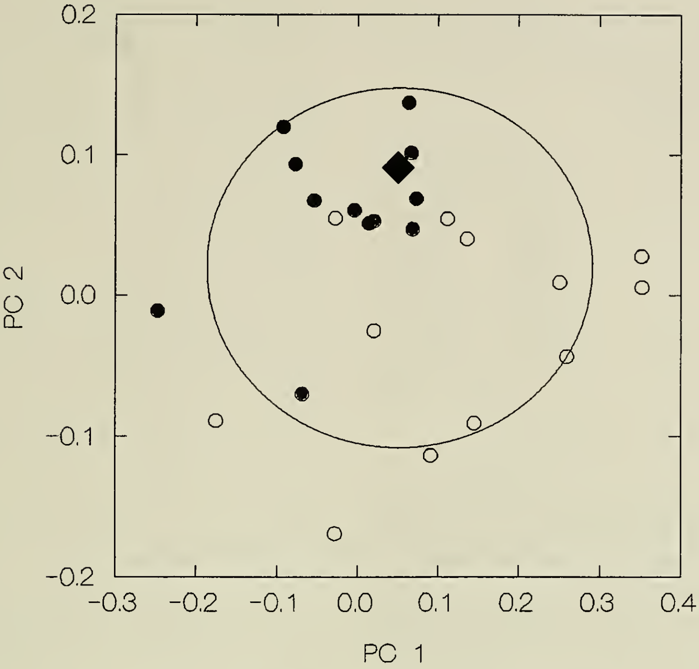

Fig. 9. Bivariate plots of factor scores from a principal components analysis of back color (see Table 4) for female *Dendroica striata* (empty circles), *D. castanea* (filled circles), and a *D. striata* × *D. castanea* hybrid (diamond).

crown feathers of both male hybrids have buffy-olive tips or margins. These cause the colorimetric values for red (*a*) and yellow (*b*) to fall outside the range of values expressed by ASY males of *D. striata.* Back color of the Michigan hybrid is intermediate between that of *D. striata* and *D. castanea,* while values for the Texas hybrid were closer to the characters means of *D. castanea.*

Colorimetric variables of female *D. striata* and *D. castanea* overlap (Table 2). Back color of the female hybrid more closely resembles that of *D. castanea.* The colorimetric values for lightness and redness of the hybrid fall narrowly outside the character ranges for *D. striata.* Crown color variables of *D. striata* and *D. castanea* also overlap, but those of *D. castanea* are significantly redder and slightly yellower. Back color of the hybrid approximates the character means of *D. striata.*

Multivariate comparisons.—Factor scores from a principal components analysis of back color of male *D. striata* and *D. castanea* overlapped slightly along the first axis, which largely reflected the difference in redness between the species (Fig. 8). The distribution of *D. castanea* along the second PCA axis, which explained only a tenth of the variance, was entirely overlapped by *D. striata.* The male hybrids most closely resembled *D. castanea* in bivariate space and occurred well within the 95% confidence ellipse for hybrids and parental species.

Factor scores for female back color of *D. striata* and *D. castanea* overlapped moderately along the first axis (PCA 1) and extensively along the second (Fig. 9, Table 4). Factor scores in the upper left hand quadrant represent specimens that are redder than average. The female hybrid most closely resembled *D. castanea* in color and fell narrowly outside the zone of overlap of the proposed parental species in bivariate space.

Table 5.—Factor loadings for the first two principal components from an analysis of external measurements of a pooled sample of males and females in definitive alternate plumage of *Dendroica striata, D. castanea,* and their hybrids.

Variable	Principal component axes	
	I	II
Wing chord	0.0076	0.0069
Tail	0.0032	0.0123
Tarsus	0.0128	0.0025
Bill	0.0130	−0.0095
Percent variance explained	40.2%	29.6%

External Morphology

As a second step in the diagnosis, hypotheses generated from analyses of plumage characters were tested with analyses of morphological size and shape. Size and shape characters in birds are assumed to be encoded by a multitude of structural and regulatory genes, resulting in additive genetic variation in hybrid morphology. In other words, the external dimensions of hybrids should fall within the cumulative mensural ranges of characters expressed by large samples of the parental species of the appropriate age and sex class.

Univariate comparisons.—External measurements of the male hybrids fell within, or narrowly outside (Texas male) the cumulative ranges of measurements, for male *D. striata* and *D. castanea* (Table 1). Measurements of the wing, tail, and tarsus of the hybrids more closely approached those of the smaller parental species (*D. castanea* in wing and tarsus, *D. striata* in tail). In fact, the wings and tails of male hybrids were more similar in size to females of *D. striata* and *D. castanea* than to males.

External measurements of the female hybrid (Table 1) also fell within the range of measurements of the hypothesized parental species, *D. striata* and *D. castanea.* Wing, tail, and bill measurements of the hybrid were smaller than the character means for females of both parental species, while the hybrid's tarsi were longer than the parental means.

Multivariate comparisons.—Factor scores for male *D. striata* and *D. castanea* overlapped extensively along the first two principal components. In bivariate space, the male hybrids were closely adjacent to individuals of both probable parental species, and well inside the 95% confidence ellipse (Fig. 10a, Table 5).

Females of *D. striata* and *D. castanea* were morphologically less variable than males and primarily occupied the lower left quadrant of the bivariate plot (Fig. 10b). Females of the two species also overlapped less extensively in bivariate space than the respective males. The female hybrid was most similar to *D. striata* in size and shape. Factor scores of the hybrid fell just inside the 95% confidence ellipse surrounding the centroid of female scores.

In conclusion, the univariate and multivariate evaluations of external morphology and plumage color were consistent with the hypotheses generated from the qualitative analyses of plumage pattern and color. This concordance of results provides strong support for the restrictive hypothesis that all three specimens represent hybrids of *Dendroica striata* and *D. castanea.*

Geographic Range.—As neither *Dendroica striata* nor *D. castanea* breed in southern Michigan, southern Ontario, or Texas, the hybrids were presumably migrating when collected. The bulk of the breeding range of *D. striata* is well north of that of *D. castanea.* However, they overlap extensively in the Northwest Territories, British Columbia, Alberta, and Saskatchewan and, to a lesser degree, in the Maritime Provinces of Canada (Godfrey 1986, Erskine 1992). The species are essentially parapatric in northern Manitoba (B. Whitney, pers. comm.) and in central Ontario (Spier 1985), approximately due north of the collection site in Michigan. It is in a region of narrow distributional overlap in Ontario and Quebec, where population densities of *D. striata* and *D. castanea* are low (see Spier 1985), that I expect that hybridization would be most likely to occur. These spe-

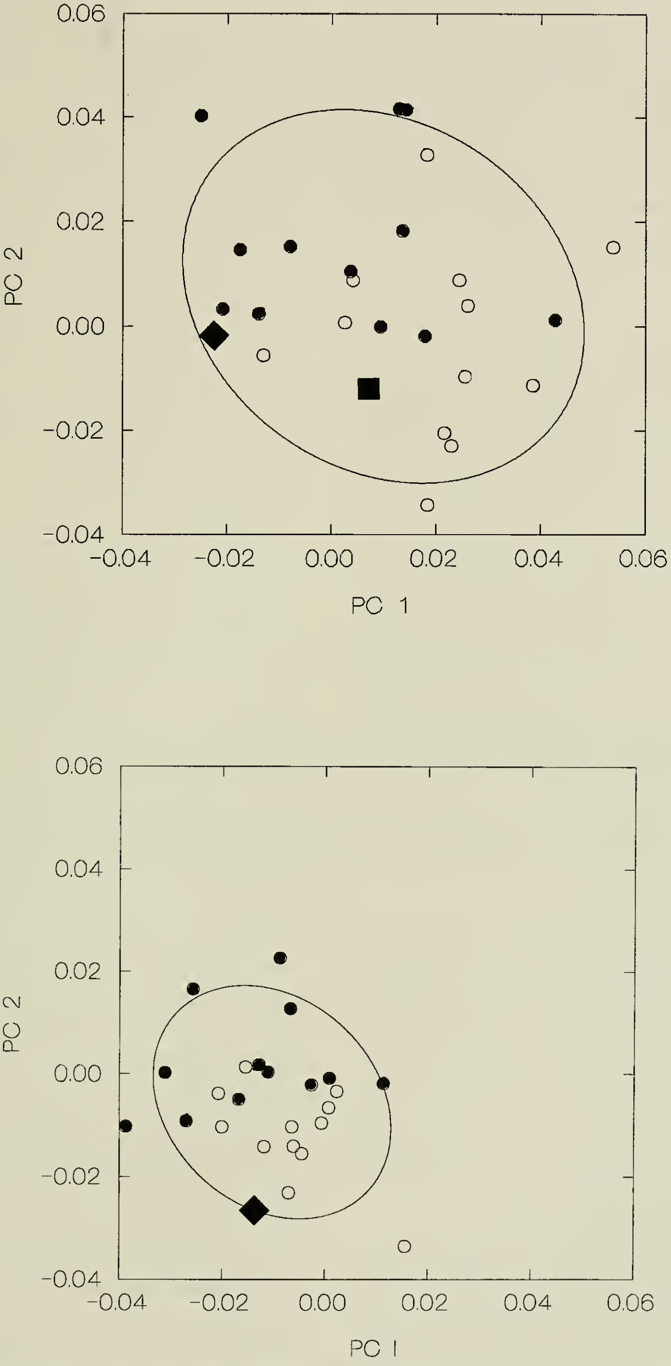

Fig. 10. Bivariate plots of factor scores from a principal components analysis of external morphology (see Table 5) for *Dendroica striata* (empty circles), *D. castanea* (filled circles), and *D. striata* × *D. castanea* hybrids (Michigan hybrid = diamond; Texas hybrid = square). Factor scores of males (top) and females (bottom) were extracted from the same principal components analysis, but projected on different plots for clarity.

cies in first basic plumage are remarkably similar and some individuals are difficult to distinguish. Juvenile hybrids would be extraordinarily difficult or impossible to detect under field conditions. Thus, surprisingly large numbers of juvenile hybrids could migrate unnoticed to their wintering grounds each autumn.

Conclusions

Hybrid intermediacy in size and shape.—Avian offspring from conspecific matings usually exhibit high heritability of morphological traits (e.g., Boag & Grant 1978, Smith & Zach 1979, Smith & Dhondt 1980, Dhondt 1982). That is, when the values for character traits of the offspring are regressed on the average of those of the parents (for monomorphic species), the slope of the resulting regression line (=heritability) approaches 1.0. These data indicate that the size and shape of passerine birds are largely determined by additive genetic processes, and to a lesser degree, by environmental factors (James 1983). As such, they constitute the empirical foundation upon which the morphological diagnosis of hybrid specimens is permitted.

With a few exceptions (e.g., MacInnes et al. 1989), there have been no comparable studies of morphological heritability in avian hybrids which, strictly speaking, are the result of interbreeding of biological species. Ornithologists have recognized, however, that mensural traits of hybrids were usually intermediate between those of their parental species long before the field of quantitative genetics blossomed (see Falconer 1981).

But what predictions can be made about the morphology of hybrids among distantly related species, especially among those classified in different genera? If the mixture of highly similar genomes results in high heritability, then hybridization between species with dissimilar genetics might be predicted to result in lower heritability. In other words, if heritability, and thus phenotypic predictability, is correlated with the degree of genomic compatibility of the parental species, then the phenotypes of true intergeneric hybrids are relatively unpredictable. Furthermore, the probability that hybrids will deviate significantly from the biparental midpoint may increase as a function of the genetic dissimilarity of the parental species (Fig. 11). In operational terms, there is no reason to expect a hybrid from an intrageneric crossing to occupy a position intermediate to the parental species in multivariate space. As a corollary, it may not be possible to distinguish F_1, F_2, or back-crosses among genetically divergent species, if they do occur, on the basis of morphology alone.

Plumage.—Two assumptions, both somewhat vague, are commonly advanced in the analysis of hybrid plumage. The first, that hybrids express plumage characters of both parental species, is bolstered by more than a century of careful study of hybrid specimens (e.g., Cabot 1854), and finds quantitative support in more recent studies that indicate that the pattern and color of most plumage tracts are polygenically controlled (see Hutt 1949, Buckley 1982).

The second assumption is that hybrids do not exhibit plumage characters of species other than their parents (e.g., Banks & Johnson 1961; Graves 1990, 1992, 1993a, 1993b; Graves & Zusi 1990). Rohwer's (1994) use of "contradictory characters" in hybrid evaluation is simply a rephrasing of that hypothesis which, in various guises, also asserts that luxuriance and atavism do not occur in hybrid plumage. As a universal statement, the latter is demonstrably incorrect, because "atavistic" characters occur with frequency in certain anseriform hybrids (Harrison and Harrison 1963). However, atavism has not been adequately documented in other avian orders, and plumage luxuriance has not been documented in any avian hybrid in nature.

In light of the aforementioned assumptions, perhaps my most noteworthy observation on the plumages of the *Dendroica striata* × *D. castanea* hybrids was the ap-

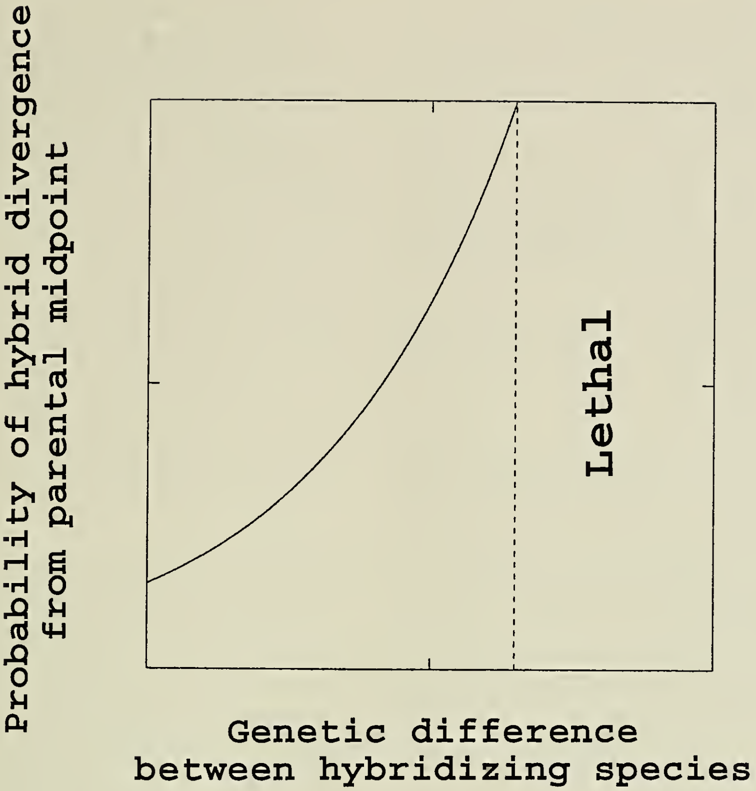

Fig. 11. Hypothetical relationship between the degree of genetic difference between hybridizing avian species and the probability that the morphology of hybrids will significantly diverge from the midpoint of their parental species. The dashed line represents the threshold beyond which hybrids die before hatching.

parent correlation between the degree of difference in colorimetric values of homologous plumage characters of the parental species and the deviation of the hybrid values from the averages of the character means of the parental species (see Table 2). The more discordant the plumage color of the parental species, the more likely that character in the hybrid closely resembled one parental species, rather than a "blended" intermediate (e.g., crown color in males). This pattern can be partially explained by the expansion of possible hybrid values when pigmentation of the parental species differed markedly. It also suggests that a small number of gene complexes control pigmentation of individual plumage tracts in *D. striata* and *D. castanea*. Crown pigmentation of *D. striata* is evidently dominant (or nearly so) to that of *D. castanea* in hybrids, and as Brodkorb (1934) noted, the male hybrid superficially resembles *D. striata* in most respects. Whether this is due to genetic dominance or chance recombination will only be determined with the discovery of additional hybrid males.

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Appendix 1

Comparative descriptions of the male hybrids, *Dendroica striata* × *Dendroica castanea,* and their parental species in definitive alternate plumage (Figs. 1–4). Hybrids are referred to as the "Texas" (SBCM) and "Michigan" (UMMZ 53692) specimens, respectively.

The crown, superciliary, and lores are semi-glossy black in *striata* (Fig. 1). In *castanea,* the forecrown is black becoming into chestnut on the crown above the eyes, and extending posteriorly to the rear crown; the superciliary and lores are black. The respective parts of the Michigan hybrid resemble those of *striata*; a few feathers above the nostrils and on the superciliary have faintly buffy-olive tips; several feathers of the hindcrown have broader buffy-olive margins. The crown of the Texas specimen is more intermediate in appearance. Feathers of the hindcrown are margined with buff-olive, imparting a streaked appearance. Several small chestnut spots occur on feathers of the midcrown.

The parental species and the hybrids have a thin nuchal collar: black streaked with white in *striata,* buffy-white in *castanea,* pale buffy-white in the Michigan hybrid, and dull olive-buffy in the Texas hybrid. Feathers on the mantle, scapulars, lower back, rump and uppertail coverts of *striata* have black center stripes and broad gray margins. The respective plumage of *castanea* is similarly patterned but the feather margins are buffy-olive on the mantle, changing to gray on the lower back, rump, and undertail coverts. In the hybrids, dorsal plumage posterior to the hindcrown is nearly intermediate in appearance to that of the parental species.

D. striata has a white facial patch that extends from the base of the lower mandible, posteriorly to the ventral eyering and the auriculars. The respective parts of *castanea* are black. In *striata,* the white facial patch of *striata* is bordered ventrally by a thin black malar stripe, which originates on the chin and extends to the upper breast, and posteriorly by vertical zebra-like striping on the nuchal collar. The black "face" of *castanea* is bordered ventrally by the chestnut throat, and posteriorly by a large buff neck patch, a ventral extension of the nuchal collar. The facial plumage of the Michigan hybrid expresses a complex mosaic of the parental characters (Fig. 4). Feathers adjacent to the bill are black with pale buffy-white tips; while those on the lower eyering and auriculars are grizzled dark gray and buffy-white. The auriculars are bordered posteriorly by a buffy-white neck patch, which is paler and smaller than that of *castanea.* Facial plumage of the Texas hybrid is considerably darker than that of the Michigan hybrid, and similar in appearance to *castanea.* The posterior auriculars are grizzled (sooty black and gray), and bordered posteriorly by a dull, silvery-buff, neck patch, which is smaller and less distinct than in *castanea.*

The remiges and wing coverts of *striata* and *castanea* are similarly patterned; the greater and middle wing coverts are tipped with white in *striata* but are more broadly tipped with pale buffy-white in *castanea.* The hybrids' wings are intermediate in pattern and color. White spots in the outer rectrices of the hybrids are intermediate in size and shape between those of *striata* and *castanea.*

The throat, breast, belly, and undertail coverts of *striata* are white bordered laterally by black streaking on the sides of the throat, breast, and flanks. The chin of *castanea* is black, bordered posteriorly by chestnut, which extends posteriorly to the upper breast along the midline and laterally to the flanks; the center of the breast, lower belly, and undertail coverts are buffy-white. The feathers of the Michigan hybrid's throat are grizzled with black and chestnut, many faintly tipped with white, especially on the chin and along the midline, imparting the appearance of wide malar stripes. The breast, belly, and undertail coverts of the Michigan hybrid are white, faintly tinted with buff; the flanks are marked with muted brownish-black spots and streaks and a strong chestnut wash. The chin, throat, upper breast, and sides of the Texas hybrid are "roan" (sooty black, subtly grizzled with chestnut and pale gray) in a pattern mirroring the distribution of chestnut in *castanea.* Center of the breast, belly and undertail coverts of the Texas specimen are pale buffy white. A few indistinct pale chestnut and sooty spots are found on the flanks.

Appendix 2

Comparative descriptions of the female hybrid (UMMZ 216628), *Dendroica striata* × *Dendroica castanea,* and its parental species in definitive plumage (Figs. 5–7).

Feathers of the crown, scapulars, and mantle of *striata* are olive to grayish-olive with pronounced blackish-brown shaft streaks. The respective plumage of *castanea* is olive-gray to gray but more heavily streaked with black; feathers of the crown, from the eyes to the nape, are chestnut distally with grayish-olive margins. The crown of the hybrid is more heavily streaked than in *striata,* but less so than in *castanea*; feather margins are olive (a few grayish-olive) and exhibit no trace of chestnut pigmentation on the basal or distal barbs under magnification (7×). The mantle of the hybrid, which contrasts with its olive crown, is intermediate in appearance between those of the parental species. The rump and uppertail coverts are olive-gray in *striata* and gray in *castanea.* The hybrid has an olive-gray rump and gray uppertail coverts.

The short superciliary of *striata* is poorly defined by pale olive to pale yellow feather tips. In *castanea* the superciliary is even more poorly defined and streaked with dark gray and black. The lores and auriculars of *striata* are mottled olive-gray, bordered posteriorly by a faintly perceptible olive-gray patch on the side of the neck. The lores and auriculars of *castanea* are more heavily pigmented and contrast with the throat and a well-defined buff neck patch. Pigmentation of the superciliary, lores, and auriculars of the hybrid falls within the range of variation found in *striata,* but the auriculars are bordered posteriorly by well-defined buffy neck patch as in *castanea.*

White tips of the middle and greater wing coverts of the hybrid are intermediate in width between those of *striata* and *castanea.* Outer margins of the rectrices are olive-gray in *striata* and the hybrid and gray in *castanea.*

The venter of *striata* is white tinted with pale yellow or olive on the throat and breast; narrow black streaking occurs on the side of the throat, breast, and flanks. The venter of *castanea* is buffy-white to buff, extensively suffused with chestnut on the throat, side of the breast, and flanks. The throat, upper breast, and flanks of the hybrid are buff, fading to pale buffy-white on the belly and undertail coverts. Several flank feathers are marked with pale chestnut and faint muted streaks appear at the side of the breast. The dried tarsi of the hybrid are intermediate in color between those of *striata* (light brown) and *castanea* (dark brown).

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Early record of indricothere (Mammalia: Perissodactyla: Hyracodontidae) from the Aral Sea region of western Kazakhstan

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Abstract.—Upper molar fragments of the indricothere rhinoceros *Paraceratherium* sp. are described from the Chilikta Formation at Altyn Chokysu, north of the Aral Sea in western Kazakhstan. Marine bivalves indicate the Chilikta Formation is of early Oligocene (Late Rupelian) age, and thus provide the first direct cross-correlation of an occurrence of *Paraceratherium* with the marine timescale. This find extends the temporal range of *Paraceratherium* in the Aral Sea region back from the late Oligocene to the early Oligocene, making it consistent with the temporal range noted for the genus in China. *Paraceratherium* thus had a geologically synchronous first appearance across Eurasia during the late early Oligocene.

The largest land mammals of all time were the indricotheres, giant rhinoceroses that lived during the early to middle Cenozoic in Eurasia. Indricothere evolution began during the middle Eocene with the pony-sized genus *Forstercooperia* and culminated during the Oligocene-early Miocene with *Paraceratherium* (=*Baluchitherium*, =*Indricotherium*), a rhinoceros that stood more than five meters tall at the shoulder, the largest land mammal of all time (Granger & Gregory 1936, Lucas & Sobus 1989).

One of the most important collecting areas for fossils of *Paraceratherium* is north of the Aral Sea in western Kazakhstan (Fig. 1). Here, the most nearly complete skeleton known of the genus was collected (Orlov 1939, Gromova 1959) from the Kumbulak Cliffs east of the town of Agyspe (Akespe) along Perovsky Bay on the northern shore of the Aral Sea. This and other specimens of *Paraceratherium* from the region north of the Aral Sea are restricted to the Aral Formation, strata of late Oligocene (Russell & Zhai 1987) or early Miocene (Akhmetyev & Sychevskaya 1994) age. Here we document a much older occurrence of *Paraceratherium* in this region that clarifies the temporal distribution of the genus. In this article, AMNH refers to the Department of Vertebrate Paleontology, American Museum of Natural History, New York; and USNM refers to the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Stratigraphy and Provenance

North of the Aral Sea, four rock-stratigraphic units of Eocene-Oligocene are exposed (Akhmetyev & Sychevskaya 1994) (Fig. 2). The oldest, the Chegan Formation, is yellowish green, bentonitic marine shale with dinocysts and molluscs of late Eocene (Priabonian) age. The Kutanbulak Formation disconformably overlies the Chegan, is as much as 28 m thick and is composed of mostly yellow, orange and brown, fine-grained quartzarenite. It is unconformably overlain by the Chilikta Formation, as much as 23 m of shale and thinly interbedded shale-sandstone. The Chilikta Formation

Fig. 1. Map of Kazakhstan showing location of Altyn Chokysu north of the Aral Sea.

produces marine bivalves (especially *Ergenica cymlanica*) that correlate it to the Solenovo horizon of the Crimea-Caucasus of late Early Oligocene (late Rupelian) age (Akhmetyev & Sychevskaya 1994).

The Chagray Formation disconformably overlies the Chilikta Formation and is as much as 33 m thick and mostly yellowish gray and brown, micaceous sandstone. The Aral Formation conformably overlies the Chagray. It is at least 24 m thick north of the Aral Sea (its top is everywhere eroded) and consists mostly of grayish yellow green, calcareous shale and claystone characterized in its lower part by numerous lenses of the euryhaline bivalve *Corbula.* All fossil mammal localities reported by previous workers (Russell & Zhai 1987, Bendukidze 1993, Akhmetyev & Sychevskaya 1994) from north of the Aral Sea are in the Aral Formation. We follow Russell & Zhai (1987) in regarding these mammals as late Oligocene in age, but Soviet scientists regard them as early Miocene in age (Akhmetyev & Sychevskaya 1994).

The new locality at which we collected

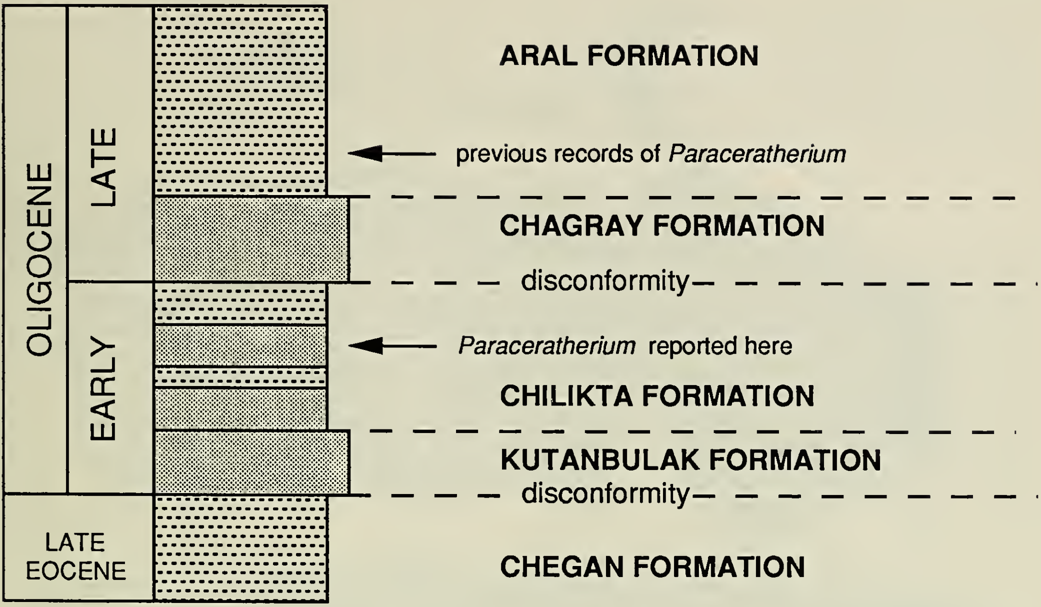

Fig. 2. Summary of Eocene-Oligocene stratigraphic units in Altyn Chokysu area showing stratigraphic levels of *Paraceratherium* occurrences (lithology schematic).

Paraceratherium tooth fragments is in the Ckilikta Formation on the escarpment of Altyn Chokysu, a plateau about 20 km northwest of the town of Saksaulskaya and about 70 km northeast of the Kumbulak Cliffs (Figs. 1–2). This locality is at UTM 3577371E, 5238795N, zone 41, stratigraphically well below Bendukidze's (1993) "Shokysu" mammal locality in the Aral Formation. The fossiliferous horizon is a 1.2-m-thick, white, fine-grained sandstone, 10.8 m above the base of the Chilikta Formation, which is 14.4 m thick at this location. The *Paraceratherium* tooth fragments were associated with a sirenian rib, fish bones and teeth of the sand tiger shark *Carcharias* sp.

Systematic Paleontology

Order Perissodactyla Owen 1848
Family Hyracodontidae Cope 1879
Subfamily Indricotheriinae Borisyak 1923
Genus *Paraceratherium* Forster Copper 1911

Paraceratherium sp.
Fig. 3

Referred specimen.—USNM 482243, approximately 50 fragments of cheek teeth, three of which, illustrated here, are parts of ectolophs of right M^1, M^2, and M^3.

Description.—The three largest tooth fragments, here referred to as 1, 2, and 3, are portions of upper molar ectolophs. Fragment 1 is right M^3 ectoloph from paracone through parastyle, and part of protoloph. Paracone forming thick rib on labial face of ectoloph and separated from parastyle by distinct cleft. Parastyle a more prominent and anteriorly-projecting rib. Ectoloph making sharp, nearly right-angled fold and becoming confluent with protoloph. Minimum crown height at paracone 59 mm.

Fragment 2 from anterior part of ectoloph of right M^2. Preserves paracone as a less prominent rib than on M^3 ectoloph. Cleft between paracone and parastyle less pronounced than on M^3. Paracone crown height about 66 mm.

Fragment 3 part of posterior portion of

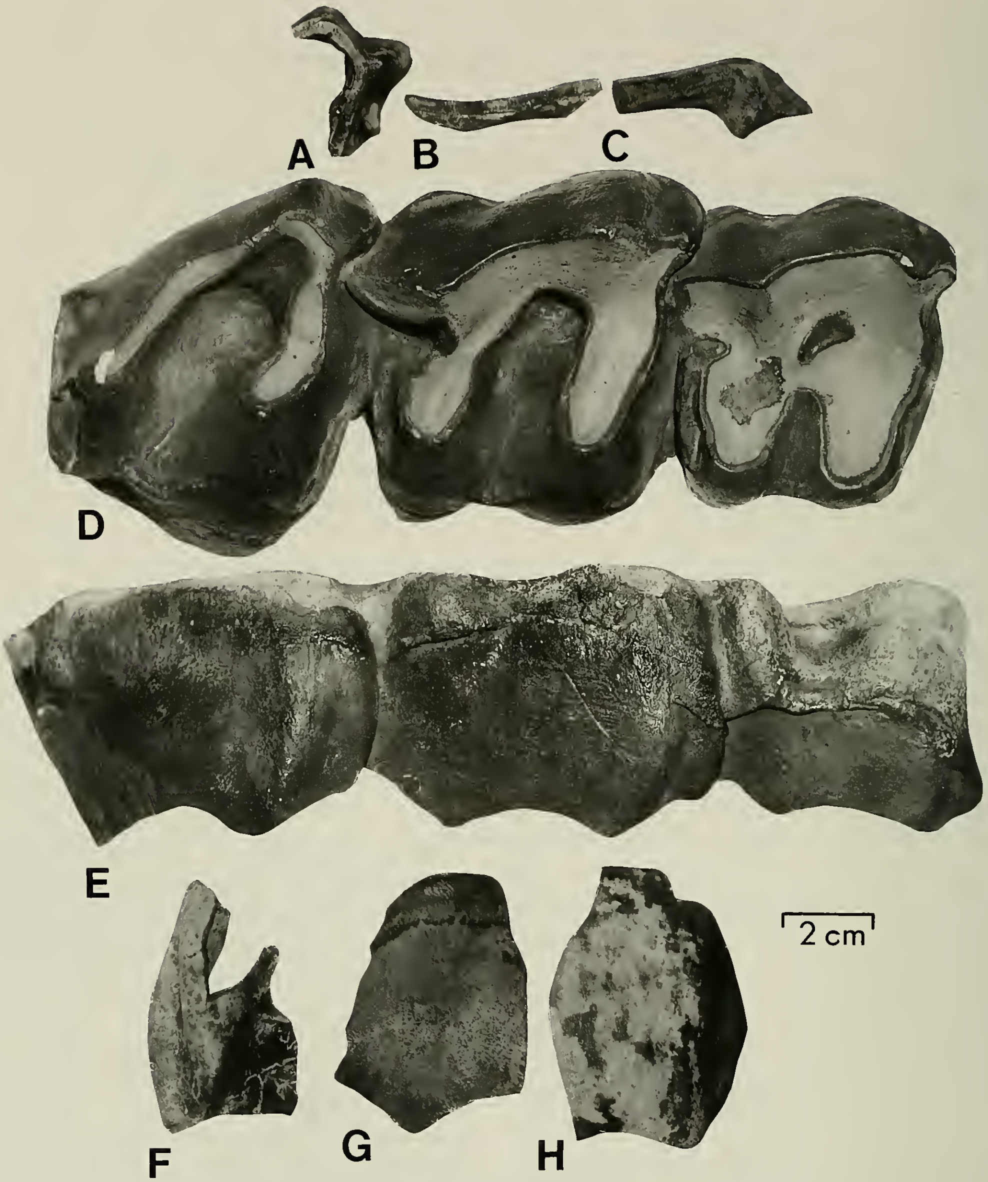

Fig. 3. Tooth fragments of *Paraceratherium* sp. from Altyn Chokysu compared to cast of holotype of *Paraceratherium asiaticum.* A–C, USNM 482243, *Paraceratherium* sp. from Altyn Chokysu: A, occlusal view of fragment of right M^3 ectoloph (fragment 1 in text); B–C, occlusal view of right M^2 ectoloph (fragments 3 and 2, respectively, in text). D–E, AMNH 26972, cast of holotype of *Paraceratherium asiaticum,* left M^{1-3} (photographs reversed): D, occlusal; E, labial views. F–H, USNM 482243: F, anterior view of fragment of right M^3 ectoloph (fragment 1 in text); G–H, labial views of fragments of right M^2 ectoloph (fragments 3 and 2, respectively, in text).

right M^2 ectoloph, probably from same tooth as fragment 2, but two pieces do not fit together. Blade-like metacone projecting from rest of ectoloph occlusal edge. Prominent basal cingulum on posterior edge of crown. Fragment 2 and 3 suggest total ectoloph length of more than 90 mm.

Identification.—We compared these

tooth fragments to casts of upper dentitions of *Paraceratherium asiaticum* from the Turgay region of central Kazakhstan (Fig. 3: Granger & Gregory 1936, figs. 2C–D). These casts are AMNH 26971, left P^2–M^3, and AMNH 26972, right P^2–M^2 (cast of holotype of *P. asiaticum*). They are very similar in size and morphology to the fragments we collected at Altyn Chokysu. Fragment 1 has a minimum crown height of 59 mm, about the same as that of AMNH 26971, which is nearly 61 mm. Fragment 2 has a paracone crown height of about 66 mm, the same as on AMNH 26971. All other rhinocerotoid genera are much smaller, so we assign USNM 482243 to *Paraceratherium* sp.

Discussion

Prior to this report, *Paraceratherium* occurrences north of the Aral Sea were restricted to the aral Formation and regarded as either later Oligocene or early Miocene in age. However, *Paraceratherium* occurrences as old as late Early Oligocene ("middle" Oligocene of some authors) are well documented in Nei Monggol, China, and the genus occurs in strata as young as late Oligocene (Russell & Zhai 1987). Specimens reported here establish a temporal range of *Paraceratherium* in western Kazakhstan coeval to that in China. They thus eliminate the possibility that *Paraceratherium* first arose in China and only reached central and western Asia (Kazakhstan) much later.

Occurrence of *Paraceratherium* in the Chilikta Formation also provides the first direct correlation of this mammal's record to the marine timescale. As stated above, marine bivalves indicate the Chilikta is late Rupelian in age. This may be the oldest age reported for the genus *Paraceratherium* across Asia. *Paraceratherium* has its youngest occurrence at Bugti in Pakistan, where it is of early Miocene age (Raza & Meyer 1984). *Paraceratherium* thus emerges as a much longer-lived genus than indicated by Lucas (1994), who assigned it a late Oligocene-early Miocene age. The genus has a range of nearly 10 million years, spanning the late Rupelian (about 30–32 Ma) to early Miocene (about 20–22 Ma).

Acknowledgments

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Late Eocene entelodonts (Mammalia: Artiodactyla) from Inner Mongolia, China

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Abstract.—Previously undescribed specimens of *Entelodon* from the late Eocene (Ergilian) of Nei Monggol, China represent two species, small and large. We identify the small species as *Entelodon gobiensis* (Trofimov, 1952), because this is the oldest valid name available for a relatively small species of Asian *Entelodon. E. diconodon* (Trofimov, 1952) is a nomen dubium, and it is probable that *E. ordosius* (Young & Chow, 1956), *E. major* Biryukov, 1961 and *E. orientalis* Dashzeveg, 1965 are junior subjective synonyms of *E. gobiensis* (Trofimov, 1952). The large species is *Entelodon dirus* Matthew & Granger, 1923, a species previously known only from its holotype M3, but to which we now refer a lower jaw with p2–m3. In Asia, *Entelodon* is more common in strata of Ergilian (late Eocene) age; its Shandgolian (early Oligocene) occurrences are few. Entelodonts originated in Asia during the middle Eocene, immigrated to North America (late Eocene) and Europe (early Oligocene) and persisted until late Oligocene in Eurasia and North America. The last entelodonts, from the early Miocene of North America, apparently arose from a separate, latest Oligocene emigration from Asia.

Entelodonts were a family of Eocene-Miocene giant suiform artiodactlys, some with skulls nearly one meter long. They are especially well represented in the fossil record in western North America (Peterson 1909) and western Europe (Brunet 1979). In Asia, the oldest entelodonts (*Eoentelodon*) are of middle Eocene (Irdinmanhan) age, and the group persisted until the late Oligocene. The genus *Entelodon* is known from the late Eocene (Ergilian) to early Oligocene (Shandgolian), and two genera, *Paraentelodon* and *Neoentelodon,* are of late Oligocene (Tabenbulukian) age. In this article, we describe a sample of *Entelodon* from the late Eocene of Nei Monggol (Inner Mongolia), China (Fig. 1), and clarify the taxonomy of the Asian species of *Entelodon* in Asia. We use the Asian "land mammal age" terminology (e.g., Irdinmanhan, Ergilian, Shandgolian) as it was established by Russell & Zhai (1987).

Abbreviations used.—When used in dental notations upper case letters denote upper (skull) teeth and lower case letters denote lower (dentary) teeth. Institutional abbreviations used are: AMNH—American Museum of Natural History, New York; IVPP—Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; KAN—Kazakh Academy of Sciences, Almaty; MAN—Mongolian Academy of Sciences, Ulan Bator; PIN—Paleontological Institute of the Russian Academy of Sciences, Moscow.

Systematic Paleontology

Family Entelodontidae Lydekker, 1883
Genus *Entelodon* Aymard, 1847

Fig. 1. Map of *Entelodon* localities in Asia. 1, Houldjin, Baron Sog and Urtyn Obo formations, Nei Monggol, China; 2, Cajiachong Formation, Yunnan, China; 3, Ergilin Dzo svita, Mongolia; 4, Kusto svita, Zaysan basin, Kazakhstan; 5, Iwaki Formation, Japan; 6, Chilikta svita at Kursay near Lake Chelkar Teniz, Kazakhstan; 7, Qingshuiying Formation, Lingwu, Ningxia, China; 8, "indricothere" svita at Dulygaly-Zhilanchik, Kazakhstan.

Entelodon gobiensis (Trofimov, 1952)

Figs. 2B, D, 3A–C

Referred specimens.—From the Baron Sog Formation at Nom Khong Obo, Holy Mesa, Nei Monggol, China: AMNH 26184, lower jaw with left and right p3 (Fig. 2B–D).

From the Baron Sog Formation at Urtyn Obo, East Mesa, Suiyuan, Nei Monggol, China: AMNH 26176, skull fragments and left and right I1–M3 (Fig. 3A–B).

From the Houldjin Formation 7 miles west of Camp Margetts, Nei Monggol, China: AMNH field number 839, right M3 (Fig. 3C).

Description.—The upper dentition of AMNH 26176 merits description as one of the best preserved upper dentitions of *Entelodon* from Asia. The I1 is an almost conical tooth with a very convex labial side, less convex lingual side and a prominent lingual cingulum. Measurements (in mm) are: length = 16.7; width = 14.6. The I2 is a larger, more caniniform tooth missing the base of the crown, so comparable measurements cannot be obtained. The I3 is a recurved tooth, with the crown more triangular in cross section than that of the I1 or I2. It is very convex labially and has a lingual cingulum. Length = 26.8, width = 22.5. The canine is a recurved tooth similar to the I3 but lacks the base of the crown.

The P1 is dominated by a single cusp,

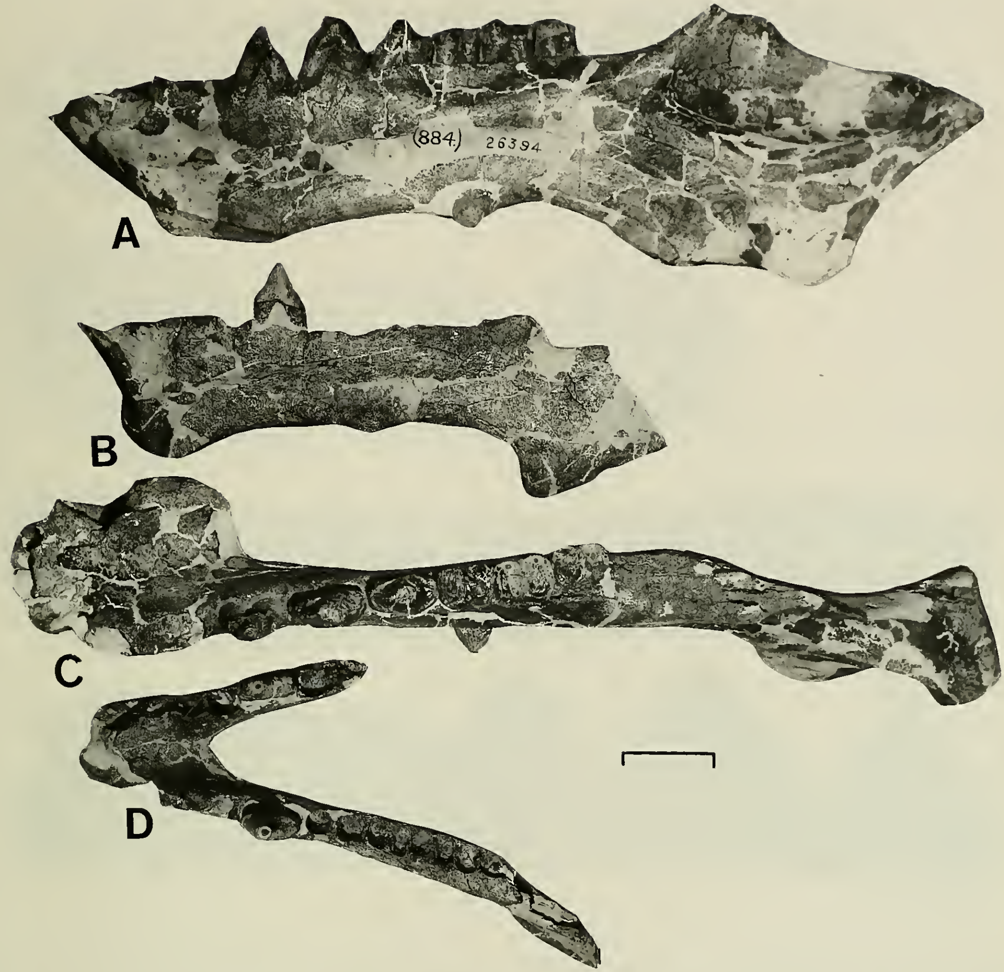

Fig. 2. Lower jaws of *Entelodon* from the upper Eocene of Nei Monggol, China. A, C, *E. dirus,* AMNH 26394, lower jaw with left p2–m3, in lateral (A) and occlusal (C) views. B, D, *E. gobiensis,* AMNH 26184, lower jaw with left and right p3, in lateral (B) and occlusal (D) views, negative reversed for easier comparison. Bar scale = 5 cm.

the paracone. The crown is curved slightly linguad. The labial face of the tooth is convex, and a ridge extends from the anterior end of the tooth to the apex of the paracone and then to the posterior base of the crown. Length = 22.2, width = 10.8.

The P2 is a larger version of P1 except that the paracone is not as lingually deflected, and it has a cingulum around the entire crown: on the labial face, beneath the paracone, the cingulum is only weakly developed. Like the P1, P2 is a trenchant tooth with two roots, one positioned anteriorly and the other posteriorly. Length = 32.8, width = 16.9.

The P3 has a triangular crown dominated by the paracone, which is deflected slightly linguad. It has a prominent posterior ridge and a less prominent anterior ridge. The basal cingulum is essentially continuous around the crown. One large root is present anteriorly, and there are two fused roots posteriorly. Length = 36.9, width = 25.6.

The crown of P4 is subtriangular in oc-

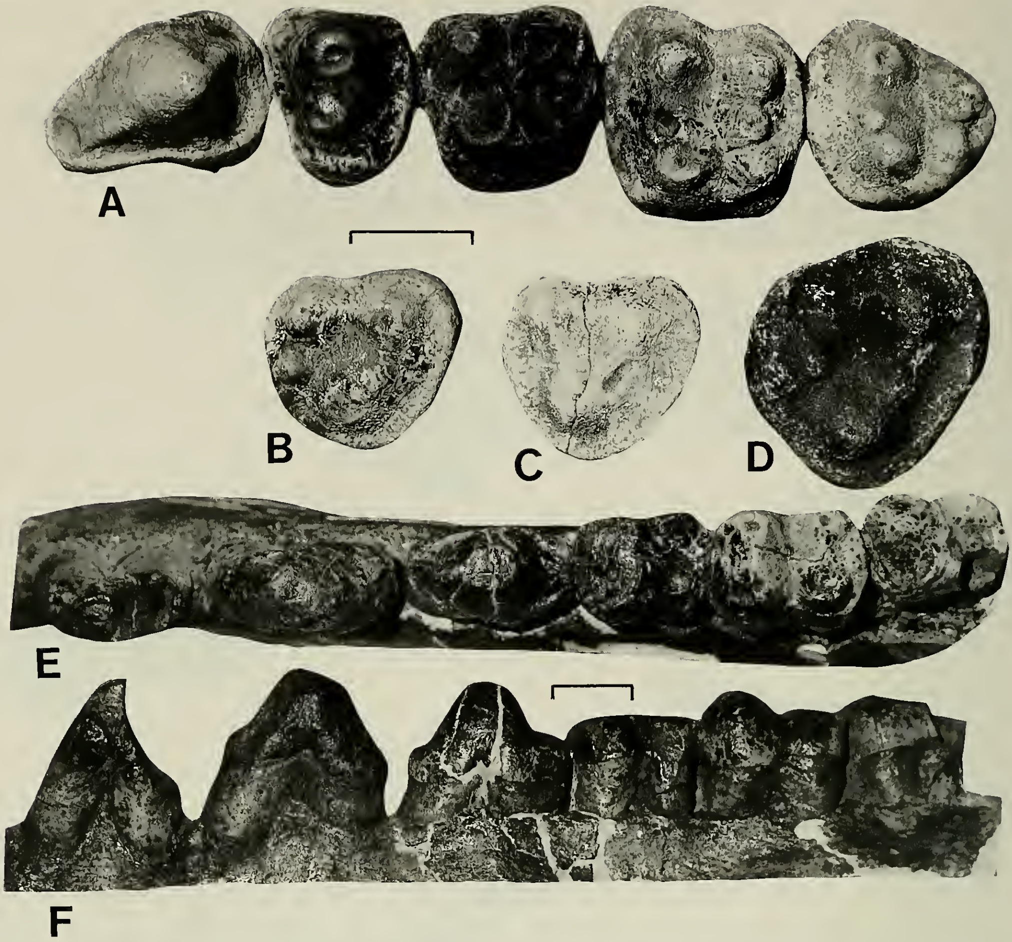

Fig. 3. Cheek teeth of *Entelodon* from the upper Eocene of Nei Monggol, China. A–B, *E. gobiensis,* AMNH 26176, occlusal view of left P3–M3 (A) and right M3 (B). C, *E. gobiensis,* AMNH field number 839, occlusal view of right M3. D, *E. dirus,* AMNH 19181 (holotype), occlusal view of right M3. E–F, *E. dirus,* AMNH 26394, occlusal (E) and labial (F) views of left p2–m3. Bar scales = 2 cm.

clusal outline, with its longer axis oriented transversely. There is a large paracone with an equally large, closely appressed protocone. A basal cingulum is prominent on the anterior, lingual and posterior margins of the tooth, and is present but weaker labially. There is a faint suggestion of a parastyle, and a convex ectoloph. The tooth has three divergent roots. Length = 25.5, width = 29.6.

The m1 is approximately square, with subequal paracone, metacone, protocone and hypocone. The anterior cingulum is prominent. The labial cingulum is faintly developed and a tiny mesostyle is present. The well worn condition of this tooth results in two lophs, one connecting the paracone and the protocone, and the other the metacone and the hypocone. A strong posthypocone crista is confluent with the posterior cingulum. It has two divergent roots labially and two fused roots lingually. For measurements of M1–M3, see Table 1.

The M2 is subrectangular in occlusal outline, and is substantially larger than M1. It also differs from M1 in having distinct

Table 1.—Measurements (in mm) of selected upper and lower cheek teeth of *Entelodon* from Asia. L = maximum antero-posterior length; W = maximum transverse width.

Specimen	M1L	M1W	M2L	M2W	M3L	M3W
E. gobiensis						
AMNH 26176	29	31	33	34	31	31
AMNH "839"					32	29
IVPP V825.1[a]	31	32				
KAN 31-181/54T[b]	28	32	33	36	29	32
MAN 27-1[c]	25	27	30	34	27	30
MAN 27-2[d]	29	31	33	37		
PIN 473-256[e]	25	32	31	39		
E. dirus						
AMNH 19181[f]						

Specimen	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W
E. gobiensis								
AMNH "839"			28	23				
IVPP V2926.1[g]			27	21	31	25	29	21
KAN 32-181/54T[h]	40	21	29	23	31	27	33	25
KAN 35(29)3837[i]	38	20	27	21	31	26	31	24
PIN 473-129[j]					35	29		
PIN 478-126[j]					32	24		
PIN 478-287[k]	32	17						
E. dirus								
AMNH 26394	41	22	33	25	38	29	33	25

[a] Holotype of *E. ordosius* (Young & Chow, 1956), [b] Holotype of *E. major* Biryukov, 1961; [c] Holotype of *E. orientalis* Dashzeveg (1965); [d] Referred specimen of *E. orientalis*; [e] Holotype of *E. gobiensis* (Trofimov, 1952); [f] Holotype of *E. dirus* Matthew & Granger, 1923; [g] Referred specimen of *E. ordosius*; [h] Holotype of *E. major* Biryukov, 1961; [i] Measurements from Emry et al. (1996); [j] Referred specimen of *E. gobiensis*; [k] Holotype of *E. diconodon* (Trofimov, 1952).

para- and metaconules, a relatively larger anterior cingulum, and a more distinct labial cingulum.

The M3 is subtriangular in occlusal outline. Its anterior part is very much like that of M2, but the posterior loph is much narrower, and lacks the metaconule. The metacone is deflected linguad. The hypocone is small but retains a posterior crista confluent with the posterior cingulum.

The lower jaw is represented by AMNH 26184. Its horizontal ramus is of nearly equal depth throughout and bears two tubercles, one beneath the p1 and anterior alveolus of p2, and the other beneath the anterior part of m1. The anterior tubercle is a convex eminence that is inclined laterally so that the horizontal ramus dorsal to it is convex laterally. The posterior tubercle is a blunt swelling that projects ventrolaterally. Two small mental foramina are on the lateral surface of the horizontal ramus, one under p1 and the other under the anterior alveolus of p3. The anteroventral aspect of the mandibular symphysis is a broad, nearly flat, sloping surface. Spacing of the alveoli of the canine and anterior premolars indicates that no diastemata separate these teeth. The canine alveolus is large, trihedral in cross section and opens anteriorly and dorsally nearly parallel to the inclination of the symphysis. The p1 alveolus is a single cavity; its cross section is ovoid with the long axis anteroposteriorly oriented. The p2 has two separate alveoli, both circular in cross section, the posterior much the larger of the two. The p3 is a trenchant tooth with a tall, pointed cuspid followed posteriorly by a short heel. The p3 is two-rooted, as were p4-m3, judging from their alveoli.

Discussion.—Brunet (1979) did much to revise the taxonomy of Asian entelodonts at the generic level. A species-level revision is overdue, and we offer some observations toward one.

Trofimov (1952) named *Entelodon diconodon* for a right p4 (he misidentified it as a left p2: Brunet 1979) from Kursay near Lake Chelkar-Teniz in Kazakhstan (Fig 1, No. 6). The paratype is a right m2 from the same locality. These specimens cannot be distinguished metrically or morphologically from those of other small *Entelodon* species from Asia or from some European *Entelodon,* although p4 is relatively smaller (Table 1) and has an accessory cuspid on the posterior slope of the trigonid, unlike other specimens. We agree with Brunet (1979) that *E. diconodon* should be considered a *nomen dubium.*

Trofimov (1952) named *Brachyodon gobiensis* for a partial skull with badly damaged left P1-M3 from Ergilin-Dzo in Mongolia. Trofimov (1958) replaced the preoccupied name *Brachyodon* with the name *Ergilobia.* Brunet (1979) synonymized *Ergilobia* with *Entelodon.* The type specimen is poorly preserved, but metrically it cannot be distinguished from the other relatively small specimens of Asian *Entelodon* (Table 1).

Young & Chow (1956, p. 41, fig. 4, pl. 1, figs. C–D) named *Archaeotherium ordosius* for an M1 (IVPP V 825.1) from Lingwu, Ningxia. They diagnosed the species by its large size and brachyodont, sexitubercular upper molar with a prominent accessory cusp on the labial cingulum. According to Young & Chow (1956), IVPP V 825.1 is indistinguishable from the M1 of *Archaeotherium* except for its larger size. However, Brunet (1979) argues that this tooth more closely resembles that of *Entelodon,* especially in its heavy labial cingulum, and created the new combination *Entelodon ordosius* for it. Nevertheless, the size and morphology of the holotype of *E. ordosius* do not distinguish it from other small *Entelodon* from Asia (Brunet 1979).

Hu (1964) referred lower jaw fragments from Urtyn Obo, Nei Monggol, to *A. ordosius.* The bilophodonty of the lower molars justify assignment to *Entelodon* (Brunet 1979). In size and morphology, these teeth cannot be distinguished from other Asian small specimens of *Entelodon* (Table 1).

Biryukov (1961) based a new species *E. major* on a skull and lower jaw from Dulygaly-Zhilanchik in Kazakhstan. This is by far the most informative type specimen of any species of *Entelodon* from Asia, but it closely resembles in size and morphology all the other names species except *E. dirus* and *E. diconodon.* Biryukov's diagnosis of *E. major* stressed its large size, massive skull, flared-out suborbital flanges, infraorbital foramen above P4, short I3-C and C-P1 diastemata, internal choanae (palatine notch) at the level of the posterior end of M3, and upper sexitubercular upper molars whose crowns are wider than long. These are features of the genus *Entelodon,* and neither these characters nor size differentiate *E. major* from the other relatively small Asian *Entelodon.*

Dashzeveg (1965) described *E. orientalis* on the basis of a left maxillary fragment with M1–3, from Khoer-Dzan, Mongolia. His diagnosis emphasized large size, low crowned and sexitubercular upper molars with anterior and posterior cingula, M3 with a protoconule but lacking a metaconule, and palatine notch at the level of the middle of M3. These features and size (Table 1) do not, however, distinguish the holotype, or the referred specimens, of *E. orientalis* from other small specimens of *Entelodon* from Asia.

It thus seems likely that only one small species of *Entelodon* is known in Asia. *Entelodon gobiensis* (Trofimov 1952) is the oldest available and valid name for that species, given that *E. diconodon* is a *nomen dubium. Entelodon ordosius* (Young & Chow 1956), *E. major* Biryukov, 1961 and *E. orientalis* Dashzeveg, 1965 are probably junior subjective synonyms of *E. gobiensis* (Trofimov, 1952). The specimens of *E. gobiensis* reported here are the first records of *Entelodon* from the Baron Sog Formation of Nei Monggol.

Entelodon dirus Matthew & Granger, 1923

Figs. 2A, C, 3D–F

Holotype.—AMNH 19181, right M3 (Fig. 3D)

Horizon and locality of holotype.—Houldjin Formation, 3 mi. (4.8 km) southwest of Iren Dabasu, Nei Monggol, China.

Referred specimens.—From the Houldjin Formation at Overnight Camp, Camp Margetts area, Nei Monggol, China: AMNH 26394, incomplete lower jaw with p2–m3 (Figs. 2A, C, 3E–F).

From the Houldjin Formation 7 miles (11.2 km) west of Camp Margetts, Nei Monggol, China: AMNH field number 36, two canine fragments; field number 839, left p2 and right m1.

Description.—The lower jaw has a flat, sloping, plate-like symphysis. This orientation gives the I1–3 a slightly procumbent flare. The anterior tubercle is a crest or ridge that begins under the canine and continues to beneath the p2–3. The posterior tubercle is a blunt spike under the m1–2 juncture. Judging from the sizes of alveoli, i1 < i2 < i3 < c. The canine alveolus is much larger than that of i3 and is round in cross section. The p1 has a single alveolus, with the cross section an antero-posteriorly elongate oval. There are no diastemata between the teeth.

The p2 is a two-rooted, trenchant tooth dominated by a large paraconid. The p3 is a similar trenchant tooth. Both p2 and p3 have a discontinuous cingulid across the lingual face of the paraconid. The p4 has a talonid and accessory cuspid on the postero-lingual base of the paraconid slope. The p2–4 are inclined slightly posteriad.

The m1 is subrectangular in occlusal outline. With advancing wear it becomes slightly bilophodont. The m2 is a larger version of m1, with more distinct lophids, a well developed hypoconulid and a labial cingulid. The m3 is well worn but similar to m2, though it is smaller and has a relatively smaller talonid.

Discussion.—Prior to this report, *E. dirus* was known only from its holotype M3. The lower jaw, AMNH 26394, is from the same stratigraphic level as the holotype, and is from a nearby locality. It is too large to belong to *E. gobiensis* (Table 1), and its m3 is of appropriate size to occlude with the holotype M3 of *E. dirus,* to which we assign it.

Biochronology and Paleobiogeography

Entelodon occurs in Asia in strata of late Eocene (Ergilian) and early Oligocene (Shandgolian) age. The Ergilian occurrences are: (1) Houldjin, Baron Sog and Urtyn Obo formations, Nei Monggol, China (Matthew & Granger 1923, Hu 1964, this paper); (2) Cajiachong Formation, Yunnan China (Wang & Zhang 1983); (3) Ergilin Dzo svita, Mongolia (Trofimov 1952, Dashzeveg 1976); (4) Kusto svita, Zaysan basin, Kazakhstan (Emry et al. 1996); and (5) Iwaki Formation, Japan (Tomida 1986). The Shandgolian occurrences are: (1) Chilikta svita at Kursay near Lake Chelkar-Teniz, Kazakhstan (Trofimov 1952); (2) Qingshuiying Formation, Lingwu, Ningxia, China (Young & Chow 1956); and (3) "indricothere" svita at Dulygaly-Zhilanchik, Kazakhstan (Biryukov 1961). *Entelodon* is much more common and widespread in Ergilian strata than in Shandgolian strata.

The oldest and most primitive known entelodont is *Eoentelodon* from the middle Eocene (Irdinmanhan) Xiangshan and Lumeiyi formations of Yunnan, China (Chow 1958; Zhang et al. 1978). The genus has been reported from strata as young as late Eocene (Ergilian) in Mongolia (Dashzeveg 1965). Entelodonts first appear in North America during the Eocene (Duchesnean) in the form of *Brachyhyops* (Lucas 1992), and first appear somewhat later in Europe, during the early Oligocene (Brunet 1979). In Europe, the subsequent diversification of entelodonts was modest and relatively short lived. In North America, entelodonts became fairly diverse and abundant during the late Eocene and early Oligocene (Chadronian-Orellan) (Effinger 1987). They declined through the later Oligocene, and at about the end of the Oligocene a reentry from Asia gave rise to the giant entelodonts of the North American early Miocene. The known record of Asian entelodonts suggests that in Asia their diversity remained low, being limited to middle-late Eocene *Eoentelodon,* late Eocene-early Oligocene *Entelodon* and two genera of late Oligocene age, *Neoentelodon* from the Aktau svita of eastern Kazakhstan (Aubekerova 1969) and *Paraentelodon* from the Pestrotsvet svita at Benara, Georgia (Gabuniya 1964).

Given the temporal and geographic distribution of entelodonts and the authors' concept of their phylogeny (to be published in detail elsewhere), we agree with Brunet (1979) that entelodonts arose in Asia during the middle Eocene. They subsequently emigrated to North America in the late Eocene and to Europe in the early Oligocene. The immigrants gave rise to separate North American and European diversifications during the early Oligocene. Entelodonts persisted in Asia, North America and Europe through the Oligocene, but became extinct in North America and Europe late in the epoch. They emigrated again from Asia to North America at about the end of the Oligocene to produce the last entelodont, *Ammodon,* of the early Miocene.

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Taxonomic status of the enigmatic *Cryptotis avia* (Mammalia: Insectivora: Soricidae), with comments on the distribution of the Colombian small-eared shrew, *Cryptotis colombiana*

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Abstract.—*Cryptotis avia* G. M. Allen 1923, from the Eastern Andean Cordillera of Colombia, is a small-eared shrew previously known from, at most, five specimens. Review of the holotype, consisting of an understuffed skin and a partial skull, and three potential topotypes indicates that they are referable to *Cryptotis thomasi* Merriam, 1897, and *C. avia* should be considered a junior synonym of that name. *Cryptotis thomasi* is restricted to highlands around Bogotá in the Eastern Cordillera. Another specimen previously referred to *C. avia* is the second known specimen of *Cryptotis colombiana* Woodman & Timm 1993. This second record expands the known distribution of *C. colombiana* to include both the Central and Eastern Cordilleras of Colombia, and emphasizes a previous hypothesis that *C. colombiana* also will be found in the Western Cordillera, geographically closer to its sister species (*Cryptotis mera, Cryptotis nigrescens*) in southern Central America.

Resumen.—*Cryptotis avia* G. M. Allen 1923, de la Cordillera Oriental de Colombia, es una musaraña conocida anteriormente de, a lo más, cinco especímenes. Estudio del holotipo, que consta de una piel poca rellenada y un cranio parcial, y tres posibles topotipos indica que todos son iguales a *Cryptotis thomasi* Merriam 1897, y *C. avia* es un sinónimo menor de *C. thomasi. Cryptotis thomasi* occurre solamente en las montañas alrededores de Bogotá en la Cordillera Oriental. Otra espécimen referida anteriormente a *C. avia* es en realidad la segunda espécimen identificada de *Cryptotis colombiana* Woodman & Timm 1993. Este segundo registro amplia la distribución de *C. colombiana* a las Cordilleras Central y Oriental de Colombia. Esta especie también debe ser encontrada en la Cordillera Occidental, la cual está más cerca geograficamente de las especies más relacionadas (*Cryptotis mera, Cryptotis nigrescens*) en el sur de Centroamérica.

Small-eared shrews of the genus *Cryptotis* are a relatively poorly studied group, notwithstanding their wide distribution in North America, Central America, and the Andean highlands of South America. *Cryptotis* reaches its greatest species diversity in southern Mexico and Central America, and most taxonomic studies of the genus have been carried out on species in this region (Choate 1970; Woodman & Timm 1992, 1993). The most recent, comprehensive compendium of mammalian species recognized 14 species of *Cryptotis* (Hutterer 1993), and subsequent studies have revealed additional species, mostly in Mexico and Central America (Woodman & Timm 1993). Little work has focused on South American taxa (Tate 1932, Hutterer 1986), and these are in need of taxonomic and systematic reevaluation (Hutterer 1993).

Most species of *Cryptotis* in South America are members of the *Cryptotis thomasi* group (sensu Choate 1970). Recently, however, Woodman & Timm (1993) described a new species of the *Cryptotis nigrescens* group (sensu Woodman & Timm 1993), *Cryptotis colombiana,* based on a specimen from the Central Cordillera of Colombia. Most other members of this latter group of shrews are found in southern Mexico and Central America, although *Cryptotis mera* is known to occur on two isolated highland areas along the border between Panama and Colombia.

One of the least known species of the *Cryptotis thomasi* group is *Cryptotis avia* from the eastern Andean cordillera of Colombia. As part of a comprehensive revision of South American members of the genus, I reviewed the holotype and other possible specimens of this species. This paper presents my conclusions concerning the taxonomic status and relationships of *C. avia* and new data on the content and distribution of *Cryptotis colombiana* and *C. thomasi.*

Taxonomic Status of *Cryptotis avia* Allen 1923

Cryptotis avia was described by G. M. Allen (1923) based on a specimen collected by Nicéforo María in October 1922 from "El Verjón" (Fig. 1); the Páramo el Verjón is at an elevation of 3400 to 3600 m in the Andean highlands east of Bogotá, Colombia (Paynter & Traylor 1981). Aside from the holotype [MCZ 20091] in the Museum of Comparative Zoology, Harvard University, few records of this species exist. Tate (1932:226) noted two individuals in the American Museum of Natural History [AMNH], "both of them from the type locality and apparently collected at the same time as the type". Although he did not provide catalog numbers, Tate almost certainly was referring to two skins lacking skulls [AMNH 62789 and 62790], collected at El Verjón in October 1922 by Nicéforo María. A fourth specimen from near the type locality, and hence, potentially referable to *C. avia,* is MCZ 19995, a skin with skull collected at "Laguna del Verjón" by Nicéforo María in March 1922. MCZ 19995 was available to Allen (1923) when he described *C. avia* (note the catalog number is lower than that of the holotype), but he did not refer this specimen to the new species or use it for comparison. [The two specimens of *C. thomasi* that Allen (1923:37) mentions in his report as "lately received by the Museum of Comparative Zoölogy from the Instituto de la Salle" with the holotype of *C. avia* probably are MCZ 20090 and 20092, from the Páramo de Choachi.] The three specimens [MCZ 19995, AMNH 62789, 62790] from the type locality of *C. avia* are identified (correctly) as *Cryptotis thomasi* in their respective collections. In my searches of North American and Colombian systematic collections, I encountered only one specimen other than the holotype that clearly was referred to *C. avia*; this is AMNH 70597, from San Juan de Ríoseco (but see below). The lack of well identified specimens of *C. avia* in itself is not surprising given the generally poor representation of South American shrews in systematic collections. However, the holotype of *C. avia* is from the vicinity of Bogotá, a region that, as far as South American shrews are concerned, is relatively well collected.

The holotype of *Cryptotis avia* consists of a skin and skull of an adult animal of unknown sex. Allen (1923) described *C. avia* as being about the size of *Cryptotis nigrescens* [a small member of the genus] and suggested a possible close phylogenetic relationship between *C. avia* and both *C. nigrescens* and *Cryptotis mexicana nelsoni.* The skin is in poor condition and is under-

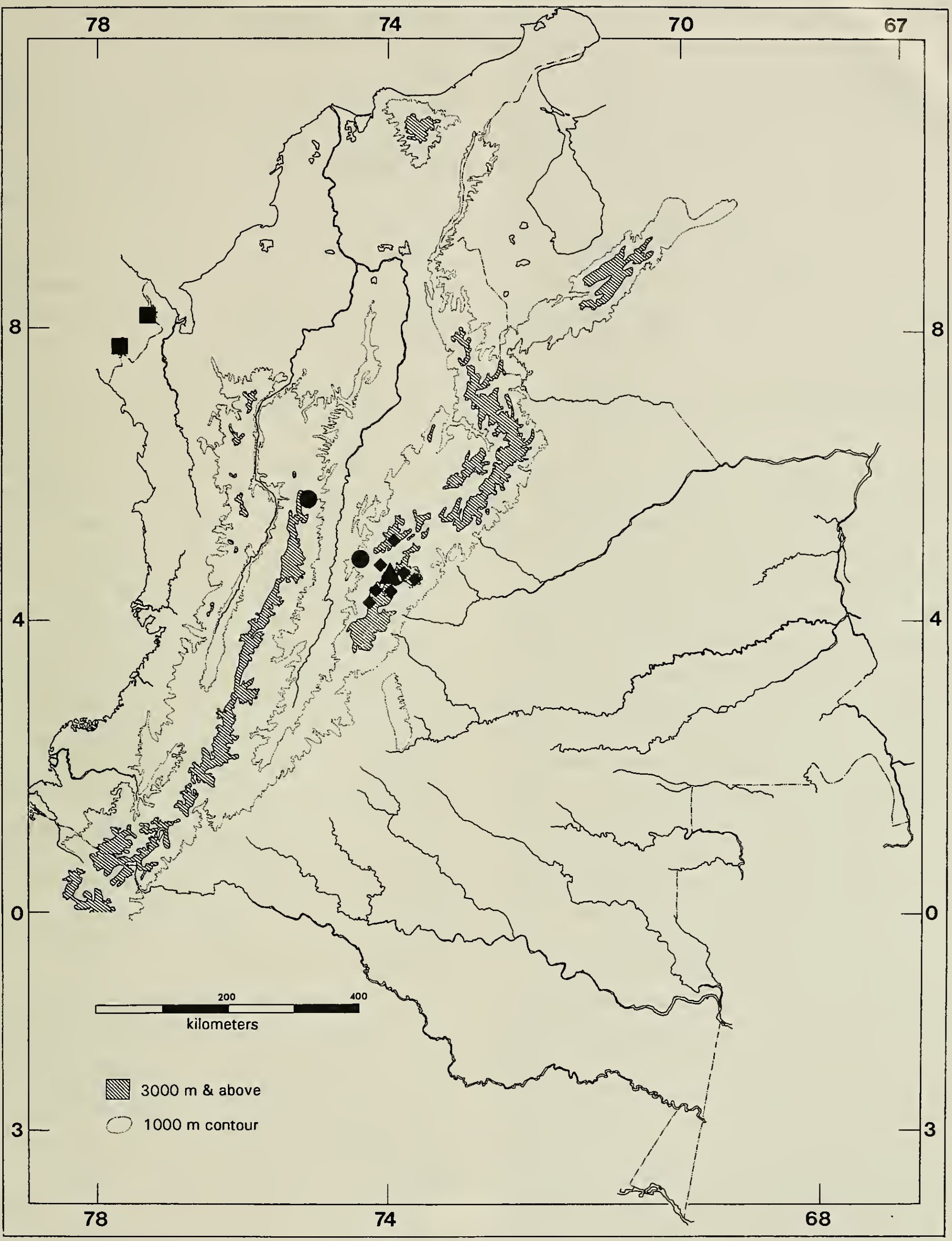

Fig. 1. Distributions of *Cryptotis mera* (solid squares) in western Panama and *Cryptotis colombiana* (filled circles) and *Cryptotis thomasi* (small, solid diamonds) in Colombia. *Cryptotis thomasi* also is know from the type locality of *Cryptotis avia* (solid triangle).

stuffed, giving the impression that it is indeed from a small animal. Unfortunately, total-length and tail-length measurements were not recorded at the time the animal was prepared, and Allen (1923) reported measurements obtained from the prepared skin. Subsequent treatments of *C. avia* have used its small size as the primary criterion for distinguishing it from *Cryptotis thomasi* and other Colombian members of the genus. Cabrera & Yepes (1960) indicated a head-and-body-length for *C. avia* of ca. 7 cm, compared to ca. 8 cm for *C. thomasi.* Choate & Fleharty (1974) distinguished *C. avia* from other South American taxa based on its shorter palatal-length and narrower maxillary-breadth, as well as its supposedly more homogeneous dorsal and ventral pelage coloration. Eisenberg (1989) gave total length of the *C. avia* as <100 mm.

In light of current knowledge of the taxonomic and morphological diversity in *Cryptotis,* Allen's (1923) description of *Cryptotis avia* no longer suffices to distinguish the species. In order to define this species more completely, I inspected the holotype and all potential topotypes of *C. avia,* reviewing the characteristics used by Allen and subsequent authors, as well as a suite of characters used to distinguish other species (Choate 1970; Woodman 1992; Woodman & Timm 1992, 1993).

Because *Cryptotis thomasi* occurs in the same region of the Eastern Cordillera as *Cryptotis avia,* it is logical to make comparisons between the two species. In order to adequately characterize *C. thomasi,* I inspected every specimen of this species readily available to me. On the basis of this study, I herein use the name *C. thomasi* only for shrews from highlands in the vicinity of Bogotá in the Eastern Cordillera of Colombia (Fig. 1); these sometimes are referred to *C. thomasi thomasi* (Cabrera 1958). *Cryptotis thomasi* (sensu stricto) is restricted to elevations above 2700 m, and the highland region around Bogotá almost certainly represents the true distributional limits of the species. Along the Eastern Cordillera, there are no specimens of *Cryptotis* from south of Paso de las Cruces, a valley that drops to below 2000 m. Similarly, there are no specimens known from the region between the northern border of Cundinamarca Dept. and the Páramo de Tama along the Venezuelan border, where *Cryptotis meridensis* occurs.

The skull of the holotype of *Cryptotis avia* is broken behind the dorsal foramina, and all of the posterior braincase is missing. This is unfortunate because several important characters can not be evaluated and because this makes the skull appear shorter than it originally was. Although the remaining rostrum and central portion of the skull and the mandible are small in comparison with many other specimens from South America, they are within the range of morphological variation for specimens of *Cryptotis thomasi,* and most craniomandibular measurements from the holotype of *C. avia* fall well within the range of size variation for that species (Table 1). To test this further, I carried out a principle components analysis of nine cranial measurements (breadth of zygomatic plate, postorbital-breadth, breadth across U1s, breadth across M2s, palatal-length, maxillary-toothrow-length, unicuspid-toothrow-length, molariform-toothrow-length, posterior width of M1) from the holotype of *C. avia* and 24 specimens of *C. thomasi.* The holotype of *C. avia* plots among the smallest specimens on the factor axis 1 (Fig. 2), which represents a combination of palatal-length and maxillary-toothrow-length (Table 2), but principle components analysis failed to identify any mensural characters or combinations of characters that clearly separate it from *C. thomasi.*

Characters preserved on the skin and skull of the holotype of *Cryptotis avia* are consistent with *Cryptotis thomasi.* As noted by Allen (1923), the foreclaws are elongate, although not particularly broad. In addition, the posterior border of the zygomatic plate is anterior to the posterior root of the maxillary process; U4 is mostly in line with the other upper unicuspids and is not obscured

Table 1.—Selected measurements of *Cryptotis* from Colombia. Measurements follow Woodman & Timm (1993).

	C. thomasi (*n* = 24)	*C. avia* (MCZ 20091 [holotype])	*C. colombiana* (FMNH 69816 [holotype], AMNH 70597)
Breadth of zygomatic plate (ZP)	2.0 + 0.2 1.7–2.4	1.9	2.0, 1.7
Postorbital-breadth (PO)	5.0 + 0.2 4.6–5.4	5.0	4.9, 4.6
Breadth across U1s (U1B)	2.7 + 0.1 2.5–2.9	2.7	2.6, x
Breadth across M2s (M2B)	6.2 + 0.2 5.9–6.5	5.8	6.3, 5.7
Palatal-length (PL)	9.3 + 0.3 8.6–9.7	8.7	8.8, 8.3
Maxillary-toothrow-length (TR)	8.1 + 0.2 7.7–8.5	7.8	7.7, 7.3
Unicuspid-toothrow-length (UTR)	2.8 + 0.1 2.4–3.0	2.6	2.5, 2.4
Molariform-toothrow-length (MTR)	5.8 + 0.1 5.5–6.0	5.5	5.8, 5.3
Posterior width of M1 (WM1)	1.9 + 0.1 1.8–2.1	1.8	1.8, 1.8
Length of mandible (ML)	7.0 + 0.2 6.6–7.4	6.5	6.9, 6.4
Height of coronoid process (HCP)	4.6 + 0.1 4.3–4.9	4.4	4.8, 4.5
Height of coronoid valley (HCV)	3.1 + 0.1 2.8–3.4	2.9	2.9, 2.8
Height of articular condyle (HAC)	4.3 + 0.1 4.1–4.6	4.0	4.1, 3.9
Breadth of articular condyle (BAC)	3.6 + 0.1 3.4–3.8	3.4	3.1, 3.0
Articular condyle to m3 (AC3)	5.7 + 0.2 5.5–5.8	5.6	4.9, 4.9
Length of lower toothrow (TRD)	6.3 + 0.2 6.2–6.7	6.0	6.0, 5.7
Length of m1 (m1L)	1.9 + 0.1 1.7–2.0	1.7	1.9, 1.8

in lateral view by P4; U1–U3 have narrow cusps with strongly concave posteroventral margins; dentition is bulbous; P4 and M1 are only slightly emarginated posteriorly; the anterior element of the ectoloph of M1 is reduced relative to the posterior element; the protoconal basin of M1 is reduced relative to the hypoconal basin; M3 is relatively complex and possesses a metacone; the coronoid process of the mandible is low and narrow, and its anterior border has a relatively shallow slope; the articular condyle is high and narrow; the lower sigmoid notch is shallow; p3 is long and low; m3 lacks an entoconid. Together, these characteristics serve to distinguish the holotype of *C. avia* from *Cryptotis parva, Cryptotis mexicana* (and its close relatives), members of the *Cryptotis nigrescens* group, and most other South American shrews.

The type locality of *Cryptotis avia* (Fig. 1) is within the established range of *Cryptotis thomasi,* and there are no characters, including size, that distinguish the holotype from that species. Similarly, the three other specimens [AMNH 62789, 62790, MCZ 19995] from El Verjón, including the two that Tate (1932) probably referred to *C. avia,* are indistinguishable from *C. thomasi.* For these reasons, *C. avia* should be considered conspecific with, and a junior synonym of, *C. thomasi.* Consequently, the synonymy of *C. thomasi* is amended as follows:

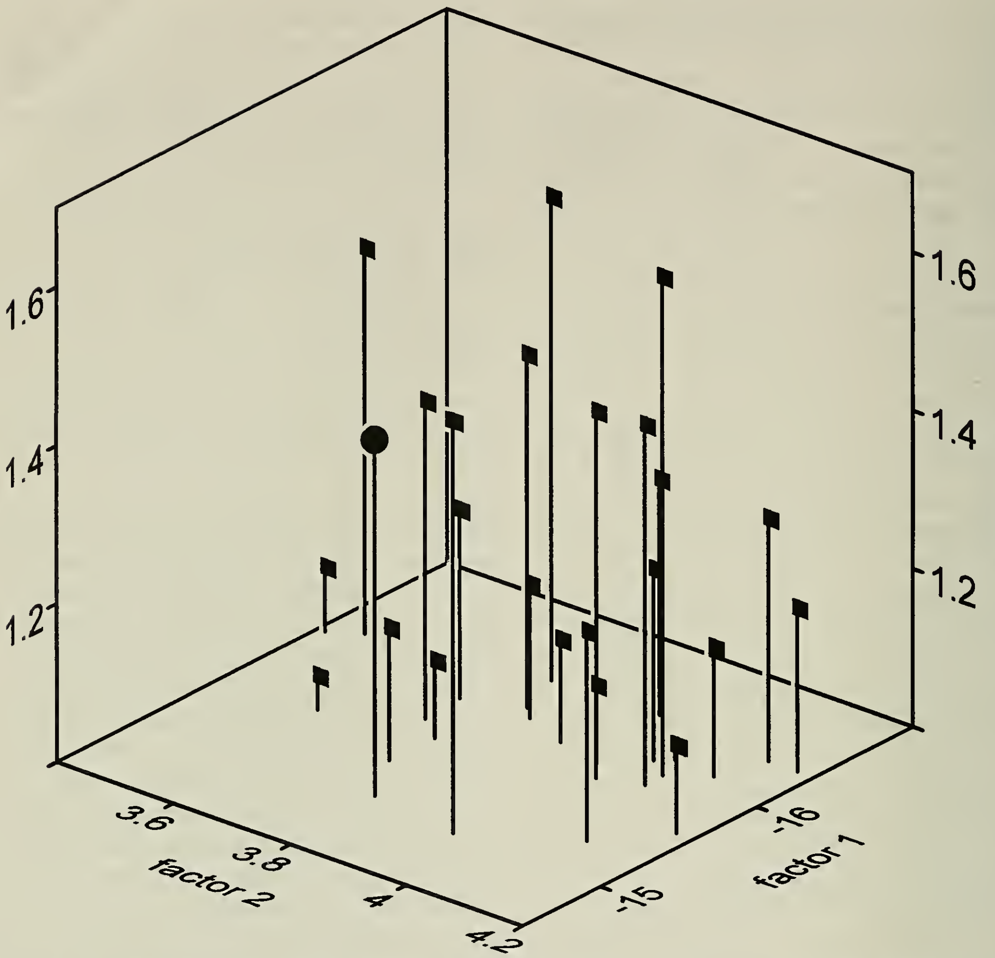

Fig. 2. Three-dimensional plot of the holotype of *Cryptotis avia* (solid circle) and 24 specimens of *Cryptotis thomasi* (solid squares) on factor axes 1, 2, and 3 from principle components analysis of nine cranial measurements. The first axis represents palatal length and maxillary toothrow length (Table 2); the second axis is postorbital breadth and breadth across M2s; the third axis is postorbital breadth and zygomatic breadth contrasted with breadth across M2s.

Cryptotis thomasi (Merriam) 1897

Blarina thomasi Merriam, 1897:227.

B.[*larina*] *Thomasi* Thomas, 1898:457.

[*Blarina*] *thomasi* Trouessart, 1905:138; Anthony, 1921:5.

B.[*larina*] *thomasi* Thomas, 1912:409; Stone, 1914:16.

C.[*ryptotis*] *thomasi* Thomas, 1921:354; Choate & Fleharty, 1974:1 (in part); Corbet & Hill, 1980:28 (in part); Corbet & Hill, 1991:32 (in part).

Cryptotis thomasi G. M. Allen, 1923:37 (in part); Tate, 1932:226; Cabrera & Yepes, 1960:54; Hershkovitz, 1969:18 (in part); Honacki et al., 1982:86 (in part); Eisenberg, 1989:71 (in part); Hutterer, 1993 (in part).

Cryptotis avia G. M. Allen, 1923:37; Tate, 1932:226; Honacki et al., 1982:85; Eisenberg, 1989:70; Hutterer, 1993.

[*Cryptotis*] *avia* Cabrera, 1925:133.

[*Cryptotis*] *thomasi* Cabrera, 1925:135.

Cryptotis avius Cabrera, 1958:46.

Cryptotis thomasi thomasi Cabrera, 1958: 46.

Table 2.—Factor loadings from principal components analysis of cranial variables of the holotype of *Cryptotis avia* and 24 *Cryptotis thomasi*. Abbreviations are explained in Table 1.

Variable	Factor 1	Factor 2	Factor 3
PL	−0.643	−0.318	−0.074
TR	−0.553	−0.220	0.134
MTR	−0.296	0.205	0.171
M2B	−0.276	0.641	−0.502
UTR	−0.231	−0.030	−0.219
ZP	−0.161	−0.064	0.434
WM1	−0.126	0.245	−0.155
PO	−0.107	0.556	0.654
U1B	−0.103	0.152	−0.081

C.[*ryptotis*] *avia* Cabrera & Yepes, 1960: 55; Choate & Fleharty, 1974:1; Corbet & Hill, 1980:27; Corbet & Hill, 1991:31.

Specimens examined (42).—Colombia: no locality (MCZ 27596). Cundinamarca: Bogotá (AMNH 34605); Bogotá, San Cristóbal, 2800–2900 m (FMNH 71030–71034, 71036, 71037); Bogotá, San Francisco, 3000–3500 m (FMNH 71023–71029, 71035); Chipague [Chipaque] (USNM 251960); El Verjón [Páramo el Verjón] (AMNH 62789, 62790, MCZ 20091—holotype of *C. avia*); Laguna del Verjón, (MCZ 19995); Fusayasugá (MCZ 27599); Hacienda Santa Barbara, Monserrate, Bogotá, D. E., 3300 m (ICN 9649, 9650, 9652, 9658); Páramo de Bogotá, 2900 m (AMNH 37381); Páramo de Chisacá, km 30, 3100 m (ICN 5223); Páramo de Choachí, 3000 m (AMNH 38405, MCZ 19885, 20090, 20092, 27597, 27598); Páramo de Monserrate, near Cerro del Rompedro, 3200 m (ROM 51870); Plains of Bogotá (USNM 80903–80906); Reserva Biológica Carpanta, Municipio Junin, 3000 m (ICN 10995, 10996); Represa del Neusa, Tausa (ICN 9659).

Distribution of *Cryptotis colombiana* Woodman & Timm (1993)

The only other specimen currently identified in a major systematic collection as *C. avia* is AMNH 70597. This consists of a skin and skull of a young adult (toothwear class 1 of Rudd 1955) of unknown sex collected in November 1925 by Nicéforo Maria (original number 111) at San Juan de Ríoseco, Cundinamarca Dept., Colombia (Fig. 1). San Juan de Ríoseco (4°51′N, 74°38′W) is at ca. 1300 m in the western foothills of the Eastern Cordillera of Colombia, about 18 km NE of Ambalema (Paynter & Traylor 1981) and ca. 70 km west of the type locality of *C. avia*. The specimen is a small- to medium-sized *Cryptotis* (Table 1), and given its similar preparation and close geographical association with the holotype of *C. avia*, it is easy to see why it was referred to that species.

The skin of the AMNH specimen is in fair condition, but the left hind leg is detached. The braincase is broken, although most pieces appear to be present. The upper dentition lacks LU1 and LU2. The right mandible is missing, and the left mandible lacks I1. This individual possesses a number of characters that distinguish it from *Cryptotis thomasi* (and other members of the *C. thomasi* group) and that place it within the *Cryptotis nigrescens* group. It has small forefeet and small foreclaws; broad upper unicuspids with straight posteroventral occlusal surfaces; a relatively shorter, broader mandible; a relatively tall coronoid process of the mandible, with steep, concave anterior border; the articular condyle is shorter and broader; p4 is shorter and higher crowned.

AMNH 70597 shares a number of cranial characteristics with the holotype of *Cryptotis colombiana*. These include: two large dorsal foramina close to the sagittal suture; no ventral extension of the sinus canal nor an associated foramen posterior to the dorsal articular facets; a moderately well-developed foramen dorsal to each dorsal articular facet; the high, wide anterior process of petromastoid (Fig. 3); a large foramen on the posteromedial edge of the tympanic process of the petromastoid. The latter two characters appear to be derived within the *Cryptotis nigrescens* group. An enlarged

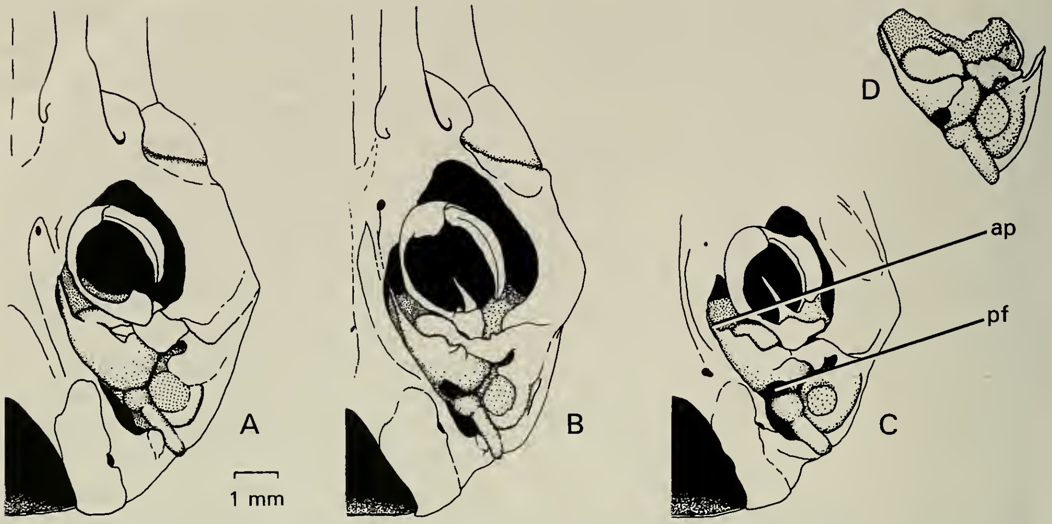

Fig. 3. Ventral view of the left tympanic region of skulls of *Cryptotis,* illustrating the location of the anterior process of the petromastoid (ap) and the foramen on the posterior edge of the tympanic process of the petromastoid (pf): A) *C. meridensis* (FMNH 12981), B) *C. thomasi* (ICN 9650), C) the holotype of *C. colombiana* (FMNH 69816), and D) the disarticulated right otic capsule of *C. colombiana* (AMNH 70597). The left anterior process of the petromastoid of FMNH 69816 is incomplete (but see Woodman & Timm 1993: Fig. 18).

anterior process of the petromastoid is not found in any other member of the genus *Cryptotis,* nor in any species of *Blarina* or *Sorex* (the sister taxa of *Cryptotis*—George 1986) that I have inspected. A large foramen in the tympanic process is found among some South American members of the *Cryptotis thomasi* group, including *C. thomasi* (Fig. 3). However, it is not found in any other member of the *C. nigrescens* group, nor is it present in any species of any other genus of soricine that I have inspected. There is a temptation to suggest that this character might be environmentally-induced, given the Andean distribution of *C. colombiana* and species in the *C. thomasi* group. However, not all Andean members of the *C. thomasi* group possess this foramen (e.g., *Cryptotis meridensis*). Moreover, *C. colombiana* and *C. thomasi* do not inhabit similar habitats within the Andes. *Cryptotis thomasi* is restricted to high elevation (>2700 m), moist paramo, whereas *C. colombiana* occurs at much lower elevations (<2000 m) and may occur in a wider variety of habitats, including the relatively dry, western side of the Eastern Cordillera.

If an enlarged anterior process of the petromastoid and a large foramen in the tympanic process are derived within the *Cryptotis nigrescens* group, the two characters link the holotype of *Cryptotis colombiana* and AMNH 70597 phylogenetically and distinguish them from all other members of the *C. nigrescens* group.

Several characters distinguish the two specimens of *Cryptotis colombiana.* The AMNH specimen is smaller overall and not as robust as the holotype; the rostrum, postorbital area, and palate are narrower; the zygomatic plate is relatively narrower; the upper molars are much smaller, resulting in a shorter molariform toothrow (Table 1); the foramen on the posterior edge of the tympanic process of the petromastoid is more medially located (Fig. 3); the articular process of the mandible is much narrower and there is a distinct notch between the upper and lower articular surfaces; there is a vestigial entoconid in the talonid of m3; the teeth are more heavily pigmented and not nearly as bulbous.

The AMNH specimen is from the Eastern Cordillera of the Colombian Andes, whereas the holotype of *Cryptotis colombiana* is from the Central Cordillera (Fig. 1). With the exception of the specialized *Cryptotis mayensis* from the Yucatan Peninsula, Mexico, the *Cryptotis nigrescens* group consists of middle- to high-elevation species that do not occur below 800 m (Woodman & Timm 1993). The Central and Eastern Cordilleras are separated by the deep valley of the Río Magdalena that flows at elevations below 500 m north of Neiva. The vegetation of the valley is quite distinct from the upper slopes of either cordillera (R. Anderson, in. lit.), and the valley probably acts as an effective barrier to gene flow. Additional collections of these shrews will help us to better understand their distribution in Colombia and to understand the range of morphological variation in the characters listed above. However, the current scarcity of specimens of *C. colombiana* prevents adequate appraisal of variation within this species, and it is most helpful at this time to refer AMNH 70597 to *C. colombiana.* The two specimens appear to be more closely related phylogenetically to each other than to any other known taxon, and whether they represent distinct species or are members of a single, morphologically diverse species, they have the same biogeographic significance relative to the distribution and history of the *C. nigrescens* group. Woodman & Timm (1993) hypothesized that *C. colombiana,* or a close relative, should occur at high elevation in the Western Cordillera of Colombia, which is located between the known geographic ranges of *C. colombiana* and its geographically closest relative in the *C. nigrescens* group, *C. mera.* The discovery of *C. colombiana* in the Eastern Cordillera reinforces that idea.

The account for *Cryptotis colombiana* is amended to include the new material:

Cryptotis colombiana
Woodman & Timm 1993

Cryptotis thomasi Hershkovitz, 1969:18 (in part).

Cryptotis colombiana Woodman & Timm, 1993.

Specimens examined (2).—Colombia: Antioquia: Sonsón, 15 km E of Río Negrito, 1750 m (FMNH 69816—holotype). Cundinamarca: San Juan de Ríoseco (AMNH 70597).

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A new Atlantic species of *Acanthemblemaria* (Teleostei: Blennioidei: Chaenopsidae): Morphology and relationships

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Abstract.—*Acanthemblemaria johnsoni* is described from six specimens collected from shallow coral reefs at the north end of the Caribbean island of Tobago. The new species differs from all other Atlantic species of *Acanthemblemaria* by the combined spinous and soft dorsal-fin ray count of XXIV, 12–13. Evolutionary relationships of the new species are discussed in relation to the phylogeny of the genus proposed by Hastings (1990).

Shallow-water rotenone collections of fishes were made at the Caribbean island of Tobago in September 1990 by members of the Division of Fishes, National Museum of Natural History, and the Marine Fisheries Section, Tobago Fisheries, in a collaborative survey of the shorefishes of Tobago. Among the fishes collected were six specimens of the chaenopsid genus *Acanthemblemaria* that could not be identified using published descriptions and keys for the Atlantic members of the genus (Smith-Vaniz & Palacio 1974, Johnson & Brothers 1989). The small blennioid fishes of the genus *Acanthemblemaria* typically inhabit tubes in shallow-water coral reefs and are distinguished from other chaenopsids by having spiny cranial bones and two rows of teeth on the palatine (Stephens 1963, Smith-Vaniz & Palacio 1974). Our investigation of Atlantic *Acanthemblemaria* indicates that the six Tobago specimens represent an undescribed species.

The addition of the new species brings the number of known species in the genus to 17 (18 including "new species A" from the eastern Pacific, see Hastings 1990); 10 in the tropical western Atlantic and 7 in the eastern Pacific, making *Acanthemblemaria* the most speciose genus in the family Chaenopsidae. The evolutionary history of the genus appears to show the influence of the emergence of the Isthmus of Panama, with two species pairs following the eastern Pacific-Caribbean distributional track (Hastings 1990). Using the characters examined by Hastings (1990), we hypothesize the phylogenetic relationships of the new species to other members of the genus and comment on its historical biogeography.

Methods

Counts and measurements generally follow Stephens (1963). Pore terminology is that of Smith-Vaniz & Palacio (1974) as modified by Johnson & Greenfield (1976) and Rosenblatt & McCosker (1988). All measurements were made to the nearest tenth of a millimeter using an ocular micrometer. Vertebral counts were made from radiographs. Tooth and gill-raker counts, as well as assessments of Hastings' (1990) os-

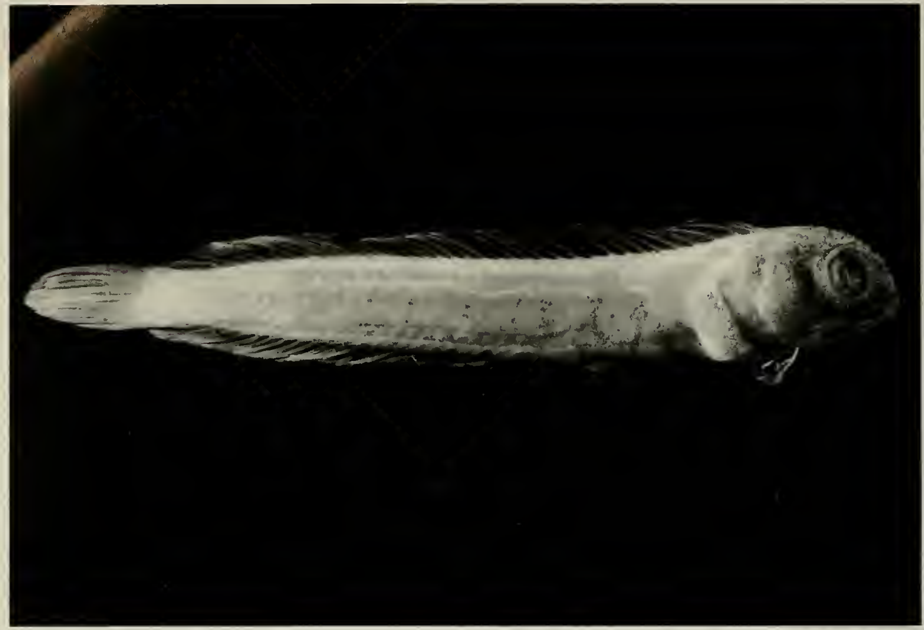

Fig. 1. *Acanthemblemaria johnsoni,* new species, holotype, USNM 317210, male, 24.0 mm SL, Tobago. Photograph by Carl Hansen, USNM.

teological characters, were made from a single cleared and stained specimen. Institutional abbreviations follow Leviton et al. (1985).

We reanalyzed Hastings' (1990) character matrix for *Acanthemblemaria* species including character states for the new species. The modified data set was analyzed using heuristic methods in PAUP 3.0. Multistate characters were treated as unordered and all characters were weighted equally.

Acanthemblemaria johnsoni, new species
Figs. 1, 2

Diagnosis.—An *Acanthemblemaria* differing from all other Atlantic members of the genus by its high number of dorsal-fin spines (XXIV) in combination with a low number of dorsal-fin soft rays (12–13, $\bar{X}$ = 12.7), and in having blunt cranial spines, each spine covered with a simple, fleshy, tapering papilla. The new species differs from all Pacific *Acanthemblemaria* in having a low number of dorsal-fin soft rays in combination with several osteological features (see "Relationships"), including equally spaced lateral ethmoid spines, the ventralmost spine not enlarged or separated from the others by a notch.

Counts and measurements in mm of holotype.—Dorsal fin XXIV, 13; anal fin II, 25; pectoral fin 13; pelvic fin I, 3; caudal fin 13 (7+6). Standard length 24.0; head length 6.0; head depth 4.0; upper jaw length 2.8; snout length 0.9; orbit length 1.8; least interorbital width 1.2; predorsal length 4.8; preanal length 10.9; caudal peduncle length 2.1; caudal peduncle depth 1.7; supraorbital cirrus length 0.8; pectoral fin length 2.3; longest dorsal-fin spine length 2.5.

Description.—Dorsal-fin spines XXIV, soft rays 12–13 ($\bar{X}$ = 12.7); total elements 36–37 ($\bar{X}$ = 36.7). Anal fin II, 24–25 ($\bar{X}$ = 24.7). Pectoral-fin rays 13. Segmented caudal-fin rays 12–13 ($\bar{X}$ = 12.8). Pelvic-fin rays I, 3. Vertebrae: precaudal 11; caudal 31–32 ($\bar{X}$ = 31.8); total 42–43 ($\bar{X}$ = 42.8).

Body elongate and slender as in other members of the genus. Similar in form to *A. greenfieldi* which lies in the middle of

Fig. 2. (Top) *Acanthemblemaria johnsoni,* holotype, USNM 317210, photograph by Carl Hansen, USNM; (Bottom) head spines of *A. johnsoni* showing fleshy papillae.

the continuum between the very slender and elongate *A. paula* and *A. chaplini,* and the more robust forms such as *A. rivasi.* Head depth 4.8 to 6.0 in SL; head length 3.5 to 4.2 in SL.

Cephalic sensory pores: common 1; mandibular 4; preopercular 4; posttemporal 4; lateral supratemporal 3; median supratemporal 3; supraorbital 4; posterior infraorbital 3; anterior infraorbital 3; frontal 3–4; median interorbital 1; anterior frontal 1; nasal 1.

Vomerine teeth 6–8, arranged in a crescent. Palatine with two rows of teeth, approximately equal numbers in each row, 7–8. Premaxilla with outer row of 10–11 teeth. Anteriormost 4 teeth relatively large and incisiform. Remaining teeth conical with tips curving slightly posteriorly, teeth decreasing in size posteriorly. Inner band of minute, conical, posteriorly or medially curved teeth. Anterior region of dentary with approximately three rows of teeth: outer row with approximately 4 large, incisiform teeth, similar to those in premaxillae; inner band with approximately 4–5 small, conical teeth; a band of minute, posteriorly curved teeth lying between inner and outer rows. Posteriorly, a single row of approximately 5–6 conical teeth occurring on each dentary, teeth decreasing in size posteriorly. Gill rakers 2 + 6.

Anterior and dorsal region of head ornamented with dorsally or anteriorly directed blunt spines, each spine covered with a simple, tapering fleshy papilla (Fig. 2B). Posterior apex of spiny patch not extending more than half the distance between posterior rim of orbit and dorsal-fin origin. Supraorbital rim of each frontal bearing a row of anterolaterally directed blunt spines beginning slightly posterior to midline of orbit and continuing onto lateral ethmoid, which bears three to four spines. Posterodorsal rim of supraorbital flange smooth. Ventral edge of anterior region of first infraorbital with several ventrally directed blunt spines. Upper margin of first infraorbital also with ventrally directed spines. Second infraorbital with a patch of rugosities centrally where infraorbital sensory canal opens in several places to surface; margins of second infraorbital smooth. Each nasal with six spines, four arranged in a semicircle around anterior nostril; a single spine projecting anteriorly from each nasal at the anterior symphysis. Nasal bones adjacent for most of their length, separating posteriorly, each limb bearing a dorsally directed spine near its posterior terminus. A row of spines on each frontal between orbits, separated by a median groove. Posterior to midorbit the interorbital rows of spines broadening into a diamond-shaped patch; weakest spine development occurring in posterior apex of this patch.

Dorsal-fin origin over posterior edge of preopercle. Membrane between spines and soft rays continuous between tips of adjacent elements, slightly incised. Each spine and soft ray curved posteriorly at distal end. Last spine approximately one half as long as first soft ray, creating a prominent notch at junction of spinous and soft portions of dorsal fin. Membrane between adjacent rays of anal fin also incised, each element in anal fin curving posteriorly at distal end. Last dorsal and anal rays connected by a membrane to caudal peduncle. Caudal fin slightly rounded, central rays longest. Membrane with notches between each ray creating a scalloped margin. Pectoral fin rounded with a weakly scalloped margin. Lower three rays thickened and bent such that distal ends curve dorsally. Central pelvic-fin ray longest. Membrane between pelvic-fin rays notched.

Supraorbital cirrus originating from dorsal membrane of eye. Cirrus usually a simple, distally tapering tentacle, rarely bifid (on right side of one male and the only female) or trifid (left side of the female); when divided, branching occurring near midpoint of cirrus. Anterior nostril surrounded by a sheath of skin which is surmounted at posterior region by a bifid or trifid cirrus. Supraorbital cirrus 1.3–2.3 in eye.

Color.—Color descriptions are based on specimens preserved in alcohol. Background color light tan. Head darkly pigmented. Scattered melanophores on dorsal surface of head, denser in larger specimens. Pigmentation darkest on cheek and opercular region with a prominent dark, oval-shaped patch of melanophores just posterior to each orbit. Heavy pigmentation of head continuing onto anterior trunk in a diagonal band that begins at dorsal-fin origin and extends to dorsal edge of pectoral-fin base. Both supraorbital and nostril cirri with heaviest pigment at distal ends but bearing melanophores along entire length. Melanophores also found on dorsal region of orbital membrane around base of supraorbital cirrus. On underside of head, pigment concentrated on branchiostegal rays such that they appear almost black. Membrane between branchiostegals lighter in color. Indistinct transverse band across middle of lower jaw. In the female specimen, transverse band unpigmented. Anterior third of lower jaw and anterior portion of upper jaw lightly pigmented relative to rest of head.

Anterior two thirds of body barred, bars well developed in larger individuals, less distinct in smaller individuals. Anteriormost bar typically beginning above pectoral-fin base and posteriormost occurring near first dorsal soft ray. Each bar approximately as wide as distance between two or three dorsal-fin elements and darkest at lateral midline of body. Posterior third of body with few scattered melanophores, but otherwise unpigmented. On ventral midline, melanophores concentrated between pelvic-fin base and vent; darkest between pectoral fins. This pigment darkest in larger specimens and may not reach all the way to the vent in smaller specimens. Ventral midline pigment extending up sides of trunk between anal-fin origin and pelvic fins, forming dorsal extensions that are confluent with barred pattern on sides of trunk.

Pigment on dorsal fin concentrated on distal ends of, and membrane between, spines I through approximately IX. Pigment darkest on and between spines I-IV, melanophores occurring along entire length of spines. Little or no pigment posterior to spine XVII or XVIII. Soft rays of dorsal fin unpigmented except for a few, faint melanophores along edges of some rays. Anal-fin pigment heaviest on spines I and II and continuing at least to ray 2 and sometimes to ray 15. Pigment heaviest on rays, but also scattered on membrane. Little or no pigment on anal fin posterior to ray 15. Single female specimen with no detectable pigment on anal fin. Caudal fin unpigmented except for faint melanophores along edges of some central elements. Pelvic fins with pigment on rays and membrane; medial rays darkest, outer rays lightest. Pectoral-fin base with even scattering of melanophores, slightly darker posteroventrally. Melanophores also occurring sometimes at proximal ends of fin rays, but central and distal regions unpigmented.

Color in life unknown.

Sex.—Individuals can be sexed based on genital morphology (Böhlke 1957). Males have a single papilla at the posterior margin of the anus whereas females have a papillar fringe surrounding the anus. There appears to be little sexual dimorphism in pigmentation or morphology, except for the lack of anal-fin pigmentation on the single female specimen. The small number of specimens, five males and one female, precludes conclusive statements regarding sexual differences.

Comparisons.—Acanthemblemaria betinensis and *A. greenfieldi* are the only other Atlantic species of *Acanthemblemaria* known to have 24 dorsal-fin spines (Smith-Vaniz & Palacio 1974). The modal number of dorsal-fin spines in *A. betinensis* is 23 ($\bar{X} = 23.2$) and 22 ($\bar{X} = 22.2$) in *A. greenfieldi* (Smith-Vaniz & Palacio 1974). *Acanthemblemaria betinensis* can be further distinguished from *A. johnsoni* by its dark background body coloration and by having two common pores versus only one in the new species. *Acanthemblemaria greenfieldi* can be further distinguished from *A. johnsoni* by its weakly developed cranial spines and complexly branched supraorbital cirri. Like, *A. johnsoni, A. maria* and *A. rivasi* usually have 12 or 13 dorsal-fin soft rays, and *A. spinosa* sometimes has 13 (Smith-Vaniz & Palacio 1974); however, *A. maria* has 23 or fewer dorsal-fin spines, and *A. spinosa* and *A. rivasi* each has 22 or fewer dorsal-fin spines (Smith-Vaniz & Palacio 1974, Johnson & Brothers 1989). The remaining Atlantic species of *Acanthemblemaria* never have 24 dorsal-fin spines or 12 or 13 dorsal-fin rays, and can be further distinguished from the new species as follows: *A. medusa* has very weak development of cranial spines, is largely unpigmented, and has a very complex and highly branched supraorbital cirrus; *A. aspera* has sharp cranial spines, a highly branched supraorbital cirrus, and very little pigment on the body; *A. paula* has a very small but elongate body and sharp cranial spines; and *A. chaplini* has a highly branched and complex supraorbital cirrus, a very elongate body, and weak development of the cranial spines.

The blunt head spines of *A. johnsoni* are more similar to those of some eastern Pacific *Acanthemblemaria* species than to those of most Atlantic species. As noted below, *A. johnsoni* shares many features with most eastern Pacific *Acanthemblemaria*.

Relationships.—Hastings (1990) hypothesized phylogenetic relationships among 17 species of *Acanthemblemaria.* In general, his phylogeny (Hastings 1990: fig. 1) suggests that the western Atlantic species are cladistically primitive members of the genus, forming a succession of sister groups to a clade comprising primarily eastern Pacific species. Exceptions include a sister-group relationship between the eastern Pacific *A. castroi* and western Atlantic *A. rivasi* within the eastern Pacific clade, and a sister-group relationship between the eastern Pacific *A. exilispinus* and western Atlantic *A. betinensis* below the eastern Pacific clade. Following Stephens (1963), and using evidence from a preliminary parsimony analysis of all chaenopsid genera, Hastings (1990) considered *Ekemblemaria* as the first outgroup for *Acanthemblemaria.* Hastings (1992a) provided an additional synapomorphy of those genera. The sister group of the *Acanthemblemaria* + *Ekemblemaria* clade was not clear from Hastings' (1990) study, and he constructed a hypothetical second outgroup for use in analyzing relationships within *Acanthemblemaria.* In a more thorough phylogenetic analysis of chaenopsids, Hastings & Springer (1994) suggested that the sister group of the *Acanthemblemaria* + *Ekemblemaria* clade is a group of seven genera that form two monophyletic groups: the "*Chaenopsis* clade," comprising *Chaenopsis, Lucayablennius, Hemiemblemaria, Emblemaria,* and *Tanyemblemaria,* and the "*Coralliozetus* clade," including *Coralliozetus, Protemblemaria,* and *Emblemariopsis.* Although a single cladistically primitive genus from these clades has not been identified, *Emblemaria* and *Tanyemblemaria* appear to be cladistically primitive members of the *Chaenopsis* clade (Hastings 1992b), and *Protemblemaria* and *Emblemariopsis* may be primitive with respect to *Coralliozetus* (P. A. Hastings, pers. comm., July, 1995). In efforts to have a tangible second outgroup for analysis of relationships of *A. johnsoni* within the genus, we added character states for *Protemblemaria* to the data matrix. Although we recognize that further study of chaenopsid phylogeny is needed to test the appropriateness of using *Protemblemaria* as a second outgroup for *Acanthemblemaria,* we note that Stephens (1963) characterized *Protemblemaria* as having numerous primitive characteristics, and he believed it is the most primitive genus in the Chaenopsidae.

Character states of *A. johnsoni* for the 60 characters of Hastings (1990) are, in numerical order, as follows: 1, 2, 2, 0, 0, 1, 1, 0, 1, 0, 1, 2, 0, 0, 1, 1, 2, 0, 1, 2, 1, 1, 0, 1, 1, 1, 0, 1, 0, 0, 0, 0, 1, 0, 0, 1, 1, 0, 0, 1, 1, 2, 0, 0, 1, 0, 0, 0, 1, 0, 2, 2, 0, 2, 0, 0, 1, 0, 0, and 0. We coded character 52, the shape of the supraorbital cirrus, as state 2 (unbranched or rarely branched once near tip). The single female specimen of *A. johnsoni* has one bifid cirrus and one trifid cirrus, and one male specimen has one bifid cirrus. The supraorbital cirri in all other specimens of the new species are simple. We coded character 53, the length of the supraorbital cirrus, as state 0 (one half to one orbital diameter) versus state 1 (less than or equal to one half the orbital diameter). The length of the supraorbital cirrus in *A. johnsoni* varies from less than one half the orbital diameter to greater than one half the orbital diameter, a condition intermediate between the two character states defined by Hastings (1990). Coding the length of the supraorbital cirrus in *A. johnsoni* as short (state 1) does not affect the topology of the tree. We coded character 54, the shape of the nasal cirrus, as state 2 (branched more than once). The nasal cirri in *A. johnsoni* are either bifid (state 1) or trifid (state 2).

Character states of *Protemblemaria* for the 60 characters of Hastings (1990) are: 0, 0, 0, 0, 0, 0, ?, 0, 0, ?, ?, 0, 1, 0, 0, ?, 0, ?, 0, 0, 0, 0, 0, 0, 0, 1, 0, 0, 0, 0, 1, 0, 0, 0, 1, 0, 0, 0, ?, 0, ?, 2, 0, 0, 0, 0, ?, 0, 1, 0, 2, 0, 0, 2, 0, ?, ?, ?, ?, and 0. Most question marks indicate characters not present in *Protemblemaria* (e.g., head spines), but we coded two characters, 39 and 47, as "?" due to the presence of a condition that does not match any states defined by Hastings (1990). The vomer of *Protemblemaria* (character 39) has three teeth forming a crescent with a single tooth posteriorly, the shape of the patch being neither a crescent nor a circle; and *Protemblemaria* has a single ossified thread (vs. none or two) on the posterior inner margin of the pelvis (character 47). Coding those characters in *Protemblemaria* with a new state number rather than a "?" has no effect on tree topology.

Although we did not stipulate a transformational order for any of the 12 multistate characters in the analysis a priori as Hastings (1990) did for three features (his characters 2, 3, and 7), our PAUP analysis yielded the same relationships as those suggested by Hastings (1990: fig. 1) for the 17 species of *Acanthemblemaria* he examined, regardless of whether we used *Protemblemaria* or Hastings' hypothetical taxon as the second outgroup. The advantage of using *Protemblemaria* is that only 12 of the 60 characters are coded as "?" (not applicable, or other than Hastings' states) versus 24 characters coded as "?" in Hastings' hypothetical second outgroup. Our phylogeny differs from Hastings only in the number of characters supporting some nodes (compare Fig. 3 and Table 1 with Hastings 1990: fig. 1 and Table 1).

Our study suggests that *A. johnsoni* is the sister group of a clade comprising *A. crockeri, A. balanorum, A. rivasi, A. castroi, A. macrospilus,* "new species A" of Hastings (1990), *A. hancocki,* and *A. stephensi* (Fig. 3), all of which are eastern Pacific taxa except *A. rivasi* and *A. johnsoni.* All eastern Pacific species except *A. exilispinus* are members of this clade, and herein we refer to species above *A. johnsoni* on the cladogram as the "eastern Pacific clade." Derived features supporting a sister-group relationship between *A. johnsoni* and the eastern Pacific clade are as follows (character numbers correspond to those of Hastings 1990): (33)—ventral portion of metapterygoid not reaching anteriorly to ectopterygoid; (49)—a notch present at the juncture between the spinous and soft dorsal fins, the last spine less than one half the length of the first ray; (51)—membrane posterior to the dorsal and anal fins attached to the caudal peduncle; and (52)—supraorbital cirrus unbranched or rarely branched once near the tip. As noted in the description of *A. johnsoni* above, the supraorbital cirrus is occasionally bifid or trifid, but it is never highly branched in a pinnate or palmate manner as in most Atlantic *Acanthemblemaria* and the Pacific *A. exilispinus.* It is thus somewhat intermediate between the primitive, highly branched condition found in primitive *Acanthemblemaria* and the unbranched condition of most eastern Pacific species; our placement of *A. johnsoni* between these two groups is con-

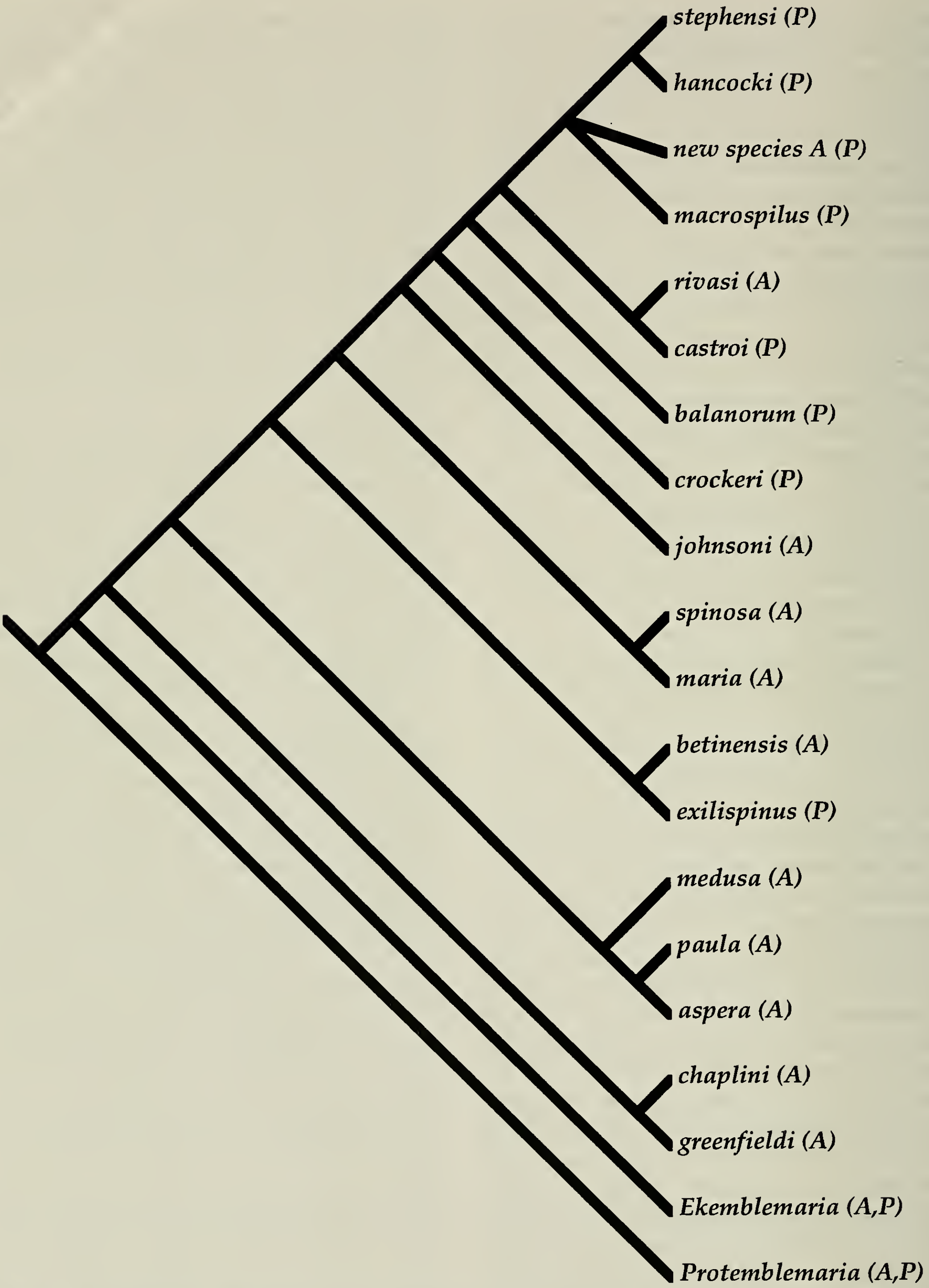

Fig. 3. Hypothesized relationships of *Acanthemblemaria* species. (A) = western tropical Atlantic; (P) = eastern Pacific.

Table 1.—List of apomorphic characters that support the hypothesized relationships among *Acanthemblemaria* species as depicted in Figure 3. For a definition of characters and states, see Hastings (1990: appendix table 1). Character states are given in parentheses. Ambiguous characters that support nodes when optimized using ACCTRAN are indicated by an "*".

Description of group	Apomorphic characters
Acanthemblemaria	6(1), 12(2), 34(2)*, 40(1)
chaplini + *greenfieldi*	44(1), 51(1), 55(1)
medusa + *aspera* + *paula* and above	2(1), 9(1)*, 19(1), 20(2), 25(1), 36(1)
medusa + *aspera* + *paula*	13(1), 23(1), 39(1), 52(1)
aspera + *paula*	34(1)*, 51(1), 57(1)
betinensis + *exilispinus* and above	1(1), 7(1), 15(1), 22(1), 26(1), 29(1)*, 34(0)*, 35(1), 37(1)*, 41(1), 42(0)
betinensis + *exilispinus*	12(1), 20(1), 56(1), 58(1), 60(1)
spinosa + *maria* and above	2(2), 14(1)*, 24(1), 28(1)
spinosa + *maria*	4(1), 5(1), 7(2), 27(1), 30(1), 37(0)*, 48(1)
johnsoni and above	29(0)*, 33(1), 49(1), 51(2), 52(2)
johnsoni	14(0)*, 16(1), 35(0), 42(2), 45(1), 57(1)
crockeri and above	11(0)*, 18(1), 31(1), 38(1), 39(2), 44(2)
balanorum and above	12(1), 20(1), 37(0)*, 43(1), 46(1), 47(1), 58(1)
rivasi + *castroi* and above	8(1), 50(1), 54(1)*, 56(1)*
rivasi + *castroi*	7(0), 10(1), 15(0), 17(1), 20(0), 32(1), 33(0), 37(1)*, 44(0)
macrospilus and above	38(0), 42(1)*, 59(1)
hancocki + *stephensi*	16(1), 53(1), 54(2)*

sistent with these data. The presence of a multiple-branched cirrus in *A. crockeri* is autapomorphic.

Acanthemblemaria johnsoni lacks the five derived features that unite the eastern Pacific clade (Fig. 3, Table 1): (18) an enlarged ventralmost lateral ethmoid spine that is well separated from others by a notch; (31) postorbital excluded from the posterior angle of the circumorbitals; (38) two rows of teeth on the ramus of the dentary; (39) vomer with two patches of teeth with a median hiatus; and (44) epineural bones (formerly epipleural ribs—see Patterson & Johnson 1995) present on all precaudal vertebrae and two or more caudal vertebrae. In *A. johnsoni,* lateral ethmoid spines are equally spaced, the ventralmost not separate; the lacrimal and postorbital both extend into the posterior angle of the circumorbitals; the ramus of the dentary bears a single row of teeth; the vomerine tooth patch is in the shape of a crescent; and epineurals are present on all precaudal vertebrae and sometimes on the first caudal vertebra.

Acanthemblemaria johnsoni has all of the derived features that diagnose the major clades leading up to the eastern Pacific clade (Fig. 3, Table 1) except characters (14) frontal with a central row of interorbital spines; (35) epihyal and ceratohyal suture complex, with seven or more interdigitations (both unite *A. betinensis* + *A. exilispinus* and above); and (45) fifth hypural ossified (equally parsimonious to hypothesize this condition as a synapomorphy of *A. betinensis* + *A. exilispinus* and above, or of *A. medusa* + *A. paula* + *A. aspera* and above). *Acanthemblemaria johnsoni* independently evolved (16) a continuous and straight row of lateral interorbital spines positioned well medial of the interorbital margin (a synapomorphy of *A. hancocki* and *A. stephensi*); and (57) anterofrontal pores fused into a single medial pore (a synapomorphy of *A. paula* and *A. aspera,* an autapomorphy of *A. spinosa*).

In summary, based on the phylogenetic data assembled by Hastings (1990), the affinities of the new species from Tobago clearly lie with the predominantly eastern

Pacific clade of *Acanthemblemaria* species. In addition to the characters listed above in support of this hypothesis, *A. johnsoni* is also more similar to eastern Pacific species in meristic features than to western Atlantic species. For example, a dorsal-fin count of XXIV, 12–13, is diagnostic for *A. johnsoni* relative to Atlantic species of the genus, but 24 dorsal-fin spines also occur in the Pacific *A. exilispinus* and *A. hancocki,* and is the modal count for *A. crockeri, A. macrospilus, A. balanorum,* and *A. stephensi* (Stephens 1963, Rosenblatt & McCosker 1988).

An analysis of the cladistic biogeography of the genus is beyond the scope of this study, but the phylogeny of species hypothesized by Hastings (1990) and expanded herein suggests a complicated biogeographical history. The initial radiation of the genus appears to have occurred in what is now the tropical western Atlantic, and, as noted by Stephens (1963), the primary radiation of the eastern Pacific species may have taken place since the last emergence of the Panamanian isthmus.

Within *Acanthemblemaria,* there are now three sister-group relationships pairing an Atlantic species with one or more eastern Pacific species (Fig. 3): *A. betinensis* and *A. exilispinus, A. rivasi* and *A. castroi,* and *A. johnsoni* and the eastern Pacific clade. Hastings (1990) noted that the distributions of *A. betinensis* and *A. exilispinus* are consistent with a hypothesis of allopatric speciation resulting from the emergence of the isthmus of Panama, and the same event could simultaneously have led to the division of *A. johnsoni* and the ancestor of the eastern Pacific clade. The ancestor of *A. rivasi* and *A. castroi* would not have been present at this time, but subsequent dispersal of that species to the Atlantic, possibly through an incompletely formed isthmus after the initial radiation of *Acanthemblemaria* in the eastern Pacific, could explain the phylogenetic affinities of *A. rivasi* with some of its eastern Pacific congeners. As noted by Hastings (1990), the distribution of the *A. rivasi* and *A. castroi* species pair, Central America and the Galapagos, respectively, is unusual.

Acanthemblemaria johnsoni is presently known only from shallow reefs at the north end of Tobago, but the historical distribution of the ancestor of *A. johnsoni* and the eastern Pacific clade must have been different from the known distribution of *A. johnsoni* today. Optimizing Atlantic and eastern Pacific distributions of *Acanthemblemaria* species on the cladogram suggests that the ancestor of *A. johnsoni* and the eastern Pacific clade inhabited Atlantic waters. It is thus reasonable to assume that this ancestor was once found along the eastern coast of Central America and the northern coast of South America. Further sampling of these areas may reveal that *A. johnsoni* is not restricted to Tobago.

Etymology.—It is our pleasure to name this species for G. David Johnson who assisted in the collection of these specimens. He has made contributions to the systematics of a broad array of teleostean taxa (including *Acanthemblemaria*), and his knowledge of teleostean anatomy and phylogeny is inspirational.

Habitat.—The specimens of *A. johnsoni* were collected at large rotenone stations and thus were not observed in their natural habitat. Presumably *A. johnsoni,* like other members of the genus, inhabits the vacated tubes of invertebrates, such as polychaetes or sipunculids.

Distribution.—Known only from shallow-water reefs at the north end of the Caribbean island of Tobago.

Holotype.—USNM 317210, 24.0 mm male taken with rotenone from an area with rock, live coral, gorgonians, rubble, and numerous, large, vertical walls on a reef north of Charlotteville, on the east side of North Point, Tobago, at a depth of 4.5–12 m on 8 Sep 1990 by J. Williams and party.

Paratypes.—USNM 317211 (4, 19.5–25.5 mm; one 21.9 mm male cleared and stained). Same locality and collection data as holotype, USNM 317210.

USNM 319706 (1, 14.8 mm); Saint Giles

Islands, Saint Giles Island, Tobago. Collected with rotenone from a rocky bottom shelf with some live and dead coral, rock, and rubble, at a depth of 6–10.5 m on 12 Sep 1990 by J. Williams and party.

Other material examined.—*Acanthemblemaria aspera,* USNM 274944 and 276049; *A. balanorum,* USNM 299794; *A. chaplini,* ANSP 100887 and 100880; *A. crockeri,* USNM 299798; *A. greenfieldi,* USNM 321067; *A. hancocki,* USNM 299791; *A. maria,* USNM 317081; *A. medusa,* USNM 317077 and 329332; *A. paula,* USNM 308400 and 327611; *A. rivasi,* ANSP 119230 and 147649; *A. spinosus,* USNM 320858, 320812, and 317072; *A. betinensis,* SIO 71-262; *Protemblemaria bicirris,* USNM 200400 and UAZ 95-1-1 (C&S).

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Protoglossus graveolens, a new hemichordate (Hemichordata: Enteropneusta: Harrimanidae) from the northwest Atlantic

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Abstract.—A new hemichordate species, *Protoglossus graveolens,* is described from Maine, U.S.A. *Protoglossus graveolens* is the second member of its genus and the only North American protoglossid. *Protoglossus graveolens* occurs intertidally, usually with another enteropneust, *Saccoglossus bromophenolosus* King et al., 1994. The new species is assigned to the genus *Protoglossus* based on the following criteria: 1) proboscis musculature; 2) proboscis coelom; 3) proboscis septa; 4) a basal sheath at the posterior end of the proboscis stalk; 5) inclination of the collar; 6) perihaemal spaces in the collar; 7) lack of esophageal pores. *Protoglossus graveolens* is differentiated from *Protoglossus koehleri* (Caullery & Mesnil, 1900) on the basis of size, coloration, proboscis and branchial skeleton morphologies, collar dimensions and internal organization of the collar.

Three harrimaniid species have been reported from coastal Maine. Two of these were considered a single species but have recently been differentiated into *Saccoglossus bromophenolosus* King et al., 1994 and *S. kowalevskii* Agassiz, 1873. *Saccoglossus bromophenolosus* occurs in colder waters, ranging from southern Maine northward at least to Nova Scotia (Prefontaine & Brunel 1962, Bromley 1979, King et al. 1994); populations are also known from Oregon and Washington (Bullock 1975, Kozloff 1987). In contrast, *S. kowalevskii* occurs from Georgia to southern Maine (Colwin & Colwin 1953, 1962; Elder 1973, Jaffe 1983, Fox & Ruppert 1985, Woodin et al. 1987, King et al. 1994). The third species reported from Maine, *Stereobalanus canadensis* (Spengel, 1893) occurs subtidally, and has been reported from Nova Scotia (Spengel 1893, 1901), Frenchman's Bay, Maine (Reinhard 1942), the Gulf of St. Lawrence (Prefontaine & Brunel 1962), the west coast of Scotland (Burdon-Jones & McIntyre 1960), San Diego, California (Bullock & Rao unpubl. observations cited in Burdon-Jones & McIntyre 1960) and the Norwegian Sea (Romero-Wetzel 1989). We describe here a fourth and new harrimanid from three adjacent sites in the Damariscotta River estuary, Maine, U.S.A. (43°56′N, 69°34′W).

The new species is presumptively assigned to the genus *Protoglossus* (van der Horst, 1927). This genus is referred to by different names throughout the literature. Placement of the first protoglossid species, *P. koehleri,* was uncertain with proposals for the genus *Balanoglossus* Delle Chiaje, 1829 and a new genus *Balanocephalus* (Harmer, 1899) (Caullery & Mesnil 1900). The latter genus was renamed *Protobalanus* (Caullery & Mesnil, 1904) and placed in a new family, Protobalanidae (Caullery & Mesnil 1904). *Protobalanus* was re-named *Protoglossus* (van der Horst, 1927) and subsequently placed in the family Harrimaniidae (Burdon-Jones 1956). Although Benito (1982) places *Protoglossus* in a separate family, Protoglossidae, the character overlap between *Saccoglossus* Shimkewitsch, 1892 and *Protoglossus* (Table

1), and the intermediate position of *P. graveolens* between these genera substantiates its placement in the family Harrimaniidae.

Materials and Methods

Specimens were collected from three tidal mudflats, Lowes Cove and Clarks Cove (43°56′N, 69°34′W) and Mears Cove (43°58′N, 69°34′W), in the Damariscotta River estuary, Maine (salinities range from 30–35 ppt; average range of diurnal tides about 3 m). The location of *P. graveolens* was approximated by inspection of the sediment surface for distinctive fecal coils that were easily distinguished from those of the co-occurring species *S. bromophenolosus* by size and coloration. Fecal coils of *P. graveolens* were generally 1–2 mm diameter and dark, while those of *S. bromophenolosus* were usually less than 1 mm diameter and lighter in color. *Protoglossus graveolens* was extracted from the sediment after overturning large portions of mud and exposing individuals in their burrows. Intact animals were seldom obtained due to their fragility, and frequent extension to >40 cm depth within the sediment. Several 1 m^2 plots were also excavated in order to quantify *P. graveolens* density. Morphological observations, measurements of body dimensions and gill pore counts were obtained from 48 freshly collected individuals following relaxation in 5% magnesium chloride. Four individuals were anaesthetized in 7.5% magnesium chloride and their proboscis skeletons examined after dissection and immersion in 4% sodium borate (Thomas 1968). Internal characters were examined using 7–13 μm thick sections through the proboscis, collar and trunk regions of three adult individuals. The specimens were relaxed in 5% magnesium chloride, fixed in Bouin's for 24–48 hours, dehydrated through several ethanol washes and embedded in paraffin (Humason 1979, K. Eckelbarger & S. Sampson, pers. comm.). Sections were obtained by the use of a manual microtome (AO Spencer Model 815 Rotary Microtome, American Optical Company) and stained with Gomori's solution (Humason 1979; K. Eckelbarger, pers. comm.). Specimens for analysis of bromophenols were placed in a small dish of clean seawater, and incubated overnight at ambient field temperature to facilitate complete discharge of sediment from the gut. After anaesthesis with 7.5% magnesium chloride, specimens were separated into proboscis, collar and trunk regions, then immediately placed in 1.8 ml screw-cap vials containing 250 μl hexane; the vials were subsequently sealed using teflon-faced neoprene septa. Tissues were extracted for 12–24 hours before 0.7–1.0 μl of the hexane was injected into a Varian 3400 gas chromatograph fitted with a flame ionization detector as described previously (King 1986, 1988). Bromophenol identification was confirmed by gas chromatography-mass spectroscopy according to King et al. (1994).

Harrimaniidae

Type genus.—*Protoglossus* (van der Horst, 1927)

Family diagnosis.—Well-developed proboscis muscles. Elongate proboscis skeleton crura divide buccal diverticulum in collar. Perihaemal spaces may exist in collar but peribuccal cavities not present. Tongue bars hang free in gill slit, varying lengths of skeletal rods in tongue bars, no synapticules. No lateral trunk septa. No hepatic sacculations or caeca. Large oocytes, ranging 200 μm to >1 mm in diameter.

Remarks.—The lack of a number of characters exclude *P. graveolens* from the Ptychoderidae: genital wing formation through a dorsolateral septum (Fig. 1); peribuccal coelomic cavities in the collar (Fig. 2); synapticules in the branchial apparatus; lateral septa and hepatic sacculations in the trunk (Fig. 3) (van der Horst 1930, 1932; Hyman 1959, Woodwick & Sensenbaugh 1985, Hayward & Ryland 1990). Similarly,

Table 1.—Comparison of commonly used internal and external characters of *Saccoglossus* and *Protoglossus* species; bold print indicates characters which *Protoglossus graveolens* shares with members of the two genera (compiled from: van der Horst 1930; Kirk 1938; Brambell & Cole 1939; Brambell & Goodhart 1941; Burdon-Jones 1951, 1956; Thomas 1956; Burdon-Jones & Patil 1960; Thomas 1968; Hadfield 1975; King et al. 1994). *S. sulcatus* Spengel, 1893 was excluded due to the lack of information.

Character	*Protoglossus graveolens* new species	*Protoglossus koehleri* (Caullery & Mesnil, 1900)	*Saccoglossus bromophenolosus* King et al., 1994	*Saccoglossus kowalevskii* Agassiz, 1873	*Saccoglossus otagoensis* (Benham, 1899)	*Saccoglossus pygmaeus* Hinricks & Jacobi, 1938	*Saccoglossus ruber* Tattersall, 1905	*Saccoglossus apantesis* Thomas, 1956
Proboscis groove	**Deep dorsal in posterior ½**	**Deep dorsal in pos terior ⅓**	Shallow dorsal groove	Shallow dorsal groove	**Deep dorsal groove**	Absent	**Dorsal groove in posterior ⅔**	Slight dorsal groove
Proboscis skeleton	**Crura extend to posterior collar**	**Crura extend to posterior collar**			**Crura extend to posterior collar**		Crura extend half into collar	Crura extend half into collar
Proboscis muscle	**Not concentric, radial sectors**	**Not concentric, radial sectors**	6–7 concentric rings	4–5 concentric rings	3–4 concentric rings	Not concentric	4–6 concentric rings	9–11 concentric rings
Proboscis coelom	**Large**	**Large**	Small	Small	Small		Small	
Proboscis complex	**Pericard large, stomoch capped**	**Pericard large, stomoch capped**			Glomerulus does not cap stomochord		**Pericardium large**	**Glomerulus caps stomochord**
Proboscis septa	**Dorsal replaced by pericardium**	**Dorsal replaced by pericardium**		Ventral short	Ventral short	Ventral short	Ventral short	
Proboscis pore	**1, dorso-left**	**1, dorso-left**					1, left side	**1, dorso-left**
Basal sheath	**Present**	**Present**	Not reported	Not reported	Not reported	Not reported	Not reported	Not reported
Collar dimensions	Broader than long	As long as broad	Longer than broad	Longer than broad	As long as broad	Broader than long	Longer than broad	
Collar inclination	**Dorso-ventrally at posterior end**	**Dorso-ventrally at posterior end**	Ventra-dorsally at anterior end	Ventra-dorsally at anterior end			Ventra-dorsally at anterior end	Ventra-dorsally at anterior end
Collar operculum	**Present, fused ventrally**	**Present, fused ventrally**	**Present,** fused	**Present**		**Present**	Absent	**Present**
Collar groove	**Present**	**Present**				Absent	**Present**	
Collar musculature	**Weak**	**Weak**		**Weak**	**Weak**			
Perihaemal cavities	**Extend through ⅔ of collar**	**Extend only to tips of crura**			Fused anteriorly	Fused in posterior third	Fused posterior to crura extension	
Collar mesenteries	**Both complete**	**Both complete**		Both incomplete	Both absent	**Both complete**	**Both complete**	
# of gill pores	>100	14–30 pairs	60–100 pairs	~100 pairs	10 to 15 pairs	9 to 22 pairs	60–95 pairs	30–45 pairs
Branchial skeleton	**Septa > tongues**	**Septa ≫ tongues**	**Septa > tongues**	**Septa > tongues**			**Septa > tongues**	
Esophageal pores	**Absent**	**Absent**	4–6 pairs	4–6 pairs	1 pair	1 pair	8–12 pairs	6–8 pairs
Gonads start at	Few mm from collar	Halfway down branchial region	Few mm from collar	1 mm behind collar	4th gill pore	None in branchial	Mid-branchial	Mid-branchial
Oocyte size	380 μm diameter	430 μm diameter	~250 μm diameter	~250 μm diameter			400 by 300 μm	310 by 285 μm

Table 1.—Extended.

Character	*Saccoglossus aulakoesis* Thomas, 1968	*Saccoglossus horsti* Brambell & Goodhart, 1941	*Saccoglossus pusillus* (van der Horst, 1930)	*Saccoglossus gurneyi* Robinson, 1927	*Saccoglossus bournei* Menon, 1904	*Saccoglossus inhacensis* Kapelus, 1936	*Saccoglossus mereschkowskii* Wagner, 1885	*Saccoglossus caraibicus* van der Horst, 1924
Proboscis groove	**Deep dorsal groove**	**Dorsal and ventral grooves**						
Proboscis skeleton	Crura extend half into collar	Crura extend ¼–⅓ into collar	**Crura extend to posterior collar**		**Crura embrace buccal cavity**		Endplate with dorsal spine	Endplate extends into proboscis
Proboscis muscle	9–10 concentric rings	>9 concentric rings	6–7 concentric rings	Not concentric	Not concentric	Not concentric	7–10 concentric rings	Not concentric
Proboscis coelom	Small	Small, 1/10 of proboscis diam	Medium					
Proboscis complex	**Glomerulus caps stomochord**	**Pericard large,** no capping	Glomerulus only ventral at tip		Pericardium small		**Glomerulus caps stomochord**	Extends dorso-anteriorly
Proboscis septa	Ventral short	Ventral short	Ventral short	Ventral extends past stomochord	Extend past stomochord	Ventral short	Ventral short	Ventral extends to tip of stomochord
Proboscis septa	**1, dorso-left**	1, left side	1, left side	1, mid-dorsal				1, mid-dorsal
Basal sheath	Not reported	Not reported	Not reported	Not reported	Not reported	Not reported	Not reported	Not reported
Collar dimensions	Longer than broad		Longer than broad	Broader than long	Broader than long		As long as broad	Longer than broad
Collar inclination	Ventra-dorsally at anterior end					Ventra-dorsally at anterior end		
Collar operculum	**Present**	Present but not pronounced	Absent					
Collar groove		Absent						
Collar musculature							Well-developed	Well-developed circular muscles
Perihaemal cavities	Extend into stalk	Extend to stalk, fused at crurae	Fused in proboscis stalk					**Do not extend to stalk, not fused**
Collar mesenteries	Both incomplete	Dorsal absent at anterior ⅓	Dorsal incomplete at anterior end	Septa complete through 4/5	Ventral absent at anterior end	Dorsal absent, ventral complete	Ventral incomplete anteriorly	**Both complete**
# of gill pores	12–25 pairs	100 to 140 pairs	60 pairs	40 to 60 pairs	>62 pairs	>82 pairs	50 pairs	>50 pairs
Branchial skeleton	Tongues > septa	Tongues > septa					**Septa > tongues**	
Esophageal pores	2–8 pairs	4–8 pairs	1 pair	**Absent?**		4 pairs	7 pairs	
Gonads start at	Collar	1 mm from collar	12–17th gill pore	Collar	Collar	4th gill pore	Mid-branchial	4th gill pore
Oocyte size		230 by 170 μm						

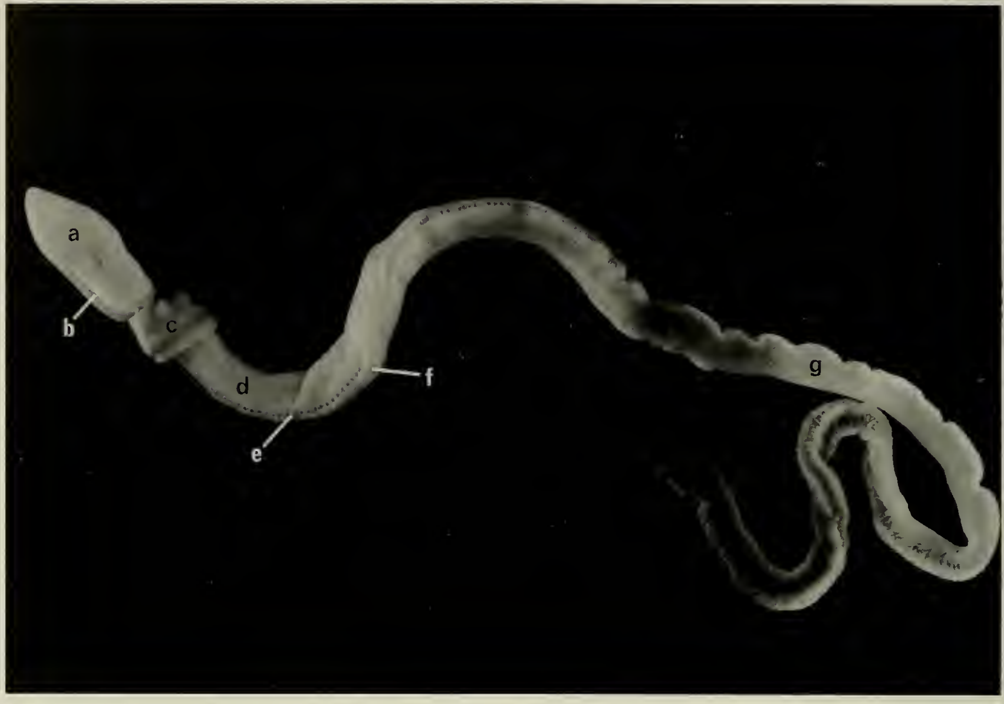

Fig. 1. *Protoglossus graveolens,* new species. Photograph of individual missing posterior portion of trunk, magnified 3×. a: proboscis, b: proboscis groove, c: collar, d: branchial region of trunk, e: gill pores, f: mid-dorsal ridge separating rows of gill pores, g: hepatic region of trunk.

lack of a proboscis appendix, esophageal pores and circular muscles in the trunk (Fig. 3) exclude *P. graveolens* from the Spengeliidae (Hyman 1959, Woodwick & Sensenbaugh 1985). The absence of both peribuccal spaces in the collar and synapticules in the branchial apparatus further differentiate *P. graveolens* from three of the Spengeliid genera, *Spengelia, Schizocardium* and *Willeyia.* Well-developed proboscis muscles (Fig. 4), division of the buccal diverticulum in the collar by the proboscis crura (Fig. 2), large oocytes (Figs. 3 & 5), and the lack of peribuccal spaces in the collar (Fig. 2), synapticulae in the branchial apparatus, lateral septa and hepatic caeca in the trunk (Fig. 3) are fundamental characters of the family Harrimaniidae (Hyman 1959, Woodwick & Sensenbaugh 1985). Since *P. graveolens* shares all of these attributes, its placement within the family Harrimaniidae is indicated.

Protoglossus (van der Horst, 1927)

Type species—Protoglossus koehleri (Caullery & Mesnil, 1900).

Genus diagnosis.—Proboscis short with deep dorsal groove along posterior ⅓ to ½. Proboscis musculature non-concentric but arranged in sectors that project into proboscis coelom along radial fissures. Proboscis coelom third to half of proboscis diameter. Large pericardium replaces dorsal proboscis septum at anterior end, glomerulus caps anterior end of short straight stomochord which extends through ¼ to ⅓ of proboscis. Basal sheath covers posterior half of proboscis stalk. Proboscis skeleton crura extend to posterior end of collar and embrace and divide buccal diverticulum. Collar inclined dorso-ventrally towards the posterior, well-defined operculum at posterior end of collar fused along ventral edge. Collar mesenteries complete, perihaemal spaces ex-

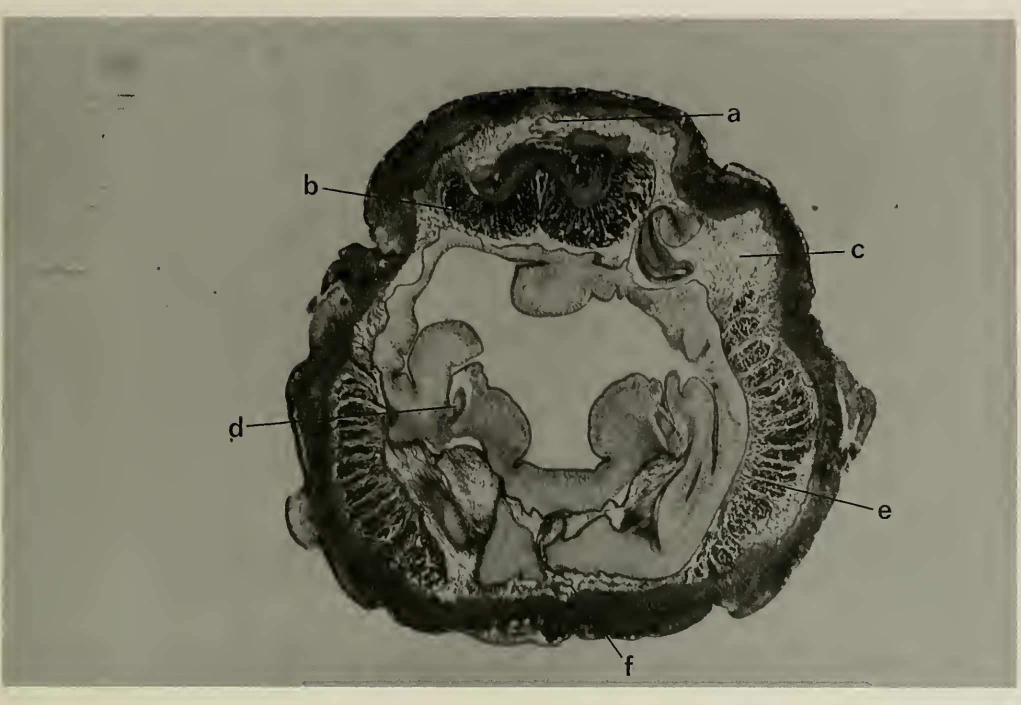

Fig. 2. *Protoglossus graveolens,* new species. Collar, transverse section through posterior end, magnified 18×. a: dorsal septum, b: perihaemal cavities, c: coelom, d: proboscis skeleton crura, e: muscles of the proboscis skeleton, f: ventral septum.

tend anteriorly only through ⅔ of collar. No esophageal pores.

Remarks.—Within the family Harrimaniidae, *P. graveolens* is readily excluded from the genera *Stereobalanus* (Spengel, 1901), *Harrimania* Ritter, 1900, and *Xenopleura* Gilchrist, 1925. Dorsolateral placement of the gonads (Fig. 3), two parallel rows of 60–143 gill pores running along a dorsal ridge in the branchial region and a comparatively higher length to width ratio of the trunk (Fig. 1) readily exclude *P. graveolens* from *Stereobalanus.* In *S. canadensis* the gonads are situated within short dorsal and ventral folds immediately behind the collar while the gill pores, which number far fewer than in *Protoglossus,* are fused to common slits that are hidden between the genital folds (Spengel 1893, Reinhard 1942, Hyman 1959, Burdon-Jones & McIntyre 1960).

Both members of the genus *Harrimania, H. kupfferi* (von Willemoes-Suhm, 1871) and *H. maculosa* Ritter, 1900, are characterized by a lower length to width ratio, two proboscis pores, radiating muscle plates and a very short bilateral coelom in the proboscis, a four-lobed branchial region, and gonads ventral and dorsal to the gill pores (Ritter 1900, Hayward & Ryland 1990). *P. graveolens* shares none of these features.

Although the description for *Xenopleura vivipara* Gilchrist, 1925 is incomplete, several key differences exclude *P. graveolens* from *Xenopleura. Xenopleura* is characterized by fusion of the posterior end of the collar to the branchial region, the presence of a differentiated buccal roof in the collar, medullary folds and internal hepatic caeca in the trunk, and the absence of an operculum (Gilchrist, 1925). These characters are not shared by *P. graveolens.*

Protoglossus graveolens shares external and internal morphological characteristics with both of the remaining harrimaniid genera, *Saccoglossus* Shimkewitsch, 1892 and

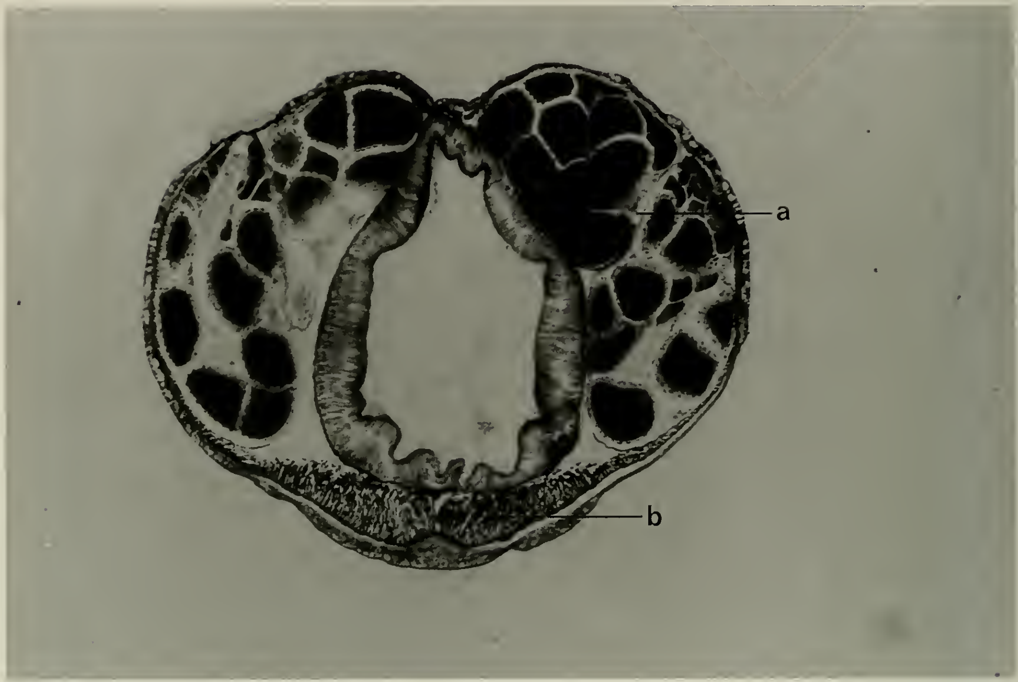

Fig. 3. *Protoglossus graveolens,* new species. Trunk hepatic region, transverse section, magnified 25×. a: dorsolaterally placed oocyte bundles, b: ventral longitudinal muscles.

Protoglossus (van der Horst, 1927). This is consistent with the results of a comparison of the commonly used characteristics of harrimaniid species which reveals a substantial overlap between the protoglossids and saccoglossids (Table 1) suggesting a close association between these genera. The anatomical organization of the *P. graveolens* proboscis stalk and collar (Figs. 2 & 6), and the morphology of its branchial skeleton (Fig. 7) are similar to the saccoglossids; the internal characters of the *P. graveolens* proboscis (Figs. 4 & 8), the extension of the perihaemal cavities in the collar (Fig. 2) and external features such as the basal sheath, inclination of the collar (Fig. 9) and lack of esophageal pores are more similar to *P. koehleri.*

The deep dorsal groove of the *P. graveolens* proboscis (Figs. 1 & 9) and the thickening of the adjacent dorsal nerve layer (Fig. 8) are characters shared with several saccoglossid species (van der Horst 1930, Brambell & Cole 1939, Brambell & Goodhart 1941, Thomas 1956, Burdon-Jones & Patil 1960, Thomas 1968) as well as *P. koehleri* (Burdon-Jones 1956) (Table 1). Other features shared between these genera include: the number and location of proboscis pores, a large pericardium (Fig. 8), the capping of the stomochord by the glomerulus (Fig. 4), the collar dimensions, the presence of a posterior collar operculum and collar groove (Fig. 9), the collar musculature and mesenteries (Fig. 2), the extension of the proboscis skeleton crurae through the collar (Fig. 2), the number of branchial gill pores, the relative proportions of tongues and septa in the branchial skeleton (Fig. 7), the starting location of gonads along the trunk and the size of oocytes (Table 1). These various characters appear unreliable as diagnostic tools both for differentiating between the two genera and within the genus *Saccoglossus.*

Burdon-Jones & Patil (1960) have pre-

Fig. 4. *Protoglossus graveolens,* new species. Proboscis, transverse section, magnified 16×. a: proboscis coelom, b: glomerulus, c: longitudinal proboscis musculature separated by radial fissures, d: anterior-most portion of stomochord.

viously questioned the taxonomic value of the posterior collar groove for saccoglossids. Inspection of Table 1 indicates that another feature commonly associated with *Saccoglossus,* the concentric arrangement of the proboscis musculature, is also an unreliable diagnostic character; five saccoglossid species lack an obvious concentric musculature. Similarly, collar mesenteries may be unreliable taxonomic indices for the genus *Protoglossus.* Complete collar mesenteries and full separation of the coelom in the collar, as observed in *P. graveolens,* have been suggested as a primitive feature characteristic of *Protoglossus* (Burdon-Jones 1956, Hyman 1959). However, complete mesenteries are also reported for *S. caraibicus* van der Horst, 1924, *S. pygmaeus* Hinrichs & Jacobi, 1938 (Brambell & Goodhart 1941) and *S. ruber* Tattersall, 1905 (Burdon-Jones & Patil 1960). Although the dorsal mesentery is absent in the anterior third of the collar in *S. horsti,* the collar coeloms are reported as being completely separated in this saccoglossid as well (Brambell & Goodhart 1941). These similarities perhaps suggest a closer phylogenetic relationship between *Protoglossus* and *Saccoglossus,* than between either of these genera and the confamilial *Stereobalanus.*

However, in spite of the similarities between *Protoglossus* and *Saccoglossus,* these genera are clearly distinct when all characters are viewed collectively. This is especially apparent for the new species reported here. When all characters are considered, it is well-differentiated from *Saccoglossus,* but closely associated with *P. koehleri* (Table 1). Three external features are diagnostic. First, *P. graveolens* is characterized by a proboscis stalk sheath, a feature thus far reported only for *P. koehleri* (Burdon-Jones 1956). Second, lack of esophageal pores is shared with *P. koehleri,* but not the saccoglossids. With only one ex-

Fig. 5. *Protoglossus graveolens,* new species. Oocytes packaged in bundles of 13–29, as observed through body wall along hepatic region of the trunk, magnified 18×.

ception, all saccoglossids possess esophageal pores, the number varying between 1–12 pairs for different species. Esophageal pores are doubted only for *S. gurneyi* (Thomas 1956). Third, the dorso-ventral inclination of the collar (Fig. 9) is not reported for any saccoglossid, but is a characteristic of *P. koehleri.* Internally, the morphology of the *P. graveolens* proboscis is unlike that of saccoglossids. The organization of the longitudinal muscles in sectors along radial fissures (Fig. 4), the wide proboscis coelom (Fig. 4 & 8) and the large pericardium that replaces the dorsal proboscis mesentery anteriorly (Fig. 8) are characteristics of the new species shared with *P. koehleri.* In contrast, the longitudinal proboscis muscles of *Saccoglossus* are typically organized either in concentric circles or form a continuous mass, the coelom is usually small, and extension of the pericardium to replace the dorsal mesentery has not been reported. The morphology of perihaemal cavities within and through the collar is also diagnostic. *P. koehleri* has no anterior extensions of the perihaemal cavities past the crura of the proboscis skeleton (Burdon-Jones 1956). Except for *S. caraibicus,* perihaemal spaces extend into or through the proboscis stalk of all described saccoglossids. The perihaemal spaces in *P. graveolens* extend past the crura but disappear ⅔ of the way through the collar (Fig. 2).

Protoglossus graveolens,
new species
Figs. 1–11

Species diagnosis.—Body large, average adult length 24 cm, largest specimen 47 cm. Collar broader than long (0.2–0.35 cm long, 0.3–0.45 cm diameter). Proboscis coloration cream-white; collar cream-white to orange-brown; branchial region translucent yellow to light orange-brown; hepatic region brown; intestinal region pale yellow,

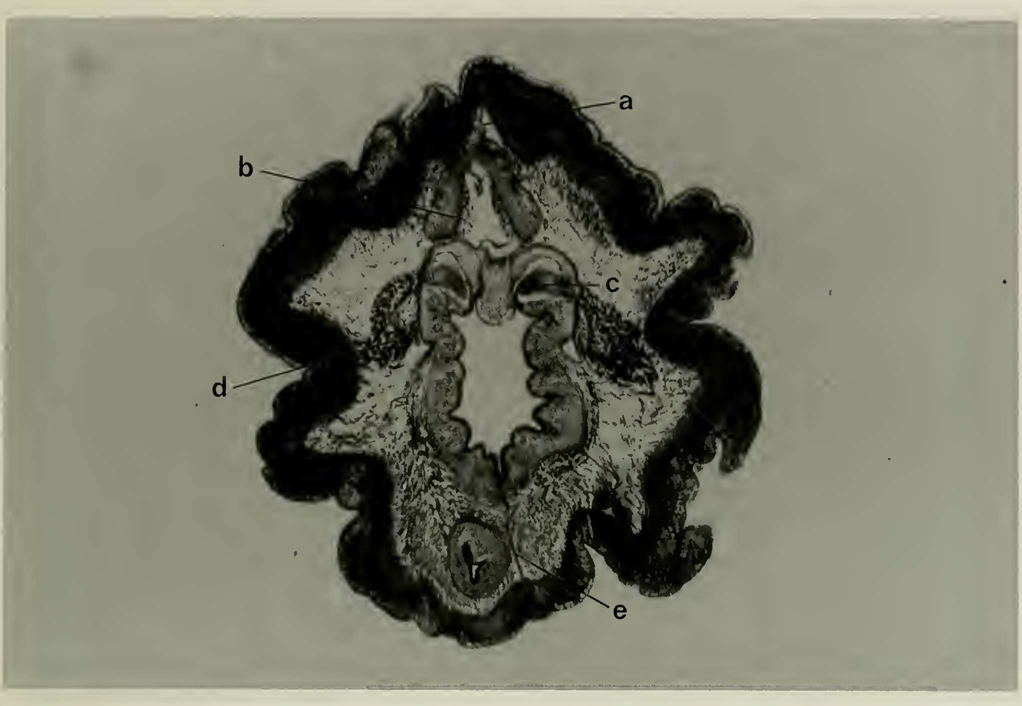

Fig. 6. *Protoglossus graveolens,* new species. Collar, transverse section mid-way through length, magnified 22×. a: dorsal septum, b: rudimentary nature of perihaemal cavities at this point along collar, c: proboscis skeleton crura, d: muscles of the proboscis skeleton, e: ventral septum.

fades posteriorly. Sixty to 142 gill pores, posterior-most 20–30 microscopic. Proboscis groove extends through posterior half of proboscis. Proboscis coelom large (⅓ to ½ of proboscis diameter). Stomochord extends through ⅓ of proboscis. Proboscis skeleton curvature approximately 90 degrees between keel and horns. Perihaemal spaces extend through ⅔ of collar, beyond posterior limit of proboscis skeleton crura. Collar coeloms occupied by muscles and interstitial tissue. Branchial skeleton made up of elongate septa and tongues, septa longer than tongues.

Fig. 7. *Protoglossus graveolens,* new species. Branchial skeleton, magnified 46×.

Remarks.—Protoglossus graveolens is easily differentiated externally from *P. koehleri* by its size and coloration. The average total length for *P. graveolens* is 24 cm while the largest specimen recorded for *P. koehleri* was only 7.5 cm (Burdon-Jones 1956). The number of gill pores is also proportionately greater in *P. graveolens,* ranging between 60–142 depending on size, while the number reported for the latter species varies between 14–30 (Burdon-Jones 1956). The coloration also differs dramatically between the two species. In *P. graveolens,* the proboscis is cream-white, the collar cream-white to orange brown, the branchial region translucent yellow to light orange brown and the intestinal region pale

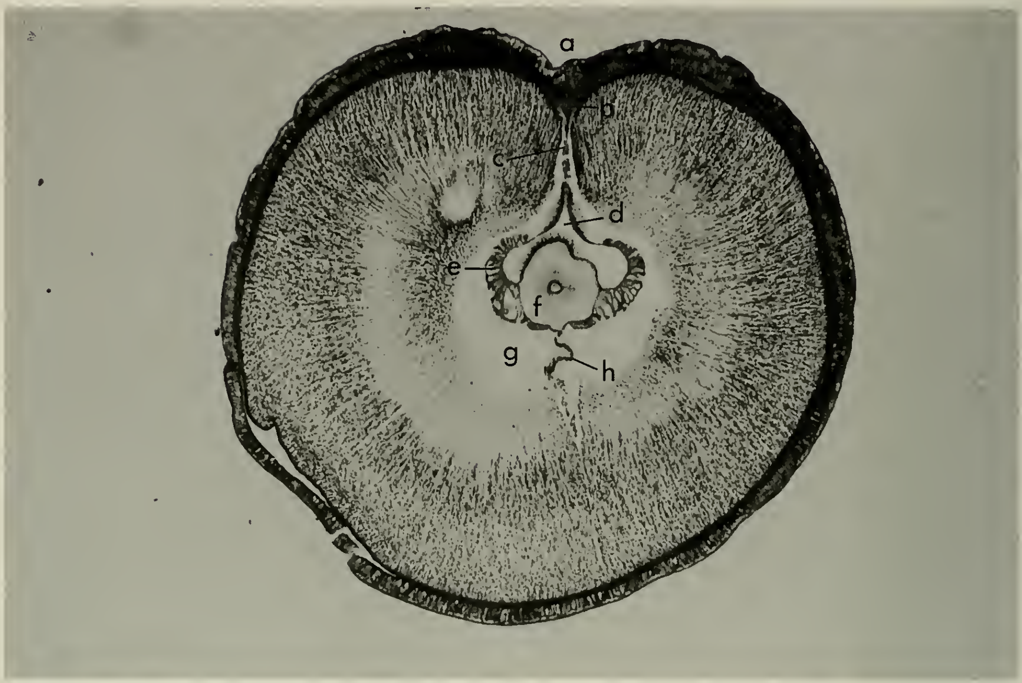

Fig. 8. *Protoglossus graveolens,* new species. Proboscis, posterior end, transverse section through proboscis complex, magnified 16×. a: dorsal groove, b: dorsal nerve layer thickening, c: dorsal septum, d: pericardium, e: glomerulus, f: stomochord, g: proboscis coelom, h: ventral septum.

yellow. In *P. koehleri* the coloration is golden yellow or honey for the proboscis and collar, with additional dark green spots that are lacking in *P. graveolens,* pale bluish green or translucent fawn for the branchial region, and amber fading to grey or cream posteriorly for the intestinal region (Burdon-Jones 1956).

The internal organization of the collar and the morphology of the proboscis and branchial skeleton also distinguish *P. graveolens* from its congener. Perihaemal cavities in *P. graveolens* extend more than halfway into the collar (Figs. 2 & 6) while in *P. koehleri* they reach only the posterior tips of the proboscis skeleton crura. The collar coelom, which is described as very distinct in *P. koehleri* (Burdon-Jones 1956), is filled with muscle and connective tissue in *P. graveolens* (Fig. 2). The proboscis skeleton of *P. graveolens* shows a greater curvature in the crura, reaching nearly 90 degrees. The branchial skeleton of *P. koehleri* is unusual among the harrimaniids because the tongue bars are short or nonexistent (Burdon-Jones 1956, Hyman 1959). On the other hand, the branchial skeleton of *P. graveolens* has well-developed tongue bars, much like those of the saccoglossids (Fig. 7).

Etymology.—The species name *graveolens* (L. 'strong smelling, noisome') describes the characteristic strong bromoform odor that emanates from the animal, associated sediment and any other surface with which it has come in contact.

Type material.—Holotype, female carrying eggs, total length 22.5 cm (USNM 173686); paratypes, 1 male, total length 20 cm (USNM 173687), 3 females, total length 23–47 cm (USNM 173688-90), 1 juvenile, total length 2.9 cm (USNM 173691) from Lowes Cove, Maine (43°56′N, 69°34′W), collected by C. Giray, 14 July 1994.

Description.—Holotype: female with eggs, total length 22.5 cm (15 cm or greater

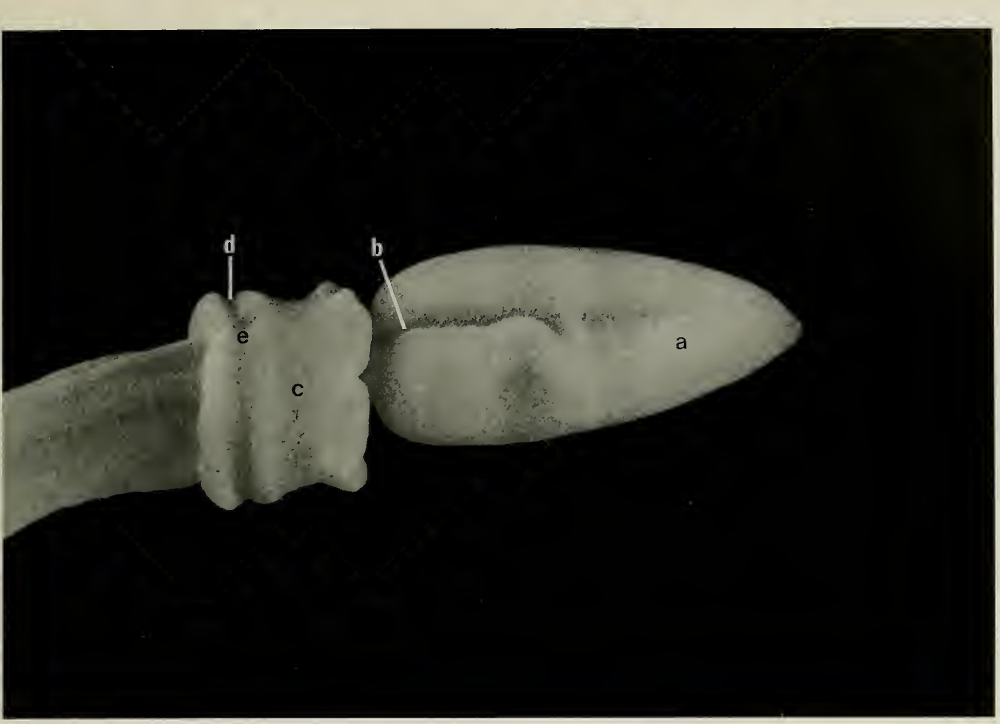

Fig. 9. *Protoglossus graveolens,* new species. Photograph of anterior end, close-up view, magnified 9.5×. a: proboscis, b: proboscis groove, c: collar, d: collar groove, e: collar operculum.

portion of trunk intestinal region lost during collection as deduced from remains recovered through further excavation).

Proboscis short and broad, tapered toward anterior tip, cream-white, 0.75 cm long, 0.45 cm wide at base. Deep, distinctive, dorsal groove extends from base of proboscis to anterior end, becoming shallower towards tip (Figs. 1 & 9); only noticeable as basal cleft post-fixation. Basal sheath covers posterior half of proboscis stalk. Single proboscis pore located just anterior of basal sheath dorsolaterally on left side of proboscis stalk. Proboscis skeleton slender, keel and horns of equal length, stalk wing not present. End plate, visible through proboscis stalk, fans out laterally, forming skewed pair of funnels. Curvature between keel and horns approximately 90 degrees, concretions not observed.

Collar 0.3 cm long by 0.45 cm in diameter. Anterior-most region of collar projects to cover most of proboscis stalk while posterior-most region, or operculum, covers first pair of gill pores (Fig. 9).

Trunk consists of three easily distinguished regions. Branchial region (Fig. 1), anterior-most and housing gill pores, 2.8 cm long, 0.35 cm diameter; greatest diameter coincides with gill pore 6 or 7; translucent yellow; surface texture smooth; pronounced mid-dorsal ridge that becomes shallower toward posterior branchial region. Gill pores, dorsal, 100 pairs, arranged in two rows parallel to mid-dorsal ridge. Anterior gill pores slit-like (200 μm maximum width); about 25–30 pair of posterior-most pores rounded and microscopic (10–20 μm maximum width, presumably gill pores in early phases of development), occupy last 0.2–0.3 cm of branchial region (Fig. 10). Hepatic, second trunk region, easily distinguished by wrinkled surface texture (Fig. 1). Occurs immediately posterior to branchial region, 13 cm long, diameter decreases from 0.35 cm at anterior end to 0.2 cm at posterior end.

Fig. 10. *Protoglossus graveolens,* new species. Trunk branchial region, posterior end, magnified 30× to show the transition from the comparatively larger gill pores which cover most of the branchial region to the posterior 25–30 smaller pores (arrow); dorsal groove also becomes significantly raised in this region.

Anterior 3 cm of hepatic region yellow, remaining length brown. Hepatic sacculations absent. Transition into third region, intestinal, marked by change in trunk coloration from brown to pale yellow. Intestinal region extends remaining length of animal, coloration fading rapidly towards posterior end. Total length of intestinal region uncertain but at least 20 cm, only 5.5 cm recovered intact. Diameter, 0.2 cm throughout most length, tapers off to 0.1 cm towards posterior end.

Gonads, dorsolateral, visible through body wall (Figs. 3 & 5), and occur in first two trunk regions; begin 1.8 cm behind collar, extend through branchial region and overlap proximal 6 cm of hepatic region; total extent along trunk, 7 cm. Body wall of gonadal region inflated to 0.35–0.4 cm diameter. Oocytes, pink, 320–380 μm diameter, in clusters of 13–29 (Fig. 5).

Variations.—Four adult paratypes, one male, three females; share similar features with holotype but greater in length by 1–1.5 cm in branchial region and 7–15 cm in total trunk; total length of most complete specimen, a female, 47 cm; longest intact intestinal region collected, 21 cm. Gill pores, 125–143 pairs, number increasing proportionately with size of individual. Proboscis, collar and branchial region of two paratypes exhibit enhanced orange shade in coloration. Male gonads, creamy white; sperm carried in irregularly shaped packets (approx. 800 μm in diameter), packets usually shed if ripe individual is disturbed. The sperm morphology of *P. graveolens* (Fig. 11) resembles that described for several saccoglossid species (Burdon-Jones 1952, Hyman 1959, Franzen et al. 1985). The head of the spermatozoa measure 3.2 μm in length and 2.2 μm in diameter at the widest part. The acrosome, nucleus and mid-piece measure 1.1, 1.0 and 1.1 μm, respectively,

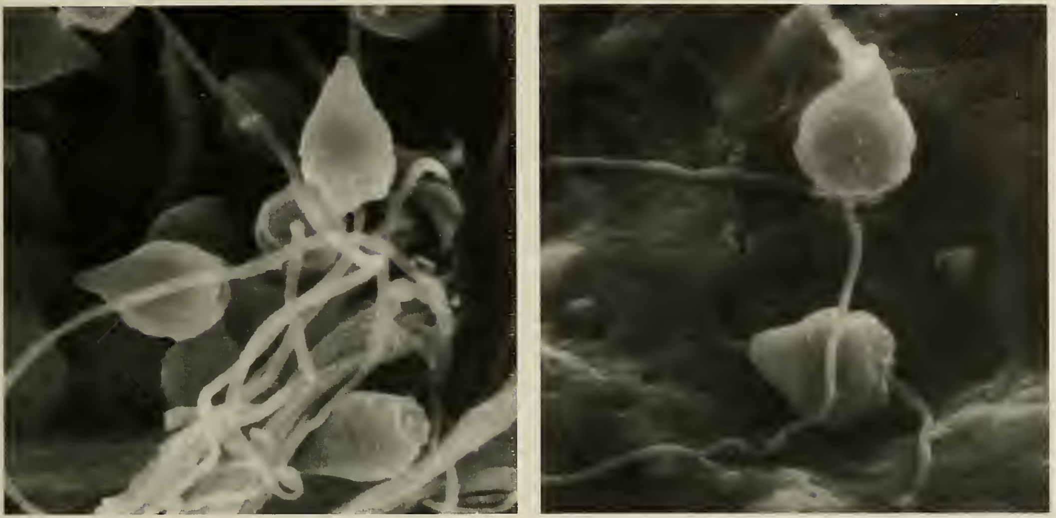

Fig. 11. Spermatozoa (SEM), magnified 10,000×. Left: *Protoglossus graveolens,* new species; total length of acrosome, nucleus and middle-piece, 3.2 μm; maximum width, 2.2 μm; length of tail 55.5 μm. Right: *Saccoglossus bromophenolosus*; total length of acrosome, nucleus and middle-piece, 3.2 μm; maximum width, 2.5 μm; length of tail, 56 μm.

while the tail has a length of 55.5 μm (measurements are average values from 12 spermatozoa). In contrast to spermatozoa of *S. bromophenolosus* (Fig. 11), the head of *P. graveolens* spermatozoa is narrower and pointed at the tip of the acrosome (Fig. 11). Female gonad coloration varies from pink to olive-gray depending on stage of development. Extent of gonads along trunk also varies with development; in fully mature individuals gonads occur up to 14 cm total length along trunk. Although specimens with developing gonads were collected as early as January, spawning was not observed until late August-early September. Fifth paratype, juvenile; total length 2.9 cm; proboscis 0.35 × 0.2 cm, collar 0.15 × 0.2 cm length and diameter, respectively; branchial region, 1 cm long; gill pores, 63 pairs; posterior trunk length, 1.4 cm; coloration, cream-white throughout.

Haloorganic content.—2,4-dibromophenol (DBP) was detected in hexane extracts of *P. graveolens,* with average concentrations from 7 μmol/g fresh weight in the post-branchial trunk to 15 μmol/g fresh weight in the proboscis and 20 μmol/g fresh weight in the collar and branchial region. A second compound, 4-bromophenol (BP), was also detected but at much smaller levels and mainly in the posterior trunk; average concentration 0.08 μmol/g fresh weight. DBP occurs in *S. bromophenolosus,* but differs considerably in concentration and distribution from that in *P. graveolens.* In the latter, the highest DBP concentrations occur in the collar, surpassing the corresponding concentration in *S. bromophenolosus* by nearly two orders of magnitude. In *S. bromophenolosus,* the highest DBP concentrations occur in the proboscis, at about double the concentrations detected for *P. graveolens.* DBP concentrations are 5–6 times greater in the branchial region of *P. graveolens* than in *S. bromophenolosus* while nearly equal levels occur in the posterior trunk regions of the two species. Bromoindoles, which occur in several other hemichordates (Higa et al. 1980), including *S. bromophenolosus* (King et al. 1994), were not detected in *P. graveolens.* Minor amounts of BP were detected in hexane extracts of both *P. graveolens* and *S. bromo-*

phenolosus with somewhat higher concentrations in the former species.

Distribution.—Protoglossus graveolens occurs intertidally, spanning from 15 to over 40 cm depth through the sediment. Its vertical position varies with sediment particle size and water content, extending to at least 50 cm in softer muds. *P. graveolens* is unusual among the harrimanids in its ability to burrow deep. *S. bromophenolosus* and *S. canadensis* in comparable substrate are found at less than 20 cm maximum sediment depth. *Protoglossus graveolens* was also collected from a shallow subtidal area. Populations of *P. graveolens* are distributed patchily within individual mudflats; densities in the Lowes and Clarks Cove sites range from 1–9 individuals m^{-2}. *Saccoglossus bromophenolosus* co-occurs with *P. graveolens* at all sampling sites, usually at greater densities. Burrows of *P. graveolens* are always deeper but not as branched as those of *S. bromophenolosus*. In addition, the burrows of *P. graveolens* lack the thick red iron oxyhydroxide coating typical of those of *S. bromophenolosus. P. graveolens* has been collected from only three adjacent sites in the Damariscotta River estuary. Therefore, its range along the eastern North American coastline is uncertain.

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Studies in aquatic insects X: Descriptions of five new species of the genus *Culoptila* Mosely (Trichoptera: Glossosomatidae) from México

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Abstract.—Five new species in the genus *Culoptila* Mosely from México are described and the male genitalia are figured. The species here described are *Culoptila acaena, C. azulae, C. denningi, C. barrerai* and *C. jamapa.*

During the last few decades, Flint, Holzenthal, Harris and the senior author have contributed significantly to our knowledge of the Neotropical caddisfly fauna. The Neotropical species of the genus *Culoptila* Mosely, however, have been little studied probably because of the infrequent collection of adults. In this paper we describe new species from the Mexican fauna. Mexican specimens of *Culoptila* are increasingly difficult to find because of the pollution and the destruction of the natural habitats of these insects.

The species described here were collected by the senior author and his students between the years 1977-1991 in the Mexican states that still have some patches of rain forest: Estado de Mexico, Guerrero, Veracruz, Oaxaca and Chiapas.

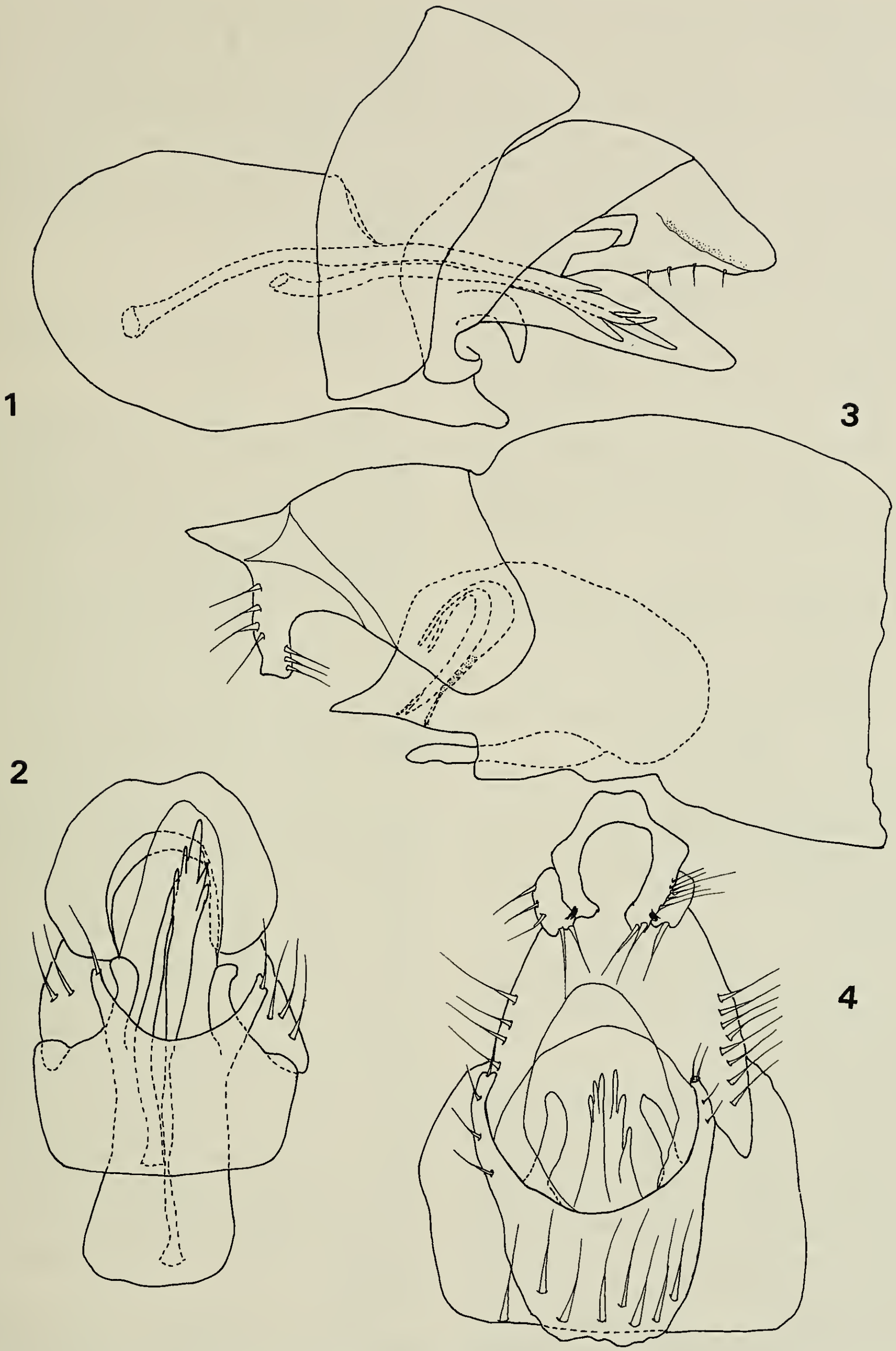
Genus *Culoptila* Mosely

Mosely (1954) originally established *Culoptila* for four Mexican species. Two decades later, Flint (1974a, 1974b) reported that number of species to be twelve, one from Guatemala, four from the United States, one from Costa Rica, and six Mexican species. In this paper we described five newly discovered species from México. Even though the larvae and pupae are not known, we are confident that the immatures of these species live in clear and unpolluted streams.

Culoptila jamapa, new species
(Figs. 1–2)

Diagnosis.—Because of the presence of two spines in the aedeagal sac, this species seems to be related to *Culoptila rusia* and *C. nahuatl.* It is also related to *C. amberia* because of the shape of the tenth tergum in ventral view. It is distinguished from these species by the apices of the two aedeagal spines, one very narrow and the other quite broad with four small subapical teeth. These characters states are not observed in any of the related species of the genus.

Description of adult.—Length of forewing 2 mm. Color in alcohol dark brown; forewing with a slight indication of a pale band at anastomosis. 6th sternum of male with a compressed apicomesal knob. Male Genitalia: 9th segment, in lateral aspect, with ventral margin shorter than dorsal margin; anterior margin slightly produced and rounded; posterior margin nearly straight. 10th tergum, in ventral aspect, clearly rounded with posterior margin slightly truncate; in lateral aspect almost straight, with ventral arms wider basally, with apices truncate and curved anteriad. Venter of capsule slightly produced posteriad, in posteroventral aspect composed of a pair of short triangular sclerites. Phallus a large internal sac bearing two spines filling more than three-fourths of sac; one spine narrow with apex straight and acute,



Figs. 1–4. *Culoptila jamapa,* new species: 1, genitalia, lateral view; 2, genitalia, ventral view; 3, 4, *Culoptila acaena,* new species: 3, genitalia, lateral view; 4, genitalia, ventral view.

the other quite broad with four small subapical teeth; in lateral aspect apicodorsal angle produced to a broad hood.

Material.—Holotype ô and 1 paratype (ô); Mexico. Veracruz: Río Jamapa, 26 May 1981, C. M. & O. S. Flint (USNM). Other paratypes are as follows: Las Minas 20 km SW from Perote, 6 Sep 1977, J. Bueno, 1ô (IBUNAM). Estado de México: Ruta 134 km 44 Toluca-Temascaltepec, 27 Apr 1990, J. Bueno y R. Barba, 6ô and 2 females (IBUNAM); Temascaltepec Real de Arriba, 2 Jun 1990, A. Rojas y R. Gaviño, 1ô; 17 Aug 1990, 1ô; 26 Apr 1991, 1ô; 16 Feb 1991, 1ô, (IBUNAM); Puebla: Puente Apulco, situated at 97.89°W and 25°N, 1400 m, 1 May 1987, J. Bueno, 2ô (IBUNAM).

Etymology.—The species epithet, *jamapa,* is the name of the river in Veracruz where this species was collected.

Culoptila acaena, new species

(Figs. 3–4)

Diagnosis.—The shape of the tenth tergum in ventral aspect and the number and length of the spines of the aedeagus distinguish this species from all others assigned to the genus.

Description of adult.—Length of forewing 2.5 mm. Color in alcohol dark brown. 6th sternum of male with a compressed apicomesal knob.

Male Genitalia: 9th tergum rectangular in lateral aspect. 10th tergum in lateral aspect with dorsal margin produced to a point, ventral arms rounded apically, each bearing a few stout anterior setae, dorsal margin clearly rectangular in posteroventral aspect; preapex of ventral arms with knobs with long and stout setae. Venter of capsule produced posteriad, in posteroventral aspect composed of a pair of long digitiform processes. Phallus a small internal sac, bearing a group of short and bent spines in lateral aspect; apicodorsal angle produced to a pointed hood, apex rounded apicoventrally.

Material.—Holotype ô; Mexico. Guerrero: Carretera 130, 80 km NW from Zihuatanejo, 1200 m, 7 Jun 1984, J. Bueno (IBUNAM). Paratype ô with same label data as the holotype (IBUNAM).

Etymology.—The species epithet, *acaena,* is a Latinized Greek word (feminine) that refers to the spines, specifically of the aedeagus.

Culoptila barrerai new species.

(Figs. 5–6)

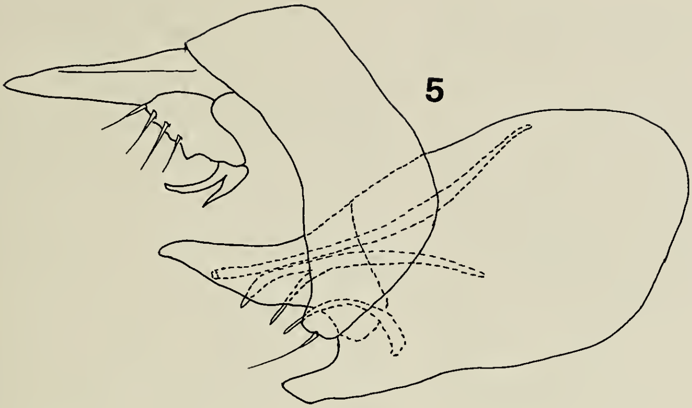
Diagnosis.—This is a very distinct species based on the shape of the tenth tergum and the ventral arms, which are wider basally and have the apices ending in two long spines curved posteriad. These character states are unique within the genus.

Description of adult.—Length of forewing 2 mm. Color in alcohol dark brown; forewing with a slight indication of a pale band at anastomosis. 6th sternum of male with a compressed apicomesal knob.

Male Genitalia: 9th segment, in lateral aspect, with ventral margin shorter than dorsal margin; anterior margin slightly produced and rounded; posterior margin nearly straight. 10th tergum, in dorsal aspect, clearly rectangular with posterior margin truncate; in lateral aspect almost straight, with ventral arms wider basally and apices ending in two long spines curved posteriad. Venter of capsule slightly produced posteriad; in posteroventral aspect, composed of a pair of very short triangular sclerites. Phallus a large internal sac bearing two spines; about half as long as sac; one spine with apex straight and acute; in lateral aspect apicodorsal angle produced to a pointed hood.

Material.—Holotype ô; Mexico. Oaxaca: Pochutla, Finca Progreso, 2 June 1987, E. Barrera (IBUNAM). Paratypes: Same label data as the holotype 4ô (IBUNAM).

Etymology.—The species epithet is a patronym we dedicated to the collector of the type series, Mr. Ernesto Barrera-Vargas.



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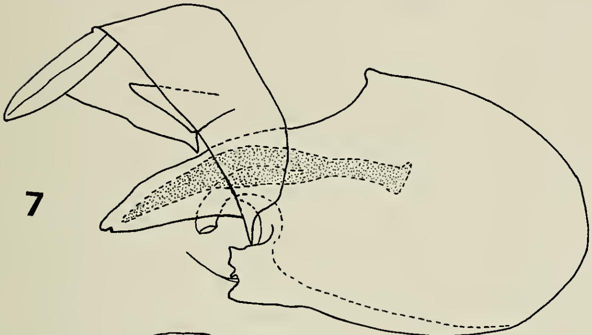

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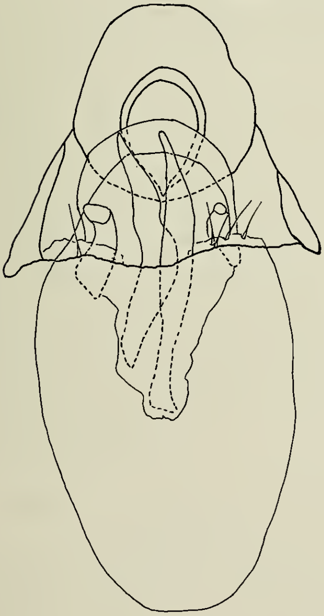

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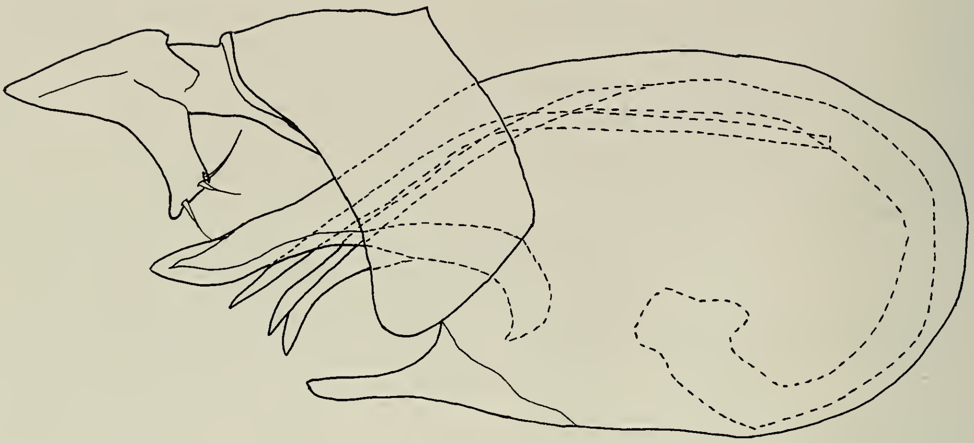
Figs. 5–8. 5, 6, *Culoptila barrerai,* new species: 5, genitalia, lateral view; 6, genitalia, ventral view; 7, 8, *Culoptila denningi,* new species: 7, genitalia, lateral view; 8, genitalia, ventral view.



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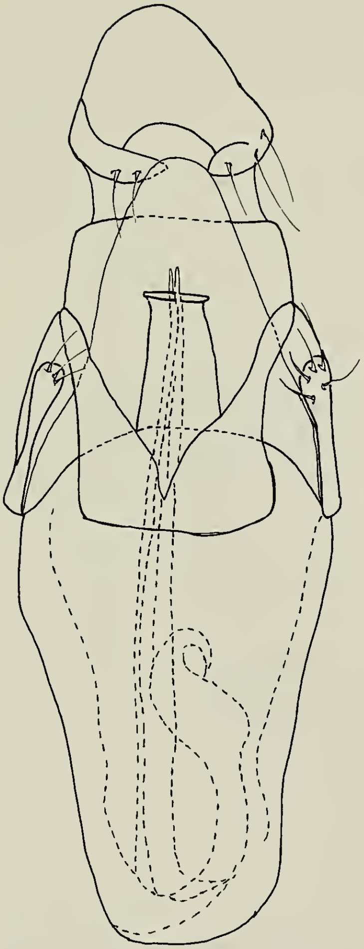

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Figs. 9–10. *Culoptila azulae,* new species: 9, genitalia, lateral view; 10, genitalia, ventral view.

Culoptila denningi new species
(Figs. 7–8)

Diagnosis.—Based on the shape and length of the internal spines of the aedeagus, *Culotila denningi* appears to be related to *C. moselyi* (Denning, 1965). However, in *C. moselyi* the spines of the internal sac of the aedeagus are of different sizes, but in *C. denningi* these spines appear to be similar in size and general appearance.

Description of adult.—Length of forewing 3 mm. Color in alcohol dark brown. 6th sternum of male with a compressed, apicomesal knob.

Male genitalia: 9th tergum narrowed ventrad. 10th tergum in lateral aspect, with ventral arms directed ventrad, tip obliquely truncate; in posteroventral aspect with dorsal margin nearly straight, inner tip of ventral arms convergent resulting in a circular opening. Venter of capsule produced to a pair of short, narrow lobes. Phallus with two short internal spines about half length of sac; apicodorsal margin produced to a long, broad hood, in posteroventral aspect widely rounded.

Material.—Holotype ♂; Mexico. Guerrero: Ruta 130, 80 km NW from Zihuatanejo, 1200 m, 7 Jun 1984, J. Bueno, (IBUNAM). Paratypes: same locality data as holotype, 2♂ (IBUNAM); Estado de México, Ruta 134, Temascaltepec Real de Arriba, Arroyo Colorado, 15 Mar 1991, A. Rojas y R. Gaviño, 2♂ (IBUNAM).

Etymology.—The species epithet is a patronym we dedicated to the memory of Dr. Donald G. Denning.

Culoptila azulae, new species
(Figs. 9–10)

Diagnosis.—Based on the shape of the aedeagus in lateral view, this species appears to be related to *C. nahuatl* Flint, but differs in having the venter of capsule composed of a pair of long digitiform sclerites, and in posteroventral aspect with the dorsal margin clearly rounded.

Description of adult.—Length of forewing 2.5 mm. Color dark brown in alcohol. 6th sternum of male with a compressed apicomesal knob.

Male Genitalia: 9th tergum rectangular in lateral aspect. 10th tergum in lateral aspect with dorsal margin produced to a point, ventral arms rounded apically, each bearing a few stout anterior setae, in posteroventral aspect with dorsal margin clearly rounded, apex of ventral arms acute. Venter of capsule produced posteriad, in posteroventral aspect composed of a pair of long digitiform processes. Phallus a large internal sac, bearing two long spines, one spine curved around apex of sac, apicodorsal angle produced into a pointed hood, apicoventrally with a complex of structures.

Material.—Holotype ♂; Mexico. Chiapas: Reserva Montes Azules, 29 Apr 1986, R. Barba (IBUNAM). Paratypes, 2♂ (IBUNAM) and 2♂ (USNM), same locality data as the holotype.

Etymology.—The species epithet, *azulae,* is feminine and refers to the Spanish word for blue.

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A new species of ghost shrimp of the genus *Sergio* Manning & Lemaitre, 1994 (Crustacea: Decapoda: Callianassidae) from the Caribbean coast of Colombia

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Abstract.—A new species of ghost shrimp, *Sergio sulfureus,* is described from shoreline habitats of Barú, on the Caribbean coast of Colombia. This new species is the seventh known of the genus *Sergio* Manning & Lemaitre, and is most similar to *S. guassutinga* (Rodrigues), from Brazil, and *S. mericeae* Manning & Felder, from Florida. The new species can be distinguished from these two primarily by characters derived from the major cheliped, including color. The new species is described in detail, and information is given on adult and immature stages, habitat, and co-occurring burrowing decapods.

A new species of the recently proposed genus *Sergio* Manning & Lemaitre, 1994, was discovered while sampling infaunal decapods from inshore habitats of the Caribbean coast of Colombia. The number of species in this genus has now nearly doubled since it was proposed. In addition to this new species, *Sergio* includes six others, all from the western Atlantic: *S. guassutinga* (Rodrigues, 1971), *S. guara* (Rodrigues, 1971), *S. mirim* (Rodrigues, 1971), *S. trilobatus* (Biffar, 1970), *S. guaiqueri* Blanco Rambla, Liñero Arana, & Lares M., 1995, and *S. mericeae* Manning & Felder, 1995. Based on morphological similarities, the new species appears to be most closely related to *S. guassutinga* and *S. mericeae.*

The specimens were collected using a yabby pump as described by Hailstone & Stephenson (1961). The material has been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and the University of Southwestern Louisiana Zoological Collections, Lafayette (USLZ). The following measurements were taken (all in millimeters): postorbital carapace length (cl); total length measured from the postorbital margin to the posterior margin of the telson (tl). Eggs were measured on their greatest diameter. All measurements were taken after preservation of specimens in 70% alcohol. Abbreviations used: M, male(s); F, female(s); ov, ovigerous; immat, immature of undetermined sex; mutl, mutilated; coll, collector.

Sergio sulfureus, new species
Figs. 1–6

Holotype.—F (cl 12.1 mm, tl 44.5 mm), Caribbean coast of Colombia, SW shoreline of Barú, beach facing Rosario Islands (on property of A. Zubiría) adjacent to Ciénaga del Pelao, 0.5 m, 20 Jul 1995, coll. R. Lemaitre, USNM 275985.

Paratypes.—Same locality as holotype: 5 M (cl 7.6–15.3 mm), 2 F (cl 7.2–15.0 mm), 1 immat (cl 5.8 mm), 1 mutl (abdomen only), 23 Jul 1994, coll. R. Lemaitre, USNM 275989. 2 M (cl 11.3–20.4 mm), 1 F (cl 13.7 mm), 3 immat (cl 5.8–7.5 mm), 20 Jul 1995, coll. R. Lemaitre, USNM 275986, 275987, 275988. 7 M, of which 5 are photo vouchers (cl 22.9–8.8 mm), 2 F photo vouchers, of which 1 ov (cl 22.1–18.7 mm), 11 Mar 1996, colls. R. Lemaitre, D. L. Felder, S. Nates and C. Moreau, USLZ 3572.

Diagnosis.—Frontal margin of carapace with 3 triangular prominences each terminating in spine; median prominence acute rostrum slightly exceeding lateral projections. Eyestalks terminating in small outwardly curved spine. Third maxilliped with moderately developed crista dentata on ischium. Major cheliped with dactyl distinctly longer than palm; dactyl with proximal half of prehensile edge bearing 2 prominent teeth (1 basal subrectangular, 1 hooked distally); distal half of prehensile edge either unarmed, or armed with 2 or 3 small rounded teeth, or row of small triangular teeth proximally; carpus more than half length of palm; merus with distinct longitudinal carina on outer surface. Major and minor chelipeds light yellow at least on lower half, often light pink dorsally; entire chelipeds sulfur yellow in large specimens (tl ≥70.0 mm).

Description.—Frontal margin of carapace (Fig. 1a, b) with 3 triangular prominences consisting of rostrum and 2 lateral projections. Rostrum acute, horizontal (in lateral view, Fig. 1c), terminating in small spine; slightly in advance of lateral projections in adults, much more prominent and distinctly exceeding lateral projections by half or more length of rostrum in immature specimens (cl ≤6.0 mm, Fig. 1b). Lateral projections terminating in inwardly curved spine. Carapace lacking rostral carina, with distinct linea thalassinica, and with a defined dorsal oval marked posteriorly by deep transverse cardiac furrow, which extends anteroventrally to either side above linea thalassinica as shallow sinuous groove demarcating posterior half of dorsal oval. Shallow cervical groove originating immediately below linea thalassinica on anterior half of branchiostegite and curved anteroventrally, intersecting raised sinuous ridge in anterior third of branchiostegite; portion of ridge anterior to intersection positioned ventrolaterally to rounded hepatic boss.

Eyestalks (Fig. 1a, c) flattened, weakly concave dorsally, length equal to or slightly less than twice basal width, tapering distally, and terminating in small distomesial spine directed slightly outward; slightly exceeding distal margin of basal antennular segment in mature specimens, or slightly shorter than basal antennular segment in immature specimens; mesial surfaces nearly in contact on proximal halves or more, slightly diverging distally; mesial margins abruptly rounded distally; anterolateral margin rounded from level of corneae to distomesial spine. Corneae dark, area of pigmentation underlying it sexually dimorphic, large and visible within much of eyestalk in males, more confined to immediate corneal area in females; rounded corneal surface more bulbous in immature than adults.

Antennular peduncle (Fig. 1a) shorter and heavier than antennal peduncle, terminal article slightly longer than penultimate and reaching to or beyond midlength of terminal article of antennal peduncle. Penultimate and terminal articles with ventromesial and ventrolateral rows of long setae (those of ventrolateral row longest, densest), and continued on ventral ramus of flagellum. Flagellum with rami subequal in length (about 4-5 times length of terminal article of peduncle); dorsal ramus with sparse tufts of long setae, distal half with heavier articles bearing dense tufts of short ventral setae, articles comprising tapered tip with dense line of short ventral aesthetascs.

Antennal peduncle (Fig. 1a) with fourth (terminal) article subequal in length or slightly longer and narrower than third article. Third article elongate, narrower than second, slightly longer than combined lengths of first two, proximolaterally with partially fused condylar process articulated to distolateral extreme of second article. Second article with deep, diagonal ventral suture, distolaterally with single tuft of setae, small rounded vestige of dorsal scale articulated at joint with third article. Basal

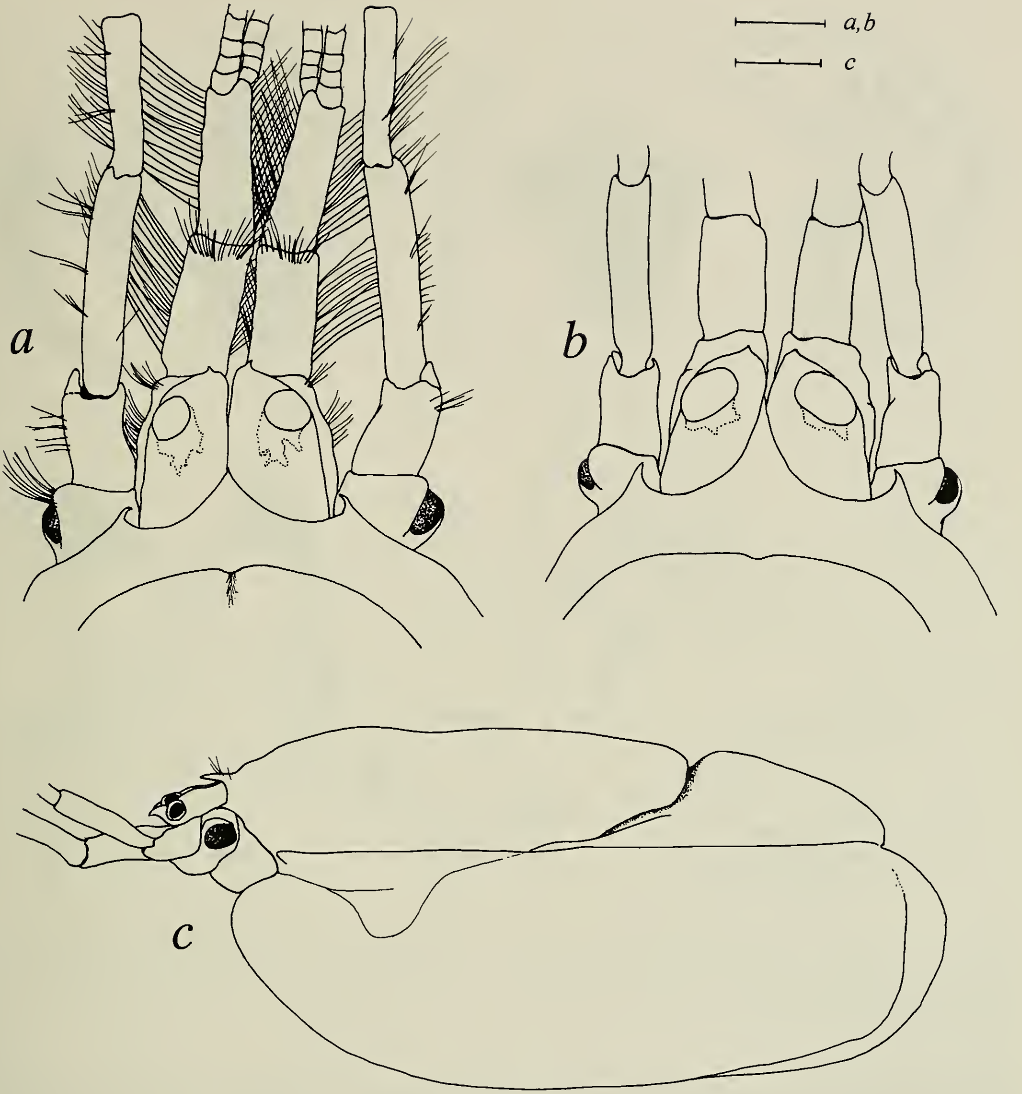

Fig. 1. *Sergio sulfureus*, new species, paratypes, USNM 275987, 275989. a,b, front of carapace and cephalic appendages, dorsal view: a, male (cl 15.3 mm); b, immature (cl 5.8 mm), setae omitted; c, carapace and cephalic appendages, female (cl 12.2 mm), lateral view. Scales equal 1 mm (a), 0.5 mm (b), and 2 mm (c).

article with dorsolateral carina above laterally produced excretory pore. Flagellum 2 to 2.5 times length of antennular flagellum.

Mandibles (Fig. 2a, b) with large 3-segmented palp, third article rounded distally and with short setae on extensor surface, second article with row of long setae on external and distal surfaces; incisor process with well developed corneous teeth on cutting margin, teeth largest on proximal half; molar process with three or four small marginal teeth; paragnath rounded. First maxilla (Fig. 2c) with long, narrow endopod deflected proximally at articulation; proximal endite with setose, sinuous margin, and terminal lobe with field of long, terminally bifid setae; distal endite narrow proximally, broadening substantially distally, with row of short stiff bristles and setae (some bifid) on distomesial margin; exopod low, truncate and setose. Second maxilla (Fig.

Fig. 2. *Sergio sulfureus,* new species, male (cl 15.3 mm), paratype, USNM 275989. Left mouthparts, all external view except b, f, and h, showing internal view: a, mandible; b, same, setae omitted; c, first maxilla; d, second maxilla; e, first maxilliped; f, same, setae omitted; g, second maxilliped; h, third maxilliped. Scales equal 1 mm (a–g), and 2 mm (h).

2d) with endopod narrow distally, tip slightly bent; first and second endite each unequally subdivided, marginally setose; exopod forming large, broad scaphognathite. First maxilliped (Fig. 2e, f) with proximal endite narrowly produced, marginally setose; distal endite subrectangular, mesial half of external surface and margins heavily setose, with longest setae distomesially, internal surface concave; exopod ovoid, setose, divided by transverse suture marking notch on mesial margin, with row of long pectinate setae on external margin near notch; epipod large, broad, anterior end tapered to elongate anterior process (Fig. 2f). Second maxilliped (Fig. 2g) with long, narrow endopod; merus more than 4 times width, flexor margin with fringe of very long setae; carpus short; propodus weakly curved, increasing slightly in width distally, with row of setae on flexor margin; dactyl short, less than ⅓ length of propodus, with terminal brush of strong, short corneous spines; exopod phylliform, setose, shorter than endopodal merus; epipod small, divided into 2 proximal lobes and minute terminal lobe. Third maxilliped (Fig. 2h) lacking exopod; endopod with long dense setation on flexor and extensor margins; combined length of ischium-merus about 2 times width; ischium subrectangular, with moderately well de-

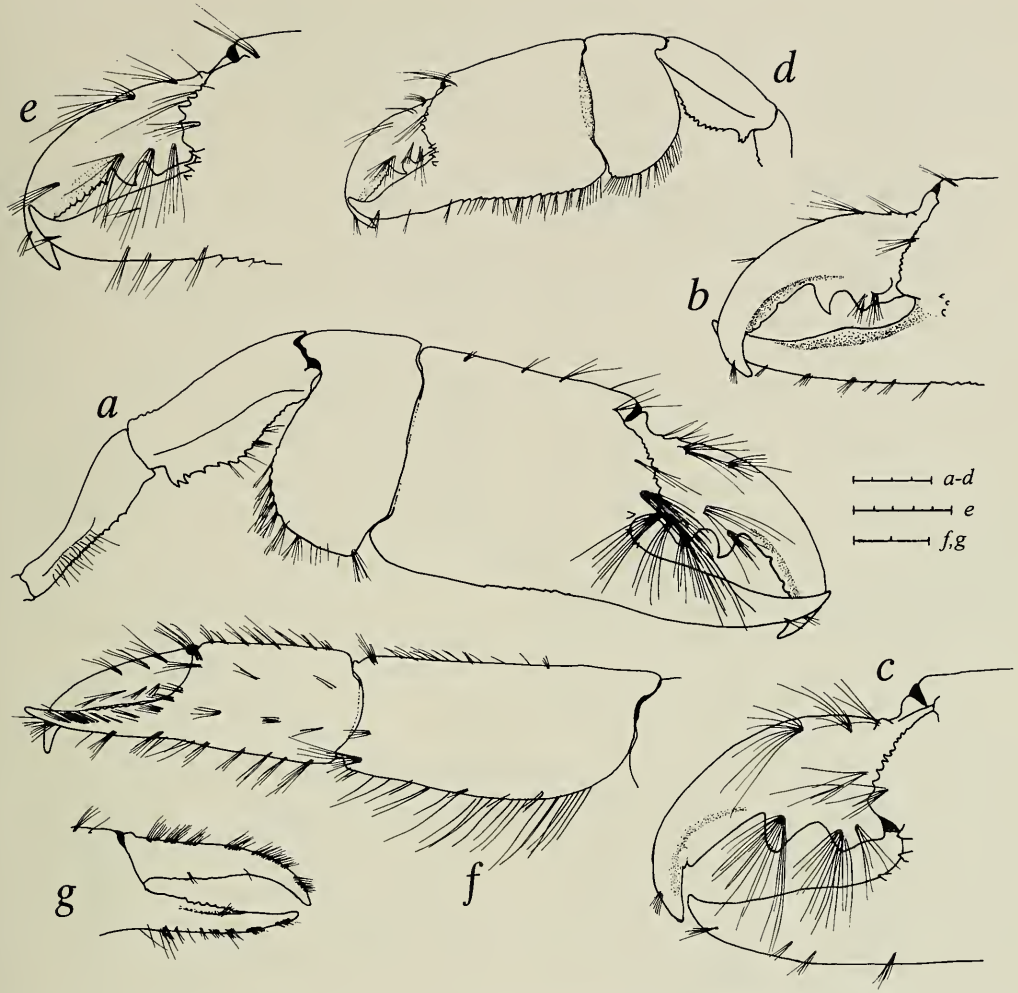

Fig. 3. *Sergio sulfureus,* new species: a–c, f, g, male paratypes, USNM 275988; d, e, holotype, USNM 275985. a, major cheliped of male (cl 15.3 mm), external; b, fingers of same, internal; c, fingers of male (cl 20.4 mm), external; d, major cheliped of female holotype (cl 12.1 mm), external; e, fingers of same, external; f, minor cheliped of male paratype (cl 15.3 mm), external; g, fingers of same, internal. Scales equal 4 mm (a-d), 5 mm (e), and 2 mm (f, g).

fined crista dentata in form of curving row of outwardly curving small spines; merus and carpus subtriangular, internal face with field of setae on distal third; propodus subquadrate (or at most height slightly exceeding length), internal face with field of setae medially; distal margin weakly emarginate; dactyl narrow, curved, with small brush of short setae terminally.

Branchial formula includes, in addition to exopods and epipods mentioned for first and second maxillipeds: rudimentary arthrobranch on second maxilliped, pair of arthrobranchs on third maxilliped, and pair of arthrobranchs on each of first to fourth pereopods.

First pereopods forming greatly dissimilar chelipeds. Major cheliped heavy, massive (less so in immature than adults) in both sexes (Fig. 3a–e). Ischium slender, increasing in width distally; dorsal margin weakly sinuous; ventral margin with row of

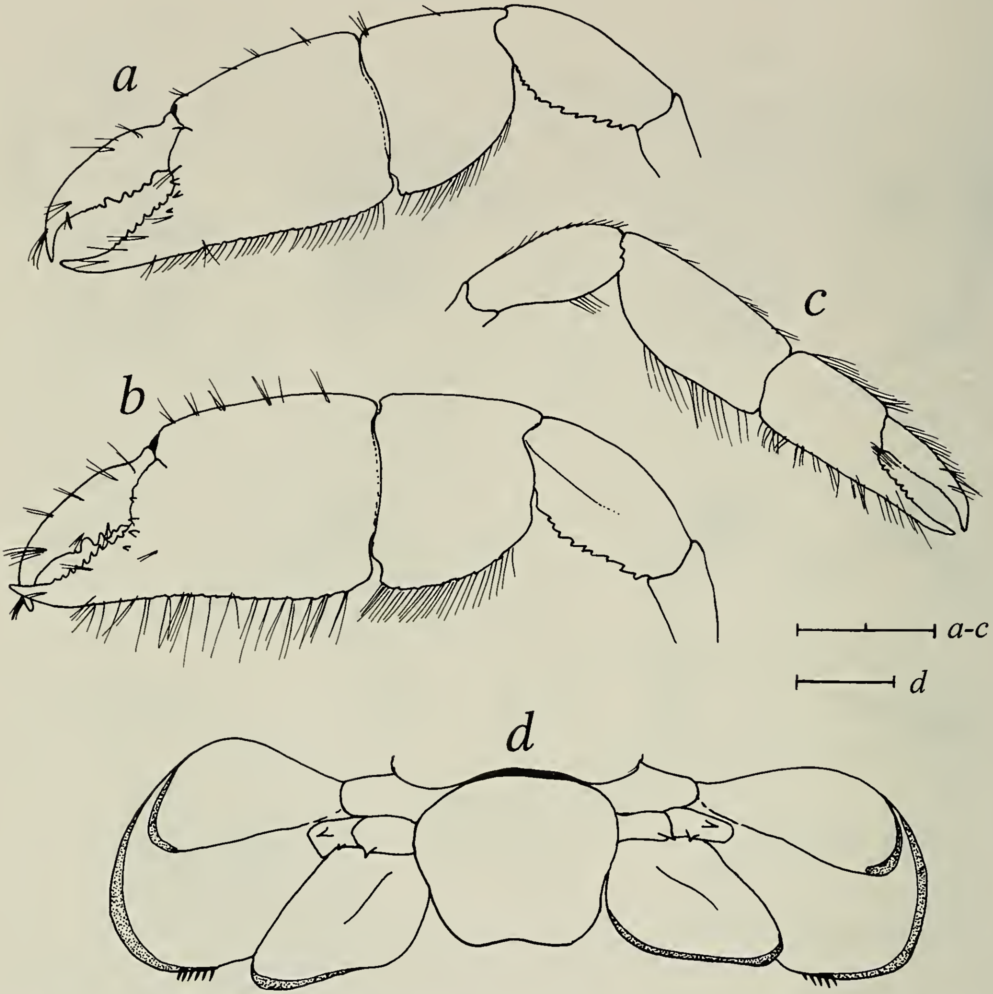

Fig. 4. *Sergio sulfureus,* new species, paratypes, USNM 275986. a, major cheliped of immature (cl 6.5 mm), external; b, major cheliped of immature (cl 7.0 mm), external; c, minor cheliped of immature (cl 6.5 mm), external; d, uropods and telson of immature (cl 6.5 mm), setae omitted, dorsal. Scales equal 2 mm (a–c) and 1 mm (d).

small denticles increasing in size and separation distally on proximal ⅔. Merus about twice as long as greatest height; outer face with median longitudinal carina visible over at least half length of merus, carina not defined in immature specimens cl ≤6.0 mm (Fig. 4a); dorsal margin weakly sinuous, keel-like, with minute tubercles proximally; ventral margin in adults strongly rounded, often ventrally produced, armed with small spines and strong bifid process proximally (Fig. 3a, d); ventral margin in immature broadly rounded, armed with small spines only (Fig. 4a, b); lateral face with longitudinal median carina. Carpus 0.6–0.8 as long as palm; shorter and higher in adults than in immature specimens (in adults length about 0.6 height, in immature length about 0.8 height); dorsal margin nearly straight, keel-like; ventral and proximal margins serrated (serrations most visible in internal view), with tufts of setae; proximal margin evenly rounded. Chela with length twice greatest height; palm about as long as high in adults (Fig. 3a, d), slightly longer than high in immature specimens (Fig. 4a, b); fingers with hooked tips crossed when closed. Palm with dorsal margin keel-like, with few tufts of setae; ventral margin serrated, with tufts of setae; outer face with 3 spines distally just proximal to gape of fingers, and row of blunt or sharp spines on upper half of distal margin. Fixed finger with prehensile margin unarmed in adults (Fig. 3a–e), or armed with small, sharp teeth in immature specimens (Fig. 4a, b). Dactyl longer than palm; dorsal margin with tufts of setae proximally; proximal half of prehensile margin with strong proximal subrectangular tooth separated by deep indentation from following hooked sharp tooth, lateral faces of teeth with 2 tufts of long setae (subrectangular tooth) or 1 tuft of setae (hooked tooth); distal half of prehensile edge slightly flared outward in large specimens (tl ≥ 70.0 mm), variable: with U-shaped indentations (Fig. 3a, b), or with subdistal rounded teeth (Fig. 3c), or with row of small, sharp teeth (Figs. 3d, e, 4a).

Minor cheliped (Figs. 3f, g, 4c) slender, elongate (more so in adults); dorsal margins of merus, carpus, and propodus keel-like. Ischium narrow unarmed. Merus twice as long as high, ventral margin with long setae. Carpus twice or more as long as high; dorsal and ventral margins with tufts of setae (longer on ventral than dorsal margin). Chela with length nearly 3 times greatest height; dorsal and ventral margins of palm and fingers with tufts of setae; fingers distally hooked, tips crossed when closed. Palm with outer surface smooth except for scattered tufts of short setae. Fixed finger subequal in length to palm, prehensile margin weakly serrate. Dactyl longer than palm; prehensile margin weakly serrate (teeth weaker than on prehensile margin of fixed finger).

Second pereopod (Fig. 5a) chelate. Ischium short, with tufts of setae on ventral margin. Merus more than 3.5 times as long as ischium; ventral margin with long setae diminishing in length distally. Carpus with long setae on dorsal and ventral margins; outer face with scattered tufts of setae, and short transverse rows of short setae subdistally on upper half. Chela triangular in shape when fingers closed; dorsal and ventral margins with long setae; outer face with scattered tufts of short setae; fingers straight, prehensile margins minutely serrate, corneous; fingers terminating in blunt corneous tip.

Third pereopod (Fig. 5b) with merus about 2.4 times as long as ischium. Merus and carpus with few setae on dorsal and ventral margins. Carpus with transverse row of stiff setae on outer face subdistally on upper half; distal margin of outer face with row of setae on lower half. Propodus with strong ventroproximal lobe bearing long setae; ventral margin with evenly spaced tufts of long setae; dorsal margin with long setae; outer face covered with numerous tufts of short setae. Dactyl tear-shaped, terminating in outwardly directed corneous tip; outer face densely setose.

Fourth pereopod (Fig. 5c) subchelate. Ischium, merus, and carpus with scattered setae. Merus about 1.7 times as long as ischium. Propodus with inferodistal corner produced in form of short fixed finger; outer surface covered with dense setation divided by naked region into upper and lower fields, lower field continued on lower half of internal face. Dactyl terminating in outwardly directed corneous tip; outer face with dense setation.

Fifth pereopod (Fig. 5d) chelate. Merus more than 3 times as long as ischium. Merus and carpus with scattered setae. Propodus with long dense setation on distal half of outer surface, and row of long setae on ventrodistal margin. Fingers with opposable surfaces excavate, spoon-like, each with row of minute, fused corneous teeth; dactyl with long setae on outer surface.

Abdomen (Fig. 6a) with dorsal surface of tergites smooth except for small, imperceptible (except under high magnification) pits. Second abdominal somite longest, about 1.3 times as long as first, and 1.7 times as long as third. Third to fifth somites each

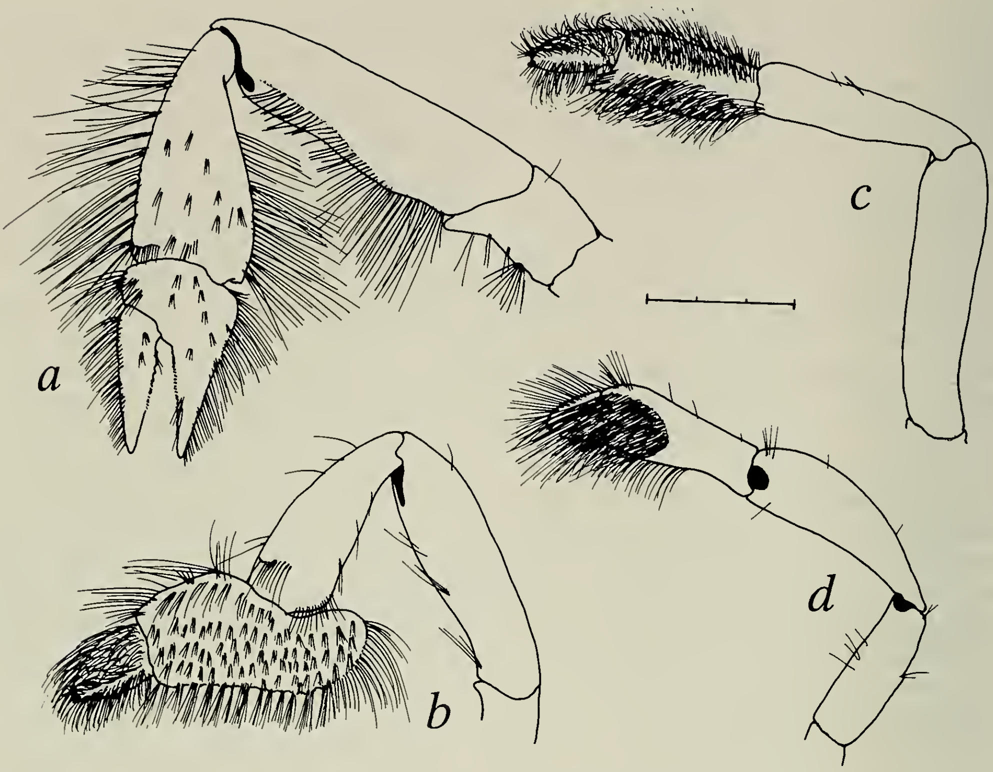

Fig. 5. *Sergio sulfureus,* new species, female (cl 12.2 mm), paratype, USNM 275989. Left second to fifth pereopods, external surface: a, second; b, third; c, fourth; d, fifth. Scale equals 3 mm.

with short transverse field of soft dense setae on lateral lobe (pleura). Sixth somite divided into unequal anterior and posterior portions by lateral constriction and transverse groove; posterior portion with short median longitudinal groove.

First pleopod of male (Fig. 6b) and female (Fig. 6c) uniramous, composed of 2 articles. In male, distal article with long setae, shorter than proximal one; subdivided into anterior and posterior lobe by weak longitudinal furrow, anterior lobe terminally rounded, posterior lobe terminally acute with tip directed anteroventrally; proximal article straight. In female, distal article with long setae, subequal in length to proximal article, anterior margin with small setose lobe at about midlength of margin; proximal article strongly curved anteriorly, with long setae on posterior margin distally. Second pleopod of male (Fig. 6d, e), and female (Fig. 6f, g) biramous. In male, exopod with long setae distally and on lateral margin; appendix masculina weakly separated from endopod, overreaching distal end of endopod; distal end of endopod terminating in minute, acute tip (Fig. 6e). In female, both rami with long setae; appendix interna small (Fig. 6g), tapered distally. Third to fifth pleopod pairs (Fig. 6h, i) forming large, posteriorly cupped fans when coupled at mesial margins of endopods; endopod of each with subtriangular, appendix interna embedded into mesial margin of endopod (Fig. 6i).

Telson (Figs. 4d, 6j) broader than long (broadest at lateral lobes) subhexagonal; dorsal surface elevated along midline on anterior half, with short transverse row of setae medially; posterior margin divided by shallow cleft into 2 lobes (cleft shallower in immature specimens, Fig. 4d), each lobe

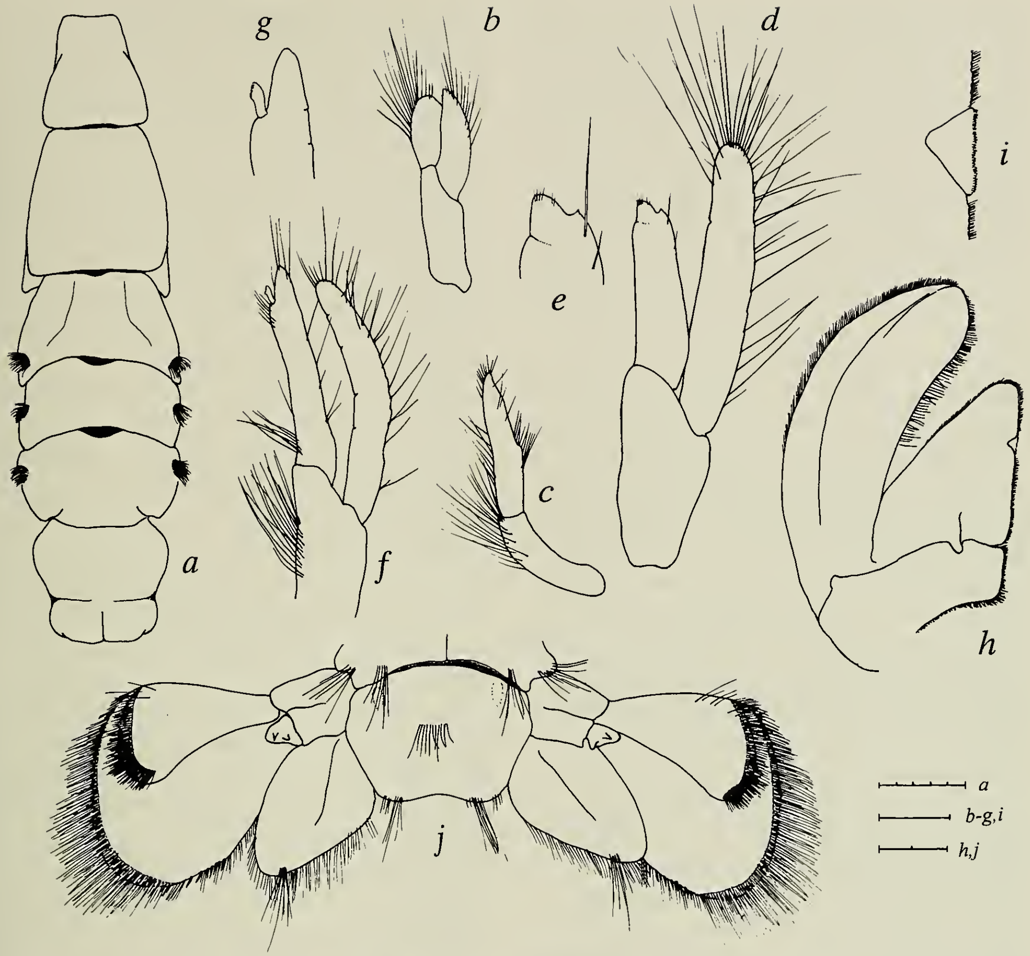

Fig. 6. *Sergio sulfureus,* new species, paratypes, USNM 275989: a, c, f, g, j: female (cl 12.2 mm); b, d, e, h, i: male (cl 15.3 mm). a, abdomen, female (cl 12.2 mm), dorsal; b, left first pleopod of male, internal; c, left first pleopod of female, lateral; d, left second pleopod of male, posterior; e, tip of endopod of same; f, left second pleopod of female, posterior; g, tip of endopod of same, showing appendix interna; h, left third pleopod, anterior; i, mesial margin of endopod of same, showing appendix interna; j, uropods and telson, female (cl 12.2 mm), dorsal view. Scales equal 5 mm (a), 1 mm (b–d, f), 0.5 mm (e, g, i), and 2 mm (h, j).

with tuft of long setae. Uropod with acute, posterolaterally directed spine on protopod, and 1 or 2 blunt or sharp dorsodistal spines. Endopod longer than broad, with tuft of setae dorsally near posterodistal corner; posterior margin setose. Exopod with anterodorsal plate falling well short of distal margin of exopod, distal edge of plate with dense setation grading posteriorly to stiff, bristle-like setae; posterior plate with dense setation on lateral and posterior edges, and row of 5–9 short corneous spines on posterodistal corner.

Size.—The largest male specimen measured cl 22.9 mm, tl 76.1 mm. The largest female, an ovigerous specimen, measured cl 22.1 mm, tl 82.1 mm; mature, eyed eggs of this female were very near hatching and measured 0.63-0.76 mm in maximum diameter. The smallest specimen, of undetermined sex, measured cl 5.8, tl 14.0 mm.

Color.—(From field notes and color photographs of fresh specimens). Large males (cl 22.9, 21.2, 20.4 mm) and female (cl 22.1 mm), all with major cheliped distinct light sulfur-yellow; minor cheliped and second to fifth pereopods light yellow, fading distally; telson light brownish distally. Otherwise overall body color whitish or transparent. Color similar in slightly smaller male (cl 17.7 mm) and female (cl 18.7 mm) except for tinges of faint pink or mauve. Specimens < cl 15.0 mm with upper surfaces of major and minor chelipeds light salmon to rose pink, darkest on carpus and merus, lower surfaces grading from white to very light yellow; pink to rose also distributed on dorsal antennular flagellum and antennal peduncle as broad band across dorsal oval of cephalothorax, and over most of cardiac region; dorsal pink to rose color on abdomen sparse on first abdominal somite, extensive on second abdominal somite, and distributed as pattern on midline and posterior margins of third to fifth abdominal somites, and more extensive pattern on sixth somite; rose color deeper and especially evident on tailfan, where most intense on uropods and distal half of telson.

Range, habitat, and commensals.—Known only from the southwestern shoreline of Barú, on the Caribbean coast of Colombia (see Lemaitre 1981, for a general description of the collecting area). The specimens were obtained on the same beach during successive years (Jul 1994, 1995, and Mar 1996), just below the lower intertidal level, mostly from sediments in depths of 0.3–0.5 m. The southwest shore of Barú is lined typically by low stands of red mangroves (*Rhizophora mangle*) alternating with short sandy beach strips ranging in length from a few to several hundred meters. Mangrove lagoons (ciénagas) are found typically on the landward side of this shore, such as the Ciénaga del Pelao, adjacent to the type locality for this new species. Suspended matter in runoff water from these lagoons heavily influences sedimentary composition of adjacent beaches, which are separated by a channel about 5 km wide from the coralline archipelago of the Rosario Islands. At the collecting site, which is immediately inshore of shallow *Thalassia* beds, the sediment is composed of a thin surface layer of coralline sand overlying a mixture of calcareous sand, mud and clay, the lower layers of which release a strong hydrogen sulfide smell when disturbed to remove the burrowing fauna. Water is frequently turbid due to wave action which makes burrow openings inconspicuous. The new species was found alongside an undetermined species of pinnotherid crab of the *P. cristata* complex, and two other callianassids, *Neocallichirus lemaitrei* Manning, 1993, and *N. grandimana* (Gibbes, 1850).

Etymology.—The specific name is from the Latin *sulfureus,* of sulfur, and is given in reference to the distinct sulfur-like color of the major cheliped and the sulfide smell released by the sediment this species inhabits.

Remarks.—This new species most closely resembles *Sergio guassutinga,* from Brazil, and *S. mericeae,* from Florida. The new species can be differentiated from these and other congeners primarily by characters of the major cheliped. The major cheliped of *S. sulfureus* differs from that of *S. guassutinga* and *S. mericeae* in the relative length and armature of the dactyl (for the latter two see Manning & Felder 1995, fig. 1b–e, h). In the new species, the dactyl is consistently longer than the palm measured dorsally (Fig. 3a, d), whereas in the other two species the dactyl is at most subequal to the length of the palm. In the new species, the distal half of the prehensile edge of the dactyl can have two or three small rounded teeth (Fig. 3a–c), or small triangular teeth proximally (Fig. 3d, e); in the other two species the distal half typically has a prominent row of sharp teeth. In live specimens of *S. sulfureus,* the major cheliped in both sexes is light pink on the dorsal surface, and light yellow elsewhere; the major cheliped of the largest specimen collected, a male tl 71.0 mm, is entirely of a distinct sulfur yellow. The major cheliped in *S. mericeae* is bright red (Manning & Felder 1995), and at least in males of *S. guassutinga,* it is pink-yellowish (Rodrigues 1971).

Comparison of the rostrum of *S. sulfureus* (Fig. 1a, b) with that of *S. mericeae* and *S. guassutinga* (see Manning & Felder (1995; figs. 1a, g, 5a, b), shows some differences that might be interpreted as diagnostic. In the new species the rostrum is more produced anteriorly than in *S. mericeae* or *S. guassutinga*; in the latter two species the rostrum is depicted by Manning & Felder as having a small slender spine terminally, whereas the rostrum of the new species usually tapers gradually to an acute tip. However, the degree of development of the rostrum and its distal termination has been observed to vary in all three species. Thus, the rostrum is not a reliable structure to use in distinguishing these species.

Sergio sulfureus shares a number of characters with *S. mericeae* and *S. guassutinga.* On the major cheliped, the armature of the dorsal and ventral margins of the merus is similar in *S. sulfureus* and *S. mericeae.* In both species, the dorsal margin has minute tubercles proximally; and the ventral margin is armed proximally with a prominent, usually bifid or trifid tooth which is separated by a distinct gap from the more distal teeth. As in *S. guassutinga,* the new species has a well defined carina on the outer face of the merus (except in smaller immature specimens), and the carpus is slightly longer than half the length of the palm. Like in *S. guassutinga,* the crista dentata on the ischium of the third maxilliped of *S. sulfureus* is moderately well developed.

Acknowledgments

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Lonchodactylus messingi, a new genus and species of Cyclodorippidae (Crustacea: Decapoda: Brachyura) from the Bahamas

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Abstract.—A new genus and species of the family Cyclodorippidae, *Lonchodactylus messingi*, is described from specimens collected in the Bahamas using a research submersible. The new genus is more closely related to two Indo-West Pacific genera (*Genkaia* Miyake & Takeda and *Phyllotymolinum* Tavares) than to any other cyclodorippid from the coasts of America. Morphological similarities and differences between these genera are discussed.

Six genera and twenty species of the family Cyclodorippidae Ortmann, 1892, are known from the western Atlantic and eastern Pacific of the Americas (Tavares 1993a). Five of these genera are restricted to the New World waters, while *Corycodus* A. Milne Edwards, 1880, has one species in the western Atlantic and four in the Indo-West Pacific (Tavares 1993b). With the present discovery in the Bahamas of a new genus and species of this family, knowledge of the western Atlantic cyclodorippid fauna is now broadened.

The description presented herein is based on two specimens collected during dives in the Bahamas of the research submersible *Johnson Sea Link I* (JSL I) in 1993. The specimens were obtained while conducting studies on the ecology and taphonomy of stalked crinoids.

The specimens have been deposited in the collections of the National Museum of Natural History, Washington, D.C. (USNM). Descriptive terminology follows that used by Tavares (1991). Measurements of carapace length × carapace width are given in millimeters (mm). Abbreviations: MXP1-3, first to third maxillipeds; P2–P5, second to fifth pereopods.

Lonchodactylus, new genus

Type-species.—*Lonchodactylus messingi*, new species, by present designation and monotypy.

Diagnosis.—Carapace longer than wide, slightly narrowing in width posteriorly. Fronto-orbital width more than half carapace width. Lateral margin between branchial tooth and posterior margin well defined. Dorsal surface weakly sculptured, frontal and hepatic regions depressed. Front bluntly subtriangular, with 1 low rounded tooth on each side. Lateral branchial tooth well developed. Lateral protogastric nodosity distinct. Mesial protogastric nodosity inconspicuous. Gastric pits well marked. Gastric and cardiac regions outlined laterally by shallow, smooth furrows.

Exorbital tooth prominent, directed anterolaterally. Orbit shallow, dorsal margin well defined, interrupted by shallow notch; ventral margin poorly defined. Lateral infraorbital tooth well developed. Eyestalk mobile, transverse in position relative to carapace axis. Antenna with article 1 mobile; articles 2, 3 fused in form of broad plate; articles 4, 5 broad.

Prostomial chamber short, shallow. Palp

of MXP3 visible in ventral view, inserted just below inner angle of merus; segments 2, 3 compressed dorsoventrally. Exopod of MXP1-3 with long flagellum.

Chelipeds similar in size and shape. P2 and P3 similar, dactyls lanceolate, laterally compressed; carpi each with 2 obtuse lobes on dorsodistal angle. P4 and P5 short, subdorsal in position; dactyls hook-like, simple; carpi each with acute lobe on dorsodistal angle.

Thoracic sternites 6–8 nearly perpendicular to plane formed by sternite 5; thoracic sternites 6, 7 contiguous. Sternal suture between sternites 7 and 8 very long, openings of spermathecae almost contiguous. Female abdomen with 7 broad segments entirely covering thoracic sternites 5–8 leaving no exposed sternal portions between lateral margins of abdomen and coxae of P2–P5. Females with first pleopod vestigial, uniramous, and inserted on ventral face of abdominal somite; pleopods 2–5 biramous; pleopod 5 shorter than pleopods 2–4, not carrying eggs.

Gender.—Masculine.

Etymology.—The generic name is formed by the combination of two Greek words, *lonche,* spear, and *daktylos,* finger, and refer to the spear-like dactyls of P2 and P3.

Remarks.—This new genus shares more characters with two Indo-West Pacific genera, *Genkaia* Miyake & Takeda, 1970, and *Phyllotymolinum* Tavares, 1993b, than with any other cyclodorippid genera from the western Atlantic or eastern Pacific. The three genera share the following characters which distinguish them from all others in the family: 1) endostome short and shallow, whereas in other genera in the family the endostome is long and deep; 2) exopod of MXP3 with a well developed flagellum, whereas all other genera in the family lack a flagellum; 3) palp of MXP3 inserted near inner angle of merus and visible in ventral view, with segments 2 and 3 compressed dorsoventrally, whereas in all other genera in the family the palp is inserted on the inner face of the merus, hidden in ventral view, with articles 2 and 3 subcylindrical; 4) abdomen in both sexes with seven segments (number of segments in male of *L. messingi* not known), whereas in all other genera the abdomen in both sexes has less than seven segments, usually five in males (5–7 fused), and six in females (6, 7 fused), except for *Corycodus* with seven segments in the female; 5) in males, the abdominal somites cover thoracic sternites 5–8 so that no sternal portions are exposed between the lateral margins of the abdomen and coxae of P2–P5; in males of all other genera in the family the abdomen is narrow, leaving exposed the sternal portions between the lateral margins of the abdomen and coxae of P2–P5.

Lonchodactylus can be differentiated from both *Genkaia* and *Phyllotymolinum* by the spermathecae (sensu Tavares & Secretan 1993) and thoracic sternites. In *Lonchodactylus,* sternal sutures 7/8 are very long, and the openings of the spemathecae, located at the end of these grooves, are almost contiguous; in *Genkaia* and *Phyllotymolinum,* the openings of the spermathecae are well separated. In *Lonchodactylus,* the openings of the spermathecae are not indicated by a distinct bulge as in *Genkaia* and *Phyllotymolinum.* In *Lonchodactylus,* sternites 6–8 are nearly perpendicular relative to the preceding sternites; in *Genkaia* and *Phyllotymolinum* the sternites are at about 50°.

Lonchodactylus can be readily separated from *Genkaia* by the shape of the plate resulting from the fusion of antennal articles 2 and 3. In *Lonchodactylus,* the plate is not expanded anteriorly (Fig. 2b); in *Genkaia* the plate is expanded, and distinctly overreaches antennal article 5 (see Tavares 1993b, fig. 11b). In *Lonchodactylus,* the epistome is twice as long (Fig. 2b) as in *Genkaia* (see Tavares 1993b, fig. 11b). In *Lonchodactylus,* the dactyls of P2 and P3 are broad, spear-like (Figs. 1, 2d); in *Genkaia* the dactyls of P2–P4 are slender (see

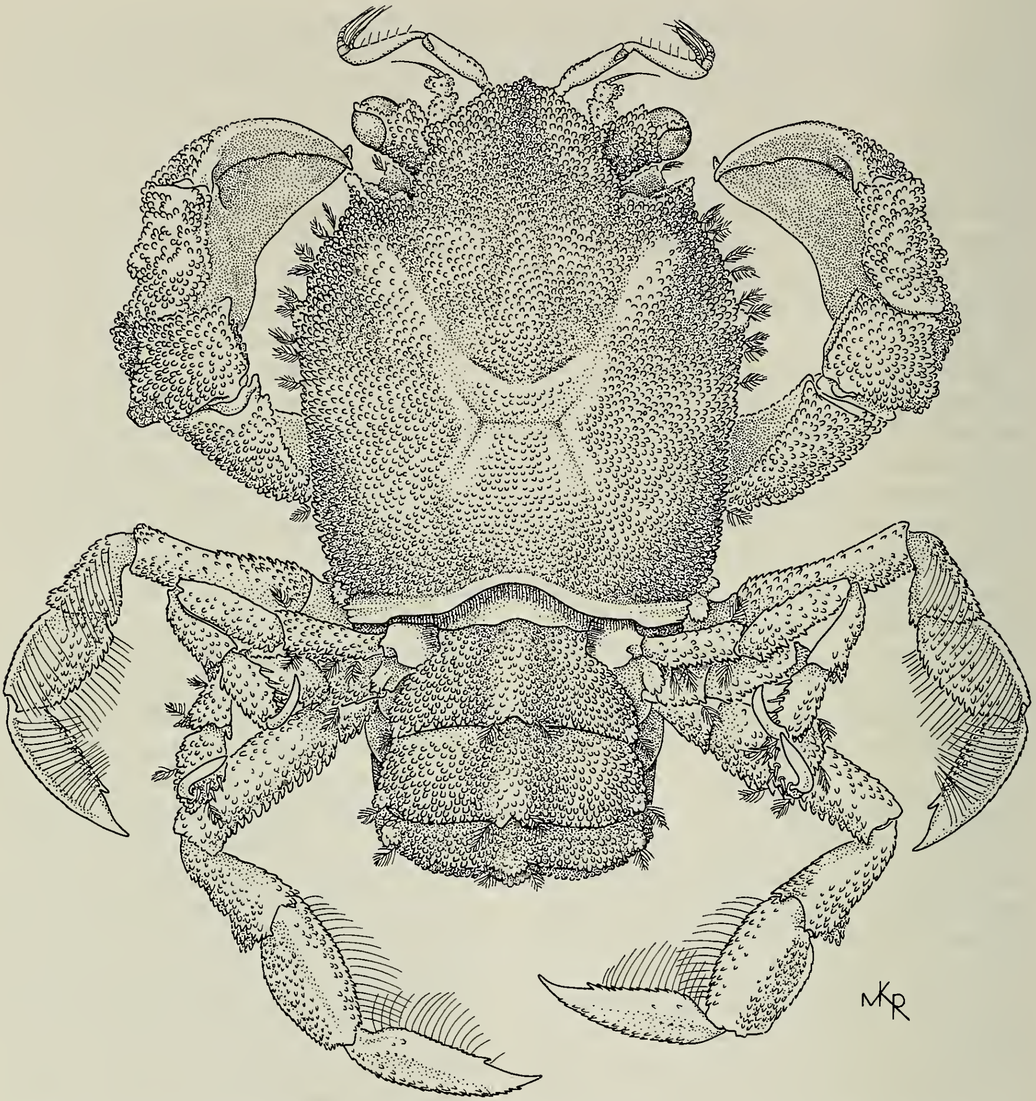

Fig. 1. *Lonchodactylus messingi,* new genus and species. Holotype, dorsal view: ovigerous female, 6.8 × 6.3 mm, Bahamas, 26°38′N, 78°58′133″W, 262 m, USNM 275920.

Tavares 1993b, figs. 10b, 11e). In females of *Lonchodactylus,* thoracic sternite 7 does not overlap sternite 6; in females of *Genkaia,* sternite 7 partially overlaps sternite 6.

Lonchodactylus differs from *Phyllotymolinum* by the presence in the former, of vestigial, uniramous pleopods on the first abdominal somite in females. First pleopods are absent in females of *Phyllotymolinum.*

Lonchodactylus messingi, new species
Figs. 1, 2

Material examined.—South of western end of Grand Bahama Island, Bahamas: holotype, ovigerous female, 6.8 × 6.3 mm, JSL I Dive 3476, 26°38′N, 78°58′133″W, 262 m, 16 May 1993, coll. C. G. Messing, USNM 275920; paratype, immature female, 3.7 × 3.2 mm, JSL I Dive 3635, 26°38.6′N,

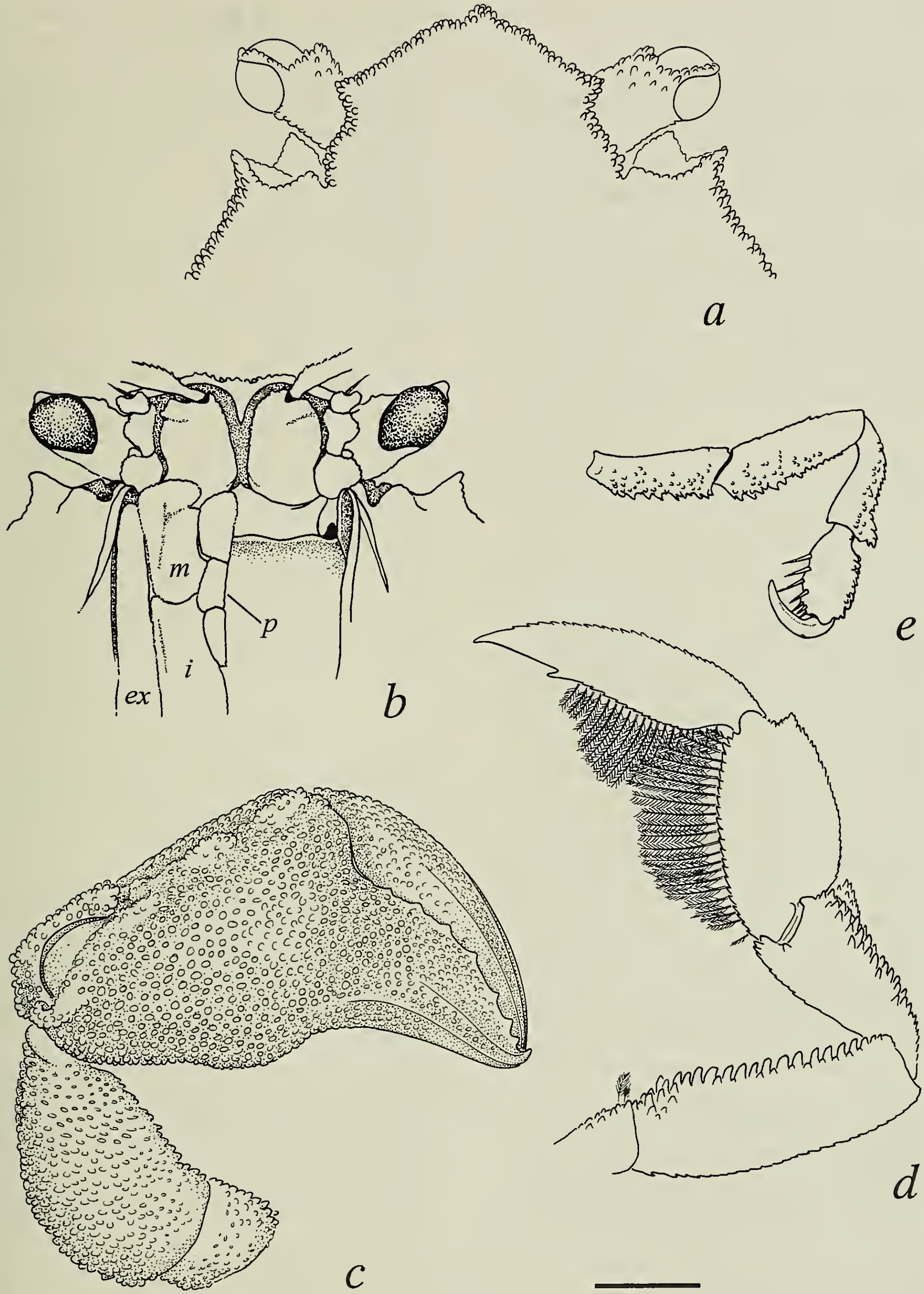

Fig. 2. *Lonchodactylus messingi*, new genus and species. Holotype, Bahamas, 26°38′N, 78°58′133″W, 262 m, USNM 275920: a, anterior region of carapace and ocular peduncles, dorsal view; b, anterior region of carapace and buccal frame with left mouthparts removed, ventral view (for right MXP3: ex, exopod, i, ischium; m, merus; p, palp); c, right cheliped, external face; d, left P3, dorsal view (not all tubercles shown, see Fig. 1); e, right P5, dorsal view. Scale equals 1 mm.

78°58.1′W, 7 Nov 1993, 265 m, coll. C. G. Messing, USNM 275982.

Description.—Carapace (Fig. 1) about 1.1 times as long as broad, with scattered, short plumose setae. Dorsal surface densely covered with small tubercles except on smooth, narrow lines defining cardiac and gastric regions. Ventrolateral surfaces of carapace densely covered with slightly smaller, more spaced tubercles than on dorsal surface. Frontal region basally forming blunt inner orbital tooth on each side. Anterolateral margin (exorbital tooth to branchial tooth) broadly rounded, less than 2 times as long as posterolateral margin (branchial tooth to posterior margin). Posterolateral margin sinuous, well defined by row of small tubercles; with low protuberance on anterior half.

Ocular peduncle (Figs. 1, 2a, b) covered with small tubercles; with blunt anterodistal lobe; corneal extension terminating in tubercle; cornea pigmented. Antennular peduncle (Figs. 1, 2b) hidden (in dorsal view) when retracted, penultimate and ultimate articles subequal in length; penultimate article armed with small spines on anterior surface. Antennal peduncle (Figs. 1, 2b) covered with small tubercles; plate resulting from fusion of articles 2, 3, slightly broader than long; articles 4, 5 increasing in width distally; article 5 produced distolaterally into rounded lobe; flagellum short, subequal to greatest width of antennal article 5.

Third maxilliped (Fig. 2b) with outer surfaces covered with small tubercles. Palp with 2 distal articles subequal in length, proximal article longest; articles setose on internal, mesial margin. Ischium and merus each more than 2 times as long as broad.

Chelipeds (Figs. 1, 2c) densely covered with small tubercles, less dense and smaller on inner surfaces; inner surfaces of merus, carpus and chela forming concave surface fitting closely to walls of carapace; dorsal and ventral margins of merus, carpus, palm, and fingers, well defined. Fingers terminating in sharp calcareous tips crossed when closed; each with 2 longitudinal ridges on outer surface; cutting edge with 7 or 8 calcareous teeth. Dactyl longer than palm, set obliquely relative to palm axis. Fixed finger 1.5 times broader basally than dactyl. Palm broader than long; dorsal margin crest-like; ventral margin with prominent rounded protuberance distally; outer surface with longitudinal row of 3 lobes on dorsolateral margin, and 1 lobe on ventroproximal angle. Merus and carpus each with blunt dorsodistal projection or spine.

P2 and P3 (Figs. 1, 2d) similar except for length and setation pattern on carpi, propodi, and dactyls. P2 shorter than P3; carpus, merus, and propodus with dorsal fringe (lacking on P3) of long plumose setae directed posteriorly over dorsal surface of segments (Fig. 1, plumose condition not shown). P2 and P3 each with propodus and dactyl with narrowly grooved ventral margins bearing row of long plumose setae (Fig. 2d), each groove flanked on each side by row of small spines; dactyls terminating in sharp tip, with larger distal spine on proximal end of distal third; meri, carpi and propodi each with blunt or sharp tubercles on lateral and mesial surfaces; meri with row of blunt or sharp spines on ventrolateral margin.

P4 and P5 (Fig. 2e) similar except for P4 with segments shorter and broader than P5. Meri and carpi with small tubercles diminishing in size and density on dorsal surfaces; with row of spines on ventral margin. Carpi each with small tubercles diminishing in size and density on ventral surface. Propodi each with row of small spines on dorsal margin; with irregular row of 7 long, slender, movable corneous spines on ventral margin.

Female abdomen densely covered with small tubercles. Somites 3–5 each with blunt median spine; somites 3, 4 each with blunt lateral spine on each side. Telson of holotype triangular with lateral margins broadly rounded; about 1.6 times as wide as long. Telson of immature paratype narrower than in holotype, triangular with lateral margins nearly straight; about 1.2 times as wide as long.

Eggs (preserved in alcohol) about 1 mm in diameter.

Distribution.—Known only from the western end of Grand Bahama Island, Bahamas; 262 m.

Etymology.—The species is named for our colleague Charles G. Messing, who collected the specimen, and in recognition of his efforts to advance our knowledge of the tropical western Atlantic invertebrate fauna.

Habitat (from C. G. Messing's field notes).—The single specimen of *Lonchodactylus messingi* was found on a gently sloping hard bottom, veneered with sediment, with a few low outcrops, and virtually barren except for scattered crinoids and *Thalassia* seagrass blades. Crinoids present about 3 m from the collecting site included the isocrinid *Cenocrinus asterius* (L.), and the comatulids *Crinometra brevipinna* (Pourtales) and *Comactinia meridionalis hartlaubi* Messing.

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We are grateful to Charles "Chuck" G. Messing (Oceanographic Center, NOVA Southeastern University, Dania, Florida), for trusting us with the study of this interesting specimen, and sharing his field notes. Raymond B. Manning and Fenner A. Chace, Jr. (both from National Museum of Natural History, Smithsonian Institution, Washington, D. C.), reviewed a draft of the manuscript, and provided us with helpful suggestions. Except for Fig. 2b, e, all illustrations are by Molly K. Ryan. MT thanks Santa Úrsula University for support in the form of grant 95.01.10, which made possible a 1-week visit to the Smithsonian Institution.

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Hermit crabs of the genus *Paguristes* (Crustacea: Decapoda: Diogenidae) from the western Atlantic
Part III. *Paguristes markhami,* a new species from the Bahama and Caicos Islands

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Abstract.—After a 20 year hiatus, a review of the western Atlantic hermit crabs of the genus *Paguristes* is reinitiated. This review resumes with the description of a new species based on specimens collected in the Bahamas and Turk and Caicos Islands. *Paguristes markhami,* new species, is described, illustrated, and compared with other known species of the genus from the western Atlantic.

The genus *Paguristes* Dana, 1851, is one of the most speciose of all hermit crab genera, and certainly is the genus having the most representatives in the western Atlantic. Alcock (1905) listed 51 species worldwide, and by the time of Gordan's (1956) bibliographic survey, 85 species and/or subspecies had been recognized. The number of western Atlantic species has never adequately been appraised. Provenzano (1959, 1961) and Holthuis (1959) provided the first critical reviews of several western Atlantic species of the genus. Subsequently, McLaughlin & Provenzano (1974) reported on seven species of the *Paguristes tortugae* Schmitt, 1933 complex, four of which were described as new species. That paper was to have been the first part of a continuing series of reports on regional *Paguristes* species. At that time, the authors acknowledged the existence of at least three additional species complexes. In the second part of the series, McLaughlin & Provenzano (1975) described an additional six new species of *Paguristes,* but none of these were associated with the three previously recognized complexes. Several circumstances apparently precluded the continuation of the series, although information on the genus continued to be accumulated by the authors. Since the publications of McLaughlin & Provenzano (1974, 1975), faunistic reports have summarized the known species (e.g., Williams 1984, Abele & Kim, 1986); however, only three new species have since been added to the fauna of the western Atlantic (Martínez-Iglesias & Gómez 1989, Campos & Sanchez 1995).

Recently I was afforded the opportunity to continue the study of regional *Paguristes* species through the auspices of the Florida Department of Natural Resources, St. Petersburg; the Smithsonian Institution, Washington, D.C.; the Rosenstiel School of Marine and Atmospheric Sciences, University of Miami; and the personal collections of Dr. P. A. McLaughlin. The present description of a new species represents the third part of this multi-part series. This distinctive, albeit small species was collected from coral and sponge habitats by Dr. John C. Markham, while SCUBA diving in various Caribbean localities in the Bahamas, and the Turk and Caicos Islands.

The holotype and one paratype have been deposited in the collections of the National

Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and two paratypes in the Swedish Museum of Natural History, Stockholm (SMNH). One measurement, shield length (SL), as measured from the tip of the rostrum to the midpoint of the posterior margin of the shield, provides an indication of specimen size. Scanning electron micrographs (SEM) of the chelae of one of the paratypes of *Paguristes markhami*, new species, were taken with a Phillips 515 scanning electron microscope.

Paguristes markhami new species

Figs. 1, 2

Holotype.—Female (SL = 2.39 mm), 13.9 km off Saddleback Cay, Andros Island, Bahamas, 24°53.0′N, 77°52.5′W, 17.5 m, 10 Sep 1973, coll. J. C. Markham, USNM 275983.

Paratypes.—2 females (1 ovigerous) (SL = 2.00, 2.42 mm), Providenciales, Turks & Caicos Islands, 21°50.5′N, 72°20.8′W, 15–20 m, 31 Aug -1 Sep 1973, coll. J. C. Markham, SMNH 4724.—1 female (SL = 1.67 mm), west side of Crooked Island, Bahamas, 22°49.2′N, 74°21.1′W, 17.5 m, 26 Aug 1973, coll. J. C. Markham, USNM 275984.

Description.—Shield (Fig. 1A) considerably longer than broad; subtriangular, anterolateral margins sloping; anterior margin between rostrum and lateral projections straight or slightly concave; posterior margin roundly truncate. Dorsal surface of shield somewhat rugose anteriorly, and with several small spines or blunt or spinulose protuberances near each lateral margin. Rostrum moderately long, distally depressed, considerably exceeding lateral projections, triangular, terminating acutely, and with small spinule or spine. Lateral projections obtusely triangular, with marginal or submarginal spine. Branchiostegites each with small spine or spinule on anterior margin, and few tufts of setae.

Ocular peduncles overreaching antennal peduncles by about ⅕ own length, broad basally and tapering to base of cornea, with few plumose setae dorsomesially in proximal half; cornea slightly dilated. Ocular acicles slender; terminating in bifid or multifid spine; separated basally by ¾ to entire basal width of 1 acicle.

Antennular peduncles moderately short, slightly shorter to slightly longer than ocular peduncles (distal margin of corneae). Ultimate segment unarmed. Penultimate segment with small spine on midventral margin. Basal segment with strong spine at ventrodistal margin, and smaller spine on lateral face dorsally.

Antennal peduncles short, often not reaching beyond proximal half of ocular peduncles, with supernumerary segmentation. Fifth segment with few short setae. Fourth segment with small spine at dorsodistal margin. Third segment produced mesioventrally and terminating in strong, acute spine. Second segment with dorsolateral distal angle produced, terminating in strong, simple or bifid spine, lateral margin with 2 or 3 smaller spines and few long setae, mesial margin unarmed; dorsomesial distal angle with a small spine. First segment with small spine on distolateral margin; ventrodistal margin produced, unarmed, but nearly obscured by long setae. Antennal acicle moderately long, usually reaching beyond proximal half of ultimate peduncular segment, terminating in strong spine; lateral margin with 3 or 4 spines and long, plumose setae; mesial margin usually with 1 or 2 spines and tufts of long, plumose setae. Antennal flagella short, not overreaching chelipeds; each article with numerous, short to moderately long setae, 1–3 articles in length.

Basis of third maxilliped with 1 or 2 small spines on inner margin; crista dentata of ischium composed of 13–15 regularly spaced small teeth, ventrodistal margin with prominent spine; merus with 2 to 4 strong spines on ventral margin, dorsodistal margin with small spine; carpus with small spine at dorsodistal margin.

Chelipeds (Figs. 1B, 2) approximately

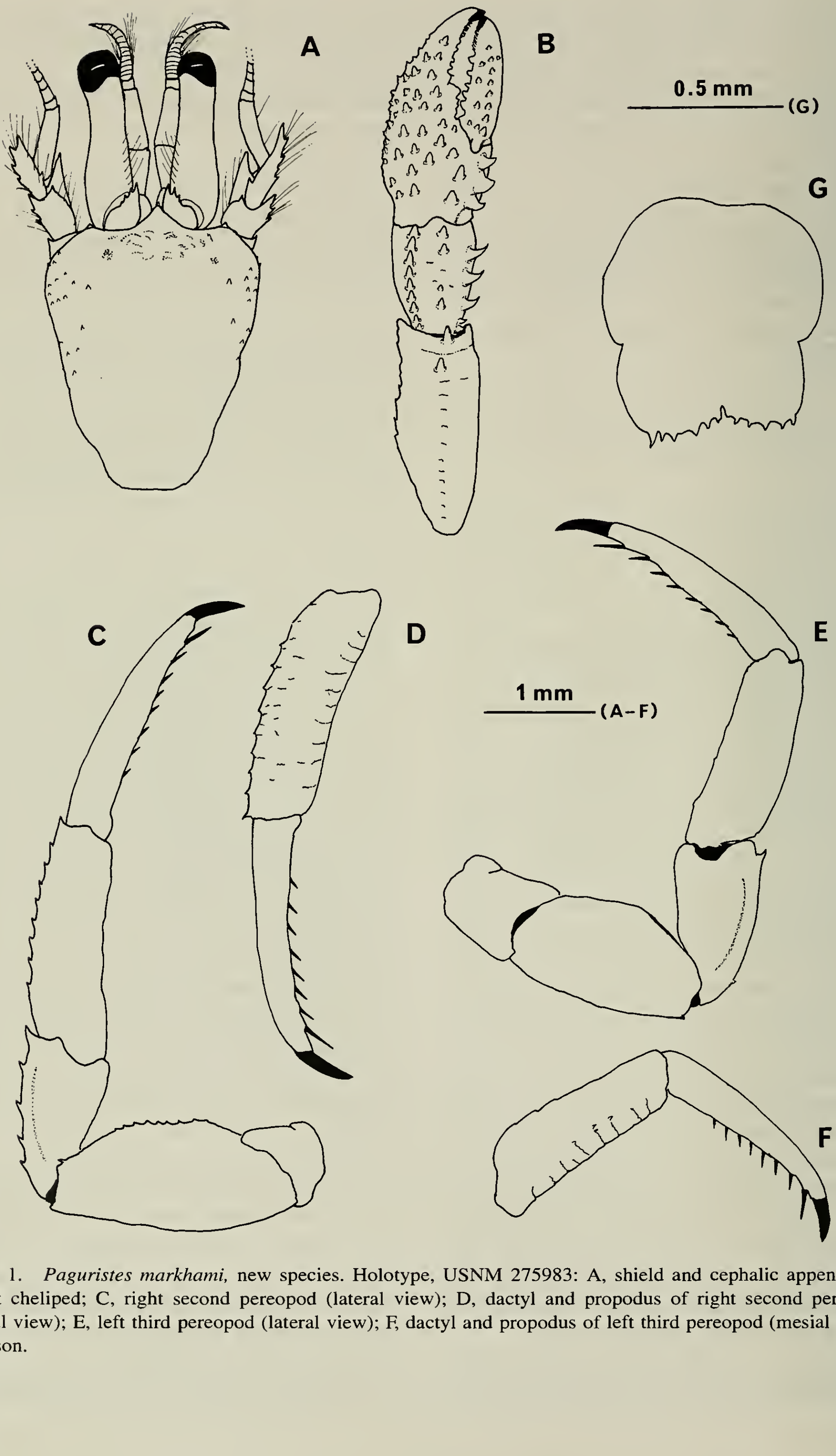

Fig. 1. *Paguristes markhami,* new species. Holotype, USNM 275983: A, shield and cephalic appendages; B, left cheliped; C, right second pereopod (lateral view); D, dactyl and propodus of right second pereopod (mesial view); E, left third pereopod (lateral view); F, dactyl and propodus of left third pereopod (mesial view); G, telson.

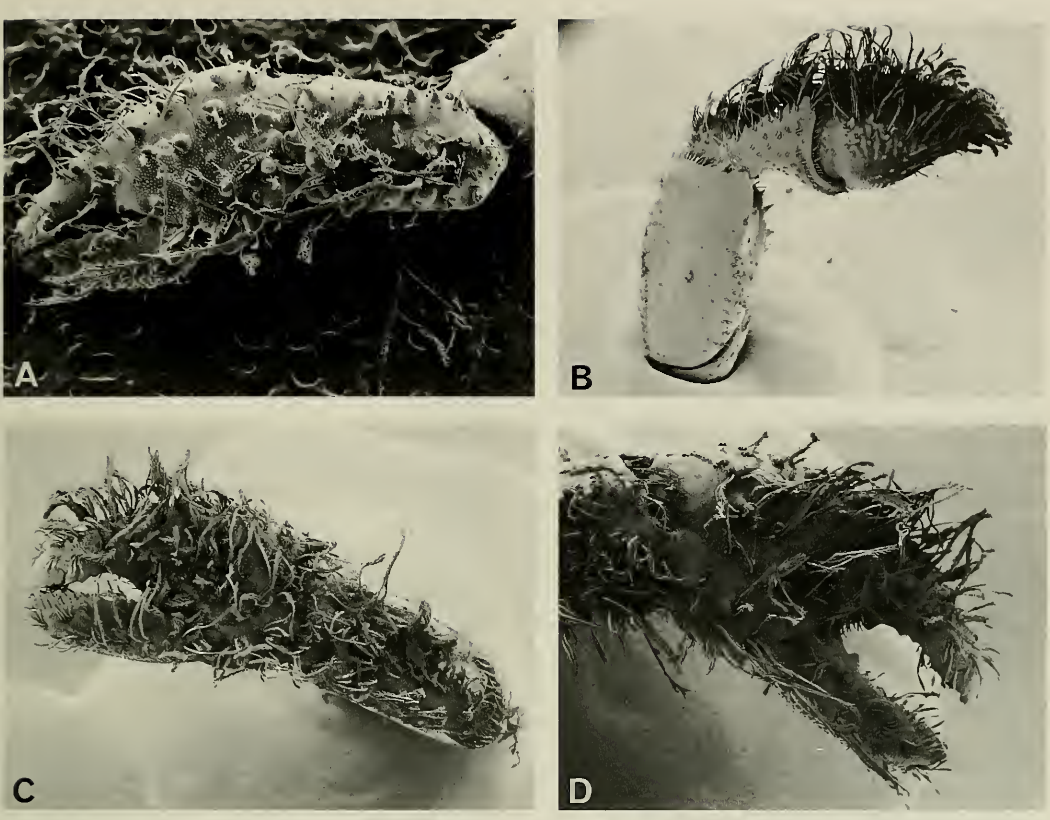

Fig. 2. *Paguristes markhami,* new species. Paratype, female (SL = 2.00 mm), Caicos Island: A, right cheliped, 31×; B, right cheliped (lateral view) 17.5×; C, chela and carpus of right cheliped, 142×; D, chela and carpus of left cheliped, 79×.

equal; moderately short and stout. Dactyl nearly twice as long as palm; cutting edge with few calcareous teeth proximally, corneous teeth distally; terminating in large, broad corneous claw; dorsal surface with few small spines or spinules; dorsomesial margin with row of small spines and tufts of long setae. Palm about ⅔ as long as carpus; dorsal surface with numerous, but randomly placed spines extending onto lateral face and partially obscured by tufts of long plumose setae, dorsomesial margin with 3 strong corneous-tipped spines; dorsolateral margin not clearly delineated, ventral surfaces with few, small spines or spinulose tubercles and tufts of setae; mesial face faintly pitted, but glabrous. Carpus considerably shorter than merus; dorsal surface with incomplete longitudinal row of small spines in midline; dorsomesial margin with row of strong spines, mesial face unarmed but with transverse rows of long, plumose setae distally; dorsolateral margin with row of moderately small spines, partially obscured by long, plumose setae, lateral face unarmed, ventrolateral distal angle strongly produced, terminating in prominent spine. Merus subtriangular; dorsal margin with row of low protuberances and tufts of long, plumose setae, 2 or 3 spines in distal third; mesial face unarmed, ventromesial margin with row of strong spines and tufts of long setae; lateral face unarmed, ventrolateral margin with row of small spines. Ischium with row of small spinules and tufts of short setae on ventromesial margin. Coxae with long setae on central surface and margins.

Second and third pereopods (Fig. 1C–F)

moderately long, overreaching outstretched chelipeds. Dactyls equalling or slightly exceeding length of propodi; in lateral view, almost straight to slightly ventrally curved; in dorsal view, straight; terminating in strong curved corneous claws; dorsal margins with tufts of dense plumose setae; lateral faces with scattered short seta; mesial faces with tufts of long plumose setae; ventral margin with row of 8 to 11 corneous spines and tufts of plumose setae. Propodi 1 ⅔ to twice as long as carpi; dorsal margins each with row of spines and tufts of long plumose setae (second) or only tufts of long plumose setae (third); mesial faces with short transverse rows of long setae, setal rows of third occasionally accompanied by small spinules; lateral faces unarmed but with transverse rows of short setae; ventral margins with scattered setae. Carpi approximately ¾ as long as meri; dorsal surfaces each with row of widely-spaced, small spines with tufts of plumose setae (second) or single dorsodistal spine and rarely 1 or 2 very small spines proximally (third), both with long plumose setae; lateral faces each with longitudinal sulcus lined with tufts of plumose setae. Meri laterally compressed; dorsal margin unarmed (second) or with very small spine at distal margin and occasionally 1 or 2 spinules in proximal half (third), mesial faces unarmed, lateral faces of second with spinule on ventrodistal margin, third unarmed; ventral margins with row of small spines or spinules and tufts of long, plumose setae (second), or with small spine at distal angle and otherwise unarmed or with few small spinules and tufts of long plumose seatae. Ischia each with small spine at ventrodistal angle, ventral and dorsal margins with row of long plumose setae. Fourth pereopods each with small spine at dorsodistal margin of carpus.

Males unknown. Female with paired first pleopods modified as gonopods; basal segment usually glabrous; distal segment with long setae. Pleopods 2–4 with both rami well developed; pleopod 5 with exopod moderately well developed, endopod vestigial. Brood pouch small, subquadrate, margins with long, plumose setae.

Telson (Fig. 1G) with posterior lobes slightly asymmetrical, left larger than right, terminal margins straight, separated by shallow median cleft; right and left terminal margins each with 4 to 6 small spines. Anterior lobes unarmed.

Coloration.—In preservative: uniformly opaque.

Habitat.—All four specimens were collected from either coral heads or rubble, or sponges.

Distribution.—Known only from localities in the Bahamas and Turk and Caicos Islands; 15–20 m.

Etymology.—The species is named for its collector, Dr. John C. Markham.

Remarks.—Because of its dense setation, *Paguristes markhami* might initially be grouped with species of McLaughlin & Provenzano's (1974) *P. tortugae* complex. As in species of the complex, *P. markhami* has a striking dense fringe of plumose setae bordering the ambulatory legs; however, in contrast to the *P. tortugae* complex species, the long plumose setae of the chelae of *P. markhami* do not occur as a marginal fringe, but instead in tufts scattered over the entire surfaces (Fig. 2A–D).

Two of the recently described species, *Paguristes mclaughlinae* Martínez-Iglesias & Gómez, 1989, and *P. werdingi* Campos & Sánchez, 1995, bear greater similarities in setation with *P. markhami.* The chelipeds of all three species appear to be similarly armed with scattered spines on the dorsal surfaces of the carpi. However, *P. maclaughlinae* is described and illustrated as having spines ventrolaterally on the propodi of the second and third pereopods, and spines on the dorsal surfaces of the carpi of the third pereopods. *Paguristes werdingi,* while apparently lacking ventral spines or spinules on the propodi of the third pereopods, is described as having a row of spines on the carpi of these appendages. In *P. markhami,* the ventrolateral surfaces of the propodi may have a series of short transverse rows of setae on the second pereopods and simply scattered setae on the third; the carpi of the third pereopods have a dorsodistal spine and rarely one or two spinules. There is also a marked difference in shape and armature between the telson of *P. markhami* and the other two species.

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Daipotamon minos, a new genus and species of potamid crab (Crustacea: Decapoda: Brachyura) from a cave in China

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Abstract.—A new genus and species of potamid freshwater crab, *Daipotamon minos,* is described from a cave in Guizhou Province, China. *Daipotamon,* new genus, is allied to *Sinopotamon* Bott, 1967, and *Tenuilapotamon* Dai, Song, Li, Chen, Wang & Hu, 1984, but differs distinctly in the form of the male abdomen and first male pleopods.

The freshwater crab fauna of mainland China is exceptionally diverse. Some 20 species and subspecies of potamid freshwater crabs have been reported from Guizhou Province in mainland China (Dai et al. 1984, 1985; Dai & Yuan 1988, Dai 1990), although none have been reported from caves thus far. Between February and March 1995, a Slovenian-Chinese caving expedition made explorations of the karst caves in Libo County, southeastern Guizhou, China. Specimens collected from one of these caves proved to belong to a new genus and species of potamid freshwater crab. The present paper describes the new taxa.

The specimens are deposited in the Department of Biology, University of Ljubljana, Slovenia (ULB); Zoological Reference Collection, Department of Zoology, National University of Singapore (ZRC); and Academia Sinica, Beijing, China (ASB). The abbreviations G1 and G2 are used for the male first and second pleopods (gonopods) respectively. The terminology adopted here essentially follows that used by Ng (1988). The synonymy of Sinopotamidae Bott, 1970, and Isolapotamidae Bott, 1970, under the Potamidae Ortmann, 1896, proposed by Ng (1988), is followed here.

Family Potamidae Ortmann, 1896

Daipotamon, new genus

Diagnosis.—Carapace broader than long, dorsal surface smooth, gently convex; epibranchial tooth small, blunt; external orbital tooth broadly triangular. Exopod of third maxilliped reaching to mid-length of merus, flagellum long, extending beyond width of merus. Male abdomen broadly triangular; telson subequal in length to segment 6; lateral margins of segment 6 concave, telson deeply concave. G1 stout, relatively short; terminal segment short, tubular, gently bent inwards towards median part of thoracic sternum. G2 subequal in length to G1; with distinct distal segment shorter than basal segment.

Type species.—Daipotamon minos, new species, by present designation. Gender neuter.

Discussion.—The establishment of a new genus is necessary because the type species, *Daipotamon minos,* new species, cannot be assigned to any known genus. *Daipotamon,* new genus, appears to be closest to *Sinopotamon* Bott, 1967 (type species *Potamon davidi* Rathbun, 1904) and *Tenuilapotamon* Dai et al., 1984 (type species *Sinopotamon joshueinse* Dai et al., 1975), with regards to the general morphology of the carapace and

Fig. 1. *Daipotamon minos,* new genus and species. Male holotype (carapace width 21.5 mm, carapace length 16.6 mm) (ZRC 1996.1044). Dorsal view.

legs, as well as the presence of a long flagellum on the exopod of the third maxilliped. However, *Daipotamon* differs in several key aspects. The lateral margins of the telson of both *Daipotamon* and *Sinopotamon* are deeply concave, but *Daipotamon* can be distinguished by its proportionately broader and shorter male abdomen, with a short telson with a more truncated tip. *Tenuilapotamon* resembles *Daipotamon* in having a broad male abdomen, but in *Tenuilapotamon* this is due to the strongly convex margins of the distal segments. In *Daipotamon,* the broad appearance of the male abdomen is due to the proportionately shorter and broader segments. The lateral margins of the male telson of *Tenuilapotamon* are gently concave while those of *Daipotamon* are deeply concave. The G1 of *Daipotamon* is also quite different from both *Sinopotamon* and *Tenuilapotamon,* being proportionately stouter, with a short and cylindrical terminal segment whose distal part lacks folds.

The characters recognized here are diagnostically significant at the generic level. The generic characters of *Sinopotamon* and *Tenuilapotamon* are constant, with some 36 and 10 species and subspecies of *Sinopotamon* and *Tenuilapotamon* respectively, already known.

Etymology.—The genus is named after Dr Dai Ai-Yun, whose detailed work on Chinese freshwater crabs over the years has provided a strong foundation for their study. The name is an arbitrary combination of her surname (Dai) and *Potamon.*

Daipotamon minos, new species
Figs. 1–3

Material examined.—Holotype: male (carapace width 21.5 mm, carapace length 16.6 mm) (ZRC 1996.1044), Jama La Tai Dong (=Cave), Jia Ban (25°10′N, 107°03′E), Libo County, southern Guizhou Province, China, leg. P. Trontelj, 6 Mar 1995. Paratypes: 2 females (larger specimen with carapace width 25.0 mm, carapace length 19.5 mm) (ZRC 1996.1045, 1046), 2 females (ULB), 1 female (AS), same data as holotype.

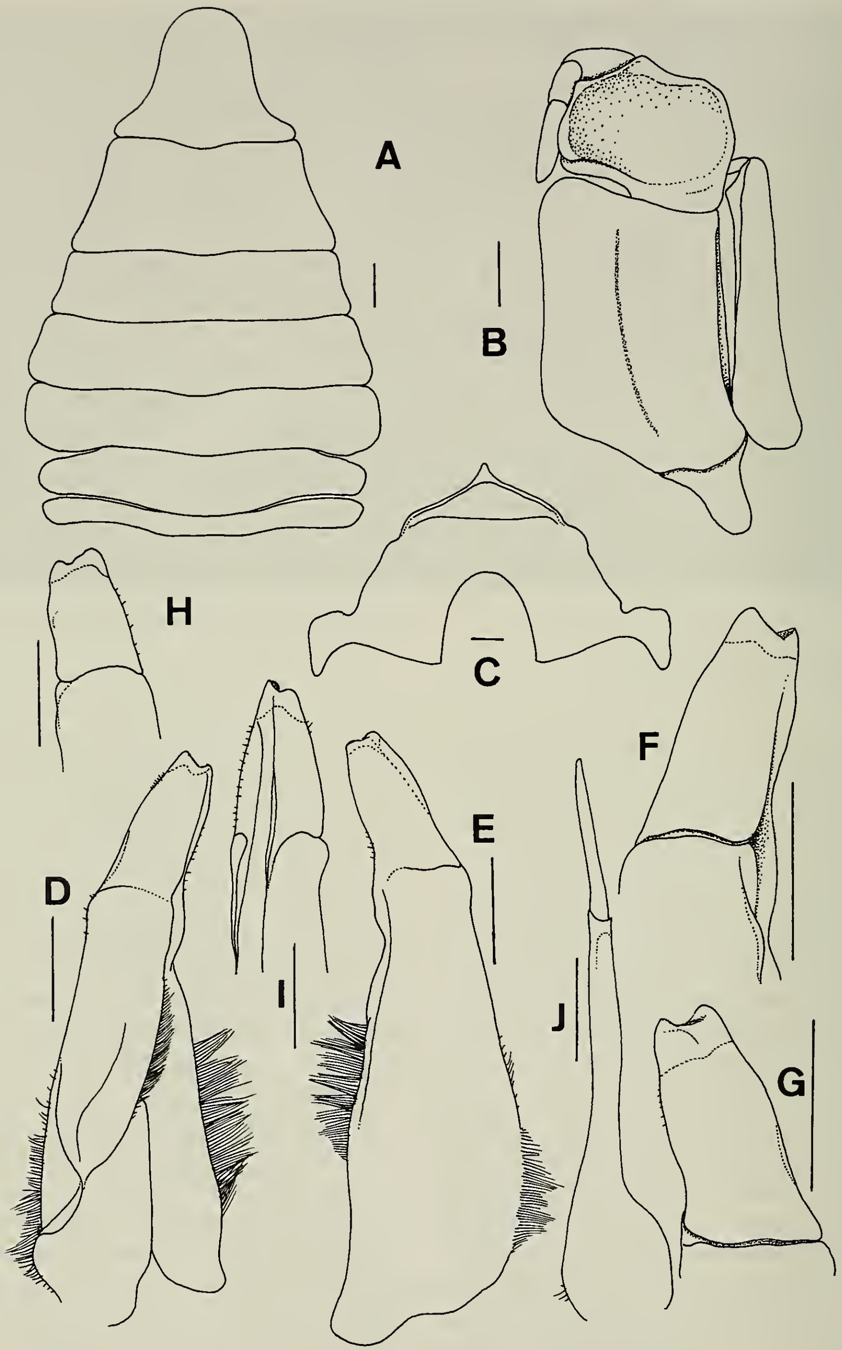

Fig. 2. *Daipotamon minos,* new genus and species. Male holotype (carapace width 21.5 mm, carapace length 16.6 mm) (ZRC 1996.1044). A, abdomen; B, left third maxilliped; C, anterior thoracic sternites; D, right G1 (ventral view); E, right G1 (dorsal view); F, right G1 terminal segment (ventral view); G, right G1 terminal segment (dorsal view); H, right G1 terminal segment (dorsomarginal view); I, right G1 terminal segment (ventromarginal view); J, left G2. Scales = 1.0 mm.

Fig. 3. *Daipotamon minos,* new genus and species. Female paratype (carapace width 25.0 mm, carapace length 19.5 mm) (ZRC 1996.1045). A, abdomen; B, right anterior sternum showing vulva. Scales = 1.0 mm.

Description of male holotype.—Carapace distinctly broader than long, not inflated or swollen; dorsal surface gently convex, smooth with numerous punctae especially on anterior ⅓; anterolateral (hepatic and branchial) regions smooth; cervical groove indistinct, very shallow, broad; H-shaped median depression shallow; cardio-intestinal region with shallow tranverse groove; pterygostomial, suborbital and sub-branchial regions smooth. Epigastric cristae very low, rugose; postorbital cristae very low, not distinct or sharp. External orbital tooth and anterolateral margin strongly convex, cristate, lined with rounded granules; external orbital tooth broadly triangular, outer margin gently convex; epibranchial tooth very small, low, blunt, separated from external orbital tooth by small but distinct notch; frontal margin smooth, gently sinuous; supraorbital margin with fine, rounded granules; infraorbital margin smooth. Ischium of third maxilliped rectangular, with shallow submedian sulcus; merus medially depressed; exopod reaching to mid-length of merus, with well developed flagellum longer than width of merus.

Outer surfaces of chelipeds gently rugose, fingers subequal to slightly longer than palm; carpus with prominent sharp tooth, with small, sharp basal granule. Second ambulatory leg longest; dactylus slender, cross-section quadrate; surfaces of meri gently rugose, dorsal margin gently serrate to uneven, without subdistal tooth or spine.

Surface of anterior thoracic sternites punctate; suture between thoracic sternites 2 and 3 gently sinuous; other anterior sternites completely fused. Male abdomen with all segments free, broadly triangular, reaching longitudinal imaginary line connecting anterior edges of cheliped bases; telson longer than segment 6; segment 6 approximately 2 times length of segment 5; lateral margins of telson deeply concave; lateral margins of segments 5 and 6 gently concave; segment 1 longitudinally narrow; transversely broad, reaching bases of coxae of fourth ambulatory legs.

G1 stout, relatively short, terminal and subterminal segments clearly demarcated; terminal segment short, approximately 0.3 times length of subterminal segment, subtubular, gently bent inwards towards median part of thoracic sternites in situ (ventral view), tip bifurcated; distal part of outer margin of subterminal segment with distinct broad cleft; groove for G2 ventral in position; G2 subequal in length to G1, distal segment well developed, approximately 0.4 times length of basal segment.

Discussion.—The exopod of the right third maxilliped of the male holotype is damaged, and reaches only to just beyond the anterior edge of the ischium. On the left third maxilliped, however, it reaches to mid-length of the merus. This condition is the same for all female paratypes.

The non-sexual characters of the female paratypes (all mature) generally agree very well with those of the male holotype. The transverse cardio-intestinal groove in the females, however, is indistinct to absent, the posterior surface of the carapace being almost flat. The female abdomen and part of the thoracic sternum with the right vulva are depicted on Fig. 2.

Daipotamon minos does not show any obvious features such as reduced eyes, the loss of body pigmentation, or elongated pereiopods to suggest it is a troglobitic species (Guinot 1988, Ng 1991, 1992). The eyes are well developed, filling most of the orbit, and the corneas are fully formed and completely pigmented. It thus seems likely that this species might also occur outside caves. It must be noted, however, that there are cave species of freshwater crabs with well developed eyes and possessing body pigmentation which are wholly troglobitic or are predominantly cavernicolous, and which make only occasional or very rare forays into epigean habitats (see Guinot 1988, Ng 1989, Ng & Goh 1987, Ng & Yussof 1990, Ng & Takeda 1994).

The type locality of *Daipotamon minos,* La Tai Cave, is northeast of Libo, at an altitude of about 600 m above sea level. The entrance of this cave is situated at the foot of a limestone mountain. A small river flows down the mountain and into the cave. At the time of the collections, the rate of flow of the river was estimated to be about 10 liters per second. In the cave itself, the main gallery follows the river until it flows through a hole. The area outside the cave is flat and is extensively cultivated (mainly rice and rape), with many small fields and irrigation ditches.

In the subterranean course of the river, the fauna was generally poor. Large amounts of empty mollusc shells (*Corbicula* sp.; some gastropods: *Gyraulus.* sp., and species of Pomatiasidae, Cyclophoridae and Pupillidae), some larvae of Plecoptera (cf. *Leuctra* sp.), and a species of surface fish, were present in the hole. The specimens of *Daipotamon minos* were caught about 400 m from the entrance in a section with slowly flowing or stagnant water about 1 m deep. The bottom was covered with stones, sand and mud. Three crabs were caught in shallow water by hand, the rest with small fish traps (plastic bottles) baited with yoghurt. Two traps were left for about two hours in the water, near the area where the first crabs had been caught.

In a lateral gallery of the same cave, the terrestrial cave life was substantially richer: Gastropoda (Pulmonata: cf. *Euplecta* sp., Ariophantidae), Isopoda Oniscidea (Trichoniscidae), Diplopoda (apparently troglomorphic Glomeridae, Doratodesmidae, and a highly troglomorphic species of Polydesmida), Orthoptera (Rhaphidophoridae), and troglomorphic Coleoptera (Carabidae: Platynini).

Etymology.—The species is named after Minos, Greek judge of the lower world. Used as a noun in apposition.

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(Kimhae), diplopods by N. Mrsic (Ljubljana), and coleopterans by T. Barr (Nashville). The study was partially supported by a research grant to the first author from the National University of Singapore.

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The subterranean asellids of Texas (Crustacea: Isopoda: Asellidae)

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Abstract.—Seven species of subterranean asellids are recognized from Texas. Four are species of *Lirceolus,* including *Caecidotea bisetus* now reassigned to *Lirceolus,* and *Lirceolus hardeni,* n. sp., described from caves and springs in east-central Texas. Previously known only from the type-locality, a new collection site for *Lirceolus pilus* is also reported. Three species of subterranean *Caecidotea* are known from the state. *Caecidotea reddelli* is redescribed and reported from both caves and collection sites that sample phreatic habitats such as wells and seeps. *Caecidotea bilineata,* n. sp., is a phreatobite occurring in non-cave groundwater habitats in northeastern Texas. A troglobitic *Caecidotea* sp. from Border Cave, Culberson County remains undescribed due to insufficient material.

The first subterranean asellid discovered in Texas was obtained from an artesian well drilled at the end of the 19th century for the United States Fish Commission in San Marcos, Texas. Eigenmann (1900) reported this isopod and named it *Caecidotea smithii,* but gave no description, thus creating a nomen nudum. Ulrich (1902) described *Caecidotea smithii* as a new species.

New material of *Caecidotea smithii* became available after the artesian well and fish hatchery at San Marcos was deeded to Southwest Texas State University in 1964, which administered the site as an aquatic station. As the morphology of *C. smithii* was clearly different from other *Caecidotea* species known at the time, the new genus *Lirceolus* was proposed by Bowman & Longley 1976.

Steeves (1968) described three additional new species of asellids collected from Texas caves, *Asellus* (=*Caecidotea*) *bisetus, A. pilus* and *A. reddelli.* Lewis (1983) examined *Caecidotea pilus* and added the species to the genus *Lirceolus* on the basis of its similar male second pleopod, oblique suture of the pleopod 3 exopod, and partial fusion of the rami of pleopods 4 and 5. The morphology of the mouthparts required emendation of the diagnosis of the genus *Lirceolus* to accommodate *C. pilus.*

Two further additions are here made to *Lirceolus, Caecidotea bisetus* (Steeves 1968) and *Lirceolus hardeni,* new species. All *Lirceolus* species are endemic to central Texas, minute in size, and share a certain uniformity of the tip elements of the male second pleopod endopod. We believe *Lirceolus* to have evolved from *Caecidotea,* with *L. bisetus* being the most morphologically similar to *Caecidotea* and *L. smithii* and *L. hardeni* the most divergent. *Caecidotea serrata* (Fleming 1973), a subterranean species known from the Ozark Plateau, shares some morphological characteristics with *Lirceolus.* Specifically, *C. serrata* is minute in size (2 mm), the gnathopod propod lacks palmar processes, the male second pleopod exopod is sparsely setose, and the third pleopod exopod has a rather oblique suture.

Species of *Lirceolus* (and *C. serrata*) are the smallest asellids known in North America. Their minute size makes them inconspicuous and therefore difficult to collect and dissect. Multiple collections available for study from Barton Springs revealed the syntopy of *L. hardeni* and *L. bisetus.* Considering that ten species of subterranean amphipods have been recovered from the artesian well at San Marcos (Holsinger & Longley 1980), it is not surprising to find syntopy among the isopods, also. Some of these species may be more widespread than is currently realized.

The addition of *Lirceolus hardeni* and *L. bisetus* makes further emendation of the diagnosis of the genus necessary.

Lirceolus Bowman & Longley, 1976

Diagnosis.—Eyeless, unpigmented, length to 4.0 mm. Mandibles with 2–3 or 4–4 cuspate incisors and lacinia mobilis. Maxilla 1, outer lobe with 10 or 13 spines, inner lobe with 4, 5 or 8 plumose setae. Pereopod 1, palmar margin of propodus without processes, dactyl flexer margin without processes. Male pleopod 1 slender, elongate, distal segment oval or subtriangular, with sparse nonplumose setation. Male pleopod 2, exopod with transverse suture, setation sparse or absent, 0–4 setae present along margins; endopod with basal spur and basal apophysis short, blunt, about equal in length. Pleopod 3 exopod with transverse to transverse/oblique suture.

Lirceolus smithii (Ulrich, 1902)
Fig. 11

Caecidotea smithii Eigenmann, 1900:302 (nomen nudem).

Caecidotea smithii Ulrich, 1902:93, plate 16, figs. 10-18.—Banta, 1907:77.—Chappuis, 1927:61.—Van Name, 1936: 472–473.—Jeannel, 1943:261.J—Nicholas, 1960:132.

Caecidotea smithsii Ulrich.—Richardson, 1905:438–439.–Creaser, 1931:6.—Miller, 1933:103.

Conasellus smithii (Ulrich).—Birstein, 1951:53.—Henry & Magniez, 1970.356. —Mitchell & Reddell, 1971.55.

Asellus smithii (Ulrich).—Chase et al. 1959:875.—Reddell, 1965, 158; 1970, 396.—Reddell & Mitchell, 1969.8. Steeves, 1968:183.—Fleming, 1973:294.

Lirceolus smithii (Ulrich).—Bowman & Longley, 1976:489–496.—Lewis, 1983: 145–148.

Description.—*Lirceolus smithii,* the type-species of the genus *Lirceolus,* was redescribed in detail by Bowman & Longley (1976).

Habitat.—This isopod is known only from the groundwaters tapped by the artesian well at San Marcos.

Range.—Known only from the type locality.

Lirceolus hardeni, new species
Figs. 1, 2

Material examined.—Texas: Blanco County: Pedernales Falls Spring, 14 m E. Johnson City, 18 Jun 1976, A. G. Grubbs, 9♂♂, 11♀♀.—Comal County: Knee Deep Cave, Guadalupe River State Park, 19 May 1985, S. J. Harden, C. F. Lindblom, 1♂, 5♀♀; 11 Jul 1986, S. J. Harden, 3♂♂; 9 Aug 1984, S. J. Harden, C. T. McAllister, 1♂, 2♀♀;—Travis County: Barton Springs (Cliff Spring), 14 Jul 1987, A. Spinelli, 4♂♂, 4♀♀; Barton Springs (Concession Spring), 7 Jul 1982, A. Spinelli, 1♂; 8 Jul 1982, A. Spinelli, 1♂; 9 Jul 1982, A. Spinelli, 1♂; 14 Jul 1983, A. Spinelli, 1♂, 12♀♀; 19 Jul 1982, D. Pate, W. Russell, 3♂♂; Barton Springs (Chair Spring), 30 Jun 1982, A. Spinelli, 2♂♂; 8 Jul 1982, A. Spinelli, 1♂, 1♀ (fragment); 14 Jul 1982, A. Spinelli, 1♂; Spicewood Springs, 7 Jun 1986, D. Pate, 2♂♂, 14 Jun 1986, D. Pate, 3♂♂, 4♀♀.

A 2.2 millimeter ♂ from Knee Deep Cave, 9 Aug 1984 is the holotype (USNM 259984), 2 ♀♀ from Knee Deep Cave, 9 Aug 1984 (USNM 259985), 3 ♂♂ from Knee Deep Cave 11 Jul 1986 (USNM 259986), and 2 specimens from Pedernales

Falls Spring (USNM 259987) are designated as paratypes.

Description.—Longest ♂ 2.2mm, longest ♀ 2mm (ovigerous); body slender, linear, about 5× as long as wide, head about 1.5× as wide as long. Antenna 1 extending only to midlength of 4th peduncular segment of antenna 2, flagellum of about 5 segments, aesthete formula 2-0. Antenna 2, flagellum quite short, of about 12-18 segments. Mandible with 4-cuspate incisors and lacinia mobilis, palp with very sparse plumose setae on distal segments. Maxilla 1, inner lobe with 4 plumose setae, outer lobe with 13 stout spines. Maxilliped with 2–13 retinacula.

Coxae visible in dorsal view. Male pereopod 1, palmar margin of propus slightly concave, slender proximal spine present; propus about 2.2× as long as wide in male and female, sexual dimorphism not apparent. Pereopod 4 sexual dimorphism apparent, carpus of male about 2.1× as long as wide, 2.5× in female.

Pleotelson about 1.4× as long as wide, caudomedial lobe not pronounced. Pleopod 1 longer than pleopod 2, protopod with 2 retinacula; exopod oval, about 1.6× length of protopod, distal margin broadly rounded, with sparse non-plumose setae. Pleopod 2, exopod proximal segment with single lateral seta, distal segment with 4 long setae; endopod, basal spur prominent, longer than knob-like basal apophysis, tip with digitiform cannula directed distolaterally, other processes absent. Pleopod 3 exopod with transverse suture, sparse setae on distal margin. Pleopod 4 exopod with weak transverse suture, proximolateral setules present, setae absent. Pleopod 5 apparently lacking sutures. Uropods about 0.5× length of pleotelson in male and female, sexual dimorphism not pronounced.

Etymology.—Named in honor of Mr. Scott Harden, the collector of this unusual species.

Habitat.—*Lirceolus hardeni* has been collected from cave streams and springs. Harden reported (pers. comm.) the stream temperature in Knee Deep Cave to be approximately 20°C. The isopods were taken from the undersides of stones starting about 60 meters from the entrance.

Range.—This species is known only from the karst area associated with the Balcones Fault Zone of central Texas.

Relationships.—*Lirceolus hardeni* is closely related to *L. smithii* and *L. bisetus.* The male second pleopod endopod tip is very similar in these species, consisting of a knob-like distolaterally projecting cannula. The first pleopod exopod is oval in both species and sparsely setose. Similarly, the gnathopods of each are similar in lacking processes along the palmar margin of the propus. Both *Lirceolus smithii* and *L. hardeni* have identical 2-0 aesthete formulas of the first antenna flagellum. In *L. bisetus* the aesthete formula is 3-0. The species of *Lirceolus* may be separated by the characters found in Table 1.

The presence of only four setae on the inner lobe of maxilla 1 was a surprising find, since other *Lirceolus* possess five or eight (*L. smithii*). All populations of *Lirceolus hardeni* examined were found to have only four setae.

Lirceolus bisetus (Steeves, 1968)
Figs. 3, 4

Asellus bisetus Steeves, 1968:183–185.—Reddell & Mitchell, 1969:7, 43.—Fleming, 1973:295, 300.

Conasellus bisetus (Steeves).—Henry & Magniez, 1970:356.—Mitchell & Reddell, 1971:54–55.

Caecidotea bisetus (Steeves).—Lewis, 1983:145.

Material examined.—Texas: San Saba County: Gorman Cave, 6 miles southwest of Bend, 15 Mar 1963, J. R. Reddell, 2♂♂, 6♀♀; 14 Sep 1985, 14♂♀. Travis County: Barton Springs (Concession Spring), 12 Jul 1982, A. Spinelli, 5♂♂, 5♀♀; 14 Jul 1982, A. Spinelli, 1♂; 8 Aug 1984, R. Herschler, 2♂♂, 25♀♀.

Description.—Longest ♂ 3.25mm, ♀

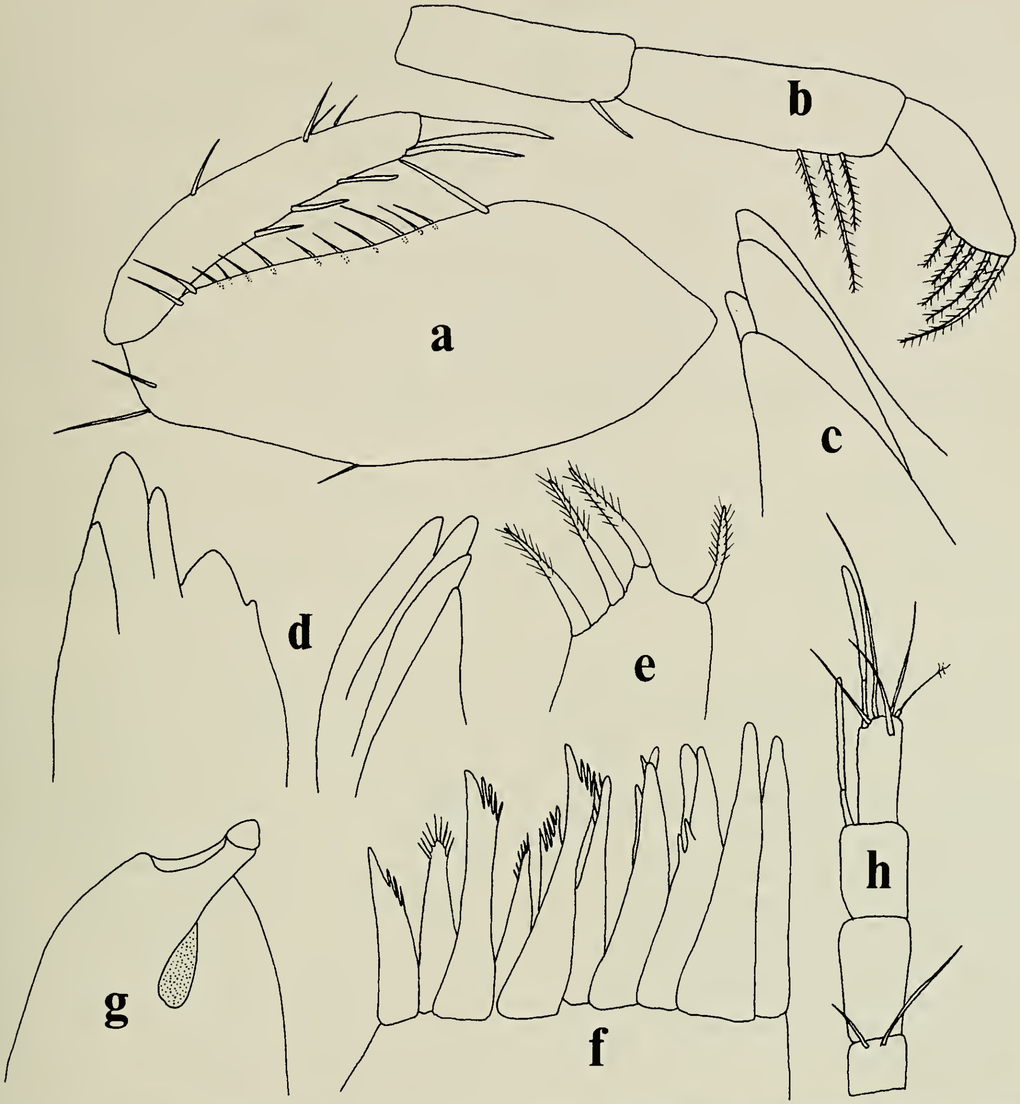

Fig. 1. *Lirceolus hardeni,* Pedernales Falls Spring, Blanco Co.: a, Pereopod 1; b, Mandibular palp; c, Incisor, right mandible; d, Incisor and lacinia mobilis, left mandible; e, Maxilla 1, inner lobe; f, Maxilla 1, outer lobe; g, Pleopod 2, endopod tip; h, Antenna 1, apical segments.

4.0mm, body slender, linear, about 4× as long as wide. Antenna 1, flagellum to about 6 segments, aesthete formula 3-0. Antenna 2 broken in all types. Mandibles with 4 cuspate incisors and lacinia mobilis, palp with plumose setae on distal segments. Maxilla 1, inner lobe with 5 plumose setae, outer lobe with 13 stout spines.

Coxae of pereopods visible in dorsal view. Pereopod 1, female propus about 3.5× as long as wide, lacking processes and proximal spine. Pereopod 4 missing in all types.

Pleotelson about 1.2× as long as wide, sides subparallel, caudomedial lobe not produced. Pleopod 1 longer than pleopod 2, protopod with 2–4 retinacula, exopod ovate, with short non-plumose setae on dis-

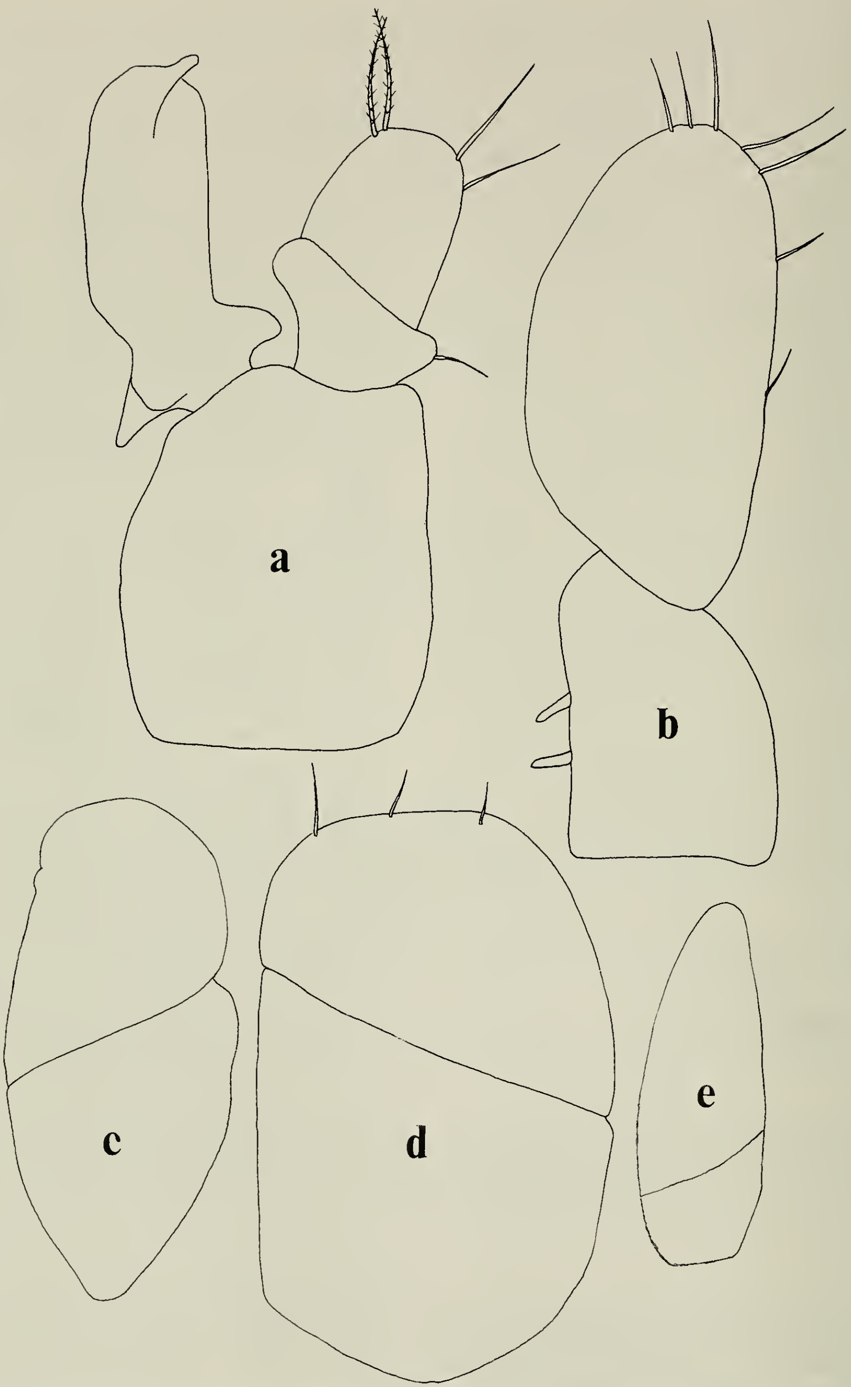

Fig. 2. *Lirceolus hardeni,* Pedernales Falls Spring, Blanco Co.: a, Pleopod 2; b, Pleopod 1; c, Pleopod 4; d, Pleopod 3; e, Pleopod 5.

Table 1.—Comparison of selected male morphology of *Lirceolus* species.

	bisetus	*pilus*	*hardeni*	*smithii*
Habitus, maximum length	4.0 mm	3.0 mm	2.2 mm	3.7 mm
Mandibles, incisors/lacinia cusps	4-4	4-4	4-4	2-3
Maxilla 1				
outer lobe spines	13	13	13	10
inner lobe plumose setae	5	5	4	8
Pleopod 1	oval	oval	oval	oval
Pleopod 2				
exopod setae	2–3	1	4	0
endopod cannula	disto-laterally extended knob	disto-laterally extended knob*	disto-laterally extended knob	disto-laterally extended knob
Pleopod 3				
exopod suture	transverse	oblique	oblique	oblique
Pleopod 4				
exopod sutures	2	1	1	membranous

* without cover slip (see text).

tal and distolateral margins. Pleopod 2, exopod proximal segment with 0-1 lateral setae, distal segment with 2–3 elongate setae. Endopod, basal spur and basal apophysis about equal in length, tip with single digitiform process, the cannula, extending somewhat obliquely across axis of endopod. Pleopod 3 exopod with transverse suture, 3 non-plumose setae on distal margin. Pleopod 4 with 2 sutures. Pleopod 5 with single suture. Uropod elongate, endopod about 1.3× as long as protopod, exopod about 0.67× length of endopod.

Etymology.—Steeves (1968) attributed the name of this species to the presence of 2 setae on the distal segment of the pleopod 2 exopod; *bisetus* is from the Latin bi = 2, and seta = hair. This is in at least some cases a misnomer; the male paratype examined had 3 setae.

Habitat.—Steeves (1968) reported that the type-series was collected from a small pool about 245 meters from the entrance of Gorman Cave.

Range.—*Lirceolus bisetus* was previously known only from the type-locality, Gorman Cave, in the Ellenburger karst area. A map and description of Gorman Cave was presented by Fieseler et al. (1978). This species is now known to co-occur with *L. hardeni* at Barton Springs, in Travis County.

Relationships.—The specimens available to Steeves for description were depauperate. He apparently misinterpreted the structure of the male second pleopod endopod tip. It was believed that the fingerlike projection of the endopod tip was the mesial process; it is interpreted here as the cannula, homologous to that of *Lirceolus smithii* and *Lirceolus hardeni.* There is an unusual sclerotized, triangular projection on the posterior side of the endopod that is hidden by the cannula except at high (1000×) magnification. This may be the structure that Steeves believed to be the cannula.

Lirceolus bisetus is most closely related to *L. smithii* and *L. hardeni* all of which share the following characteristics: (1) antenna 1 with consecutive aesthetes on the distal 2–3 segments; (2) pleopod 1 exopod oval, with sparse non-plumose setae along the apical margin; (3) pleopod 2 exopod distal segment sparsely setose, with only 0–3 setae present; (4) pleopod 2 endopod tips nearly identical in all three species, with the

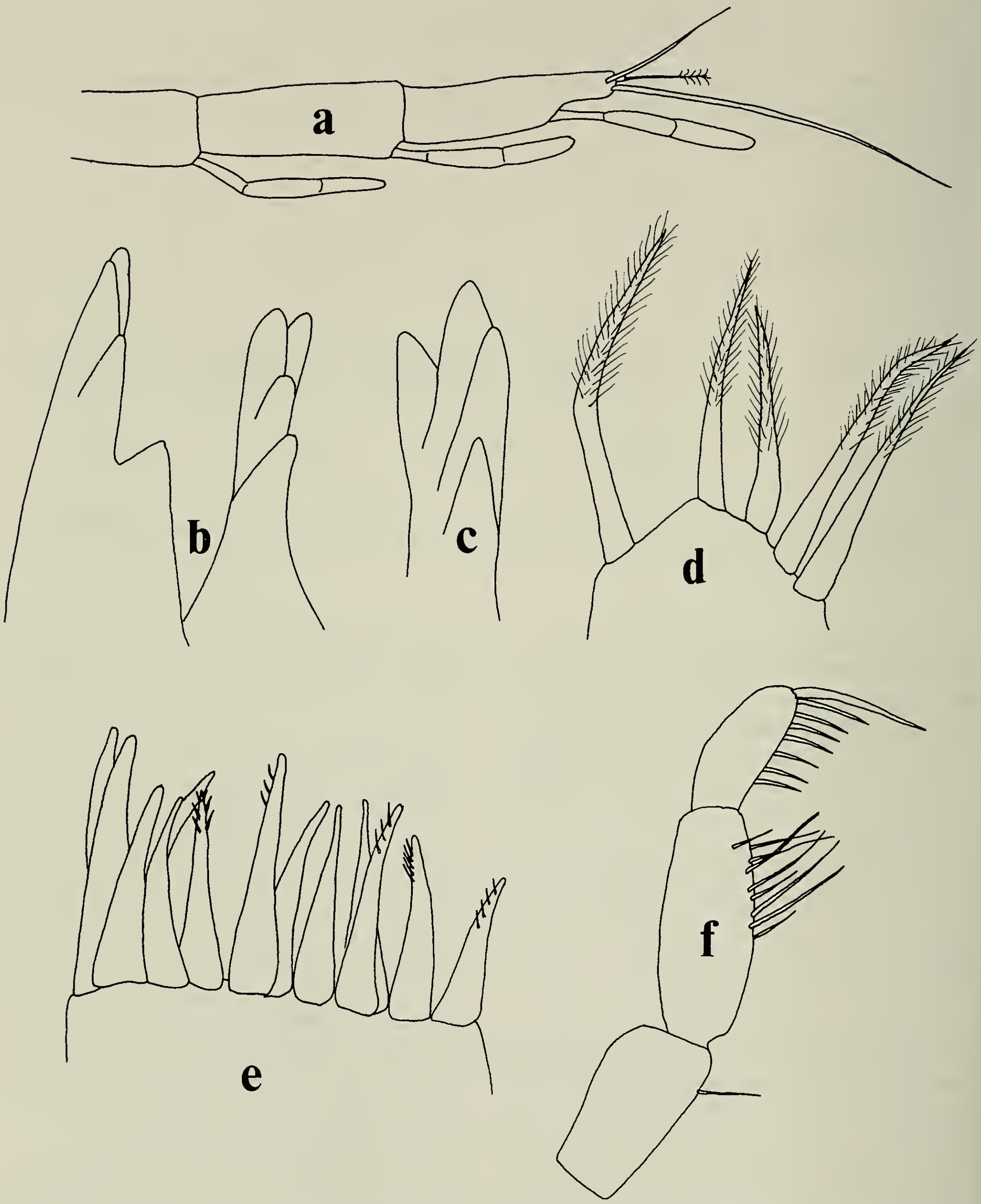

Fig. 3. *Lirceolus bisetus,* Gorman Cave, San Saba Co.: a, Antenna 1, apical segments; b, Incisor and lacinia mobilis, left mandible; c, Incisor, right mandible; d, Maxilla 1, inner lobe; e, Maxilla 1, outer lobe; f, Mandibular palp.

cannula somewhat more elongate in *L. bisetus.*

Lirceolus bisetus can be separated from *L. smithii* or *L. hardeni* by the number of setae on the inner lobe of maxilla 1: four in *Lirceolus hardeni,* five in *Lirceolus bisetus,* and eight in *L. smithii.* The male second pleopod endopod tip of all three species

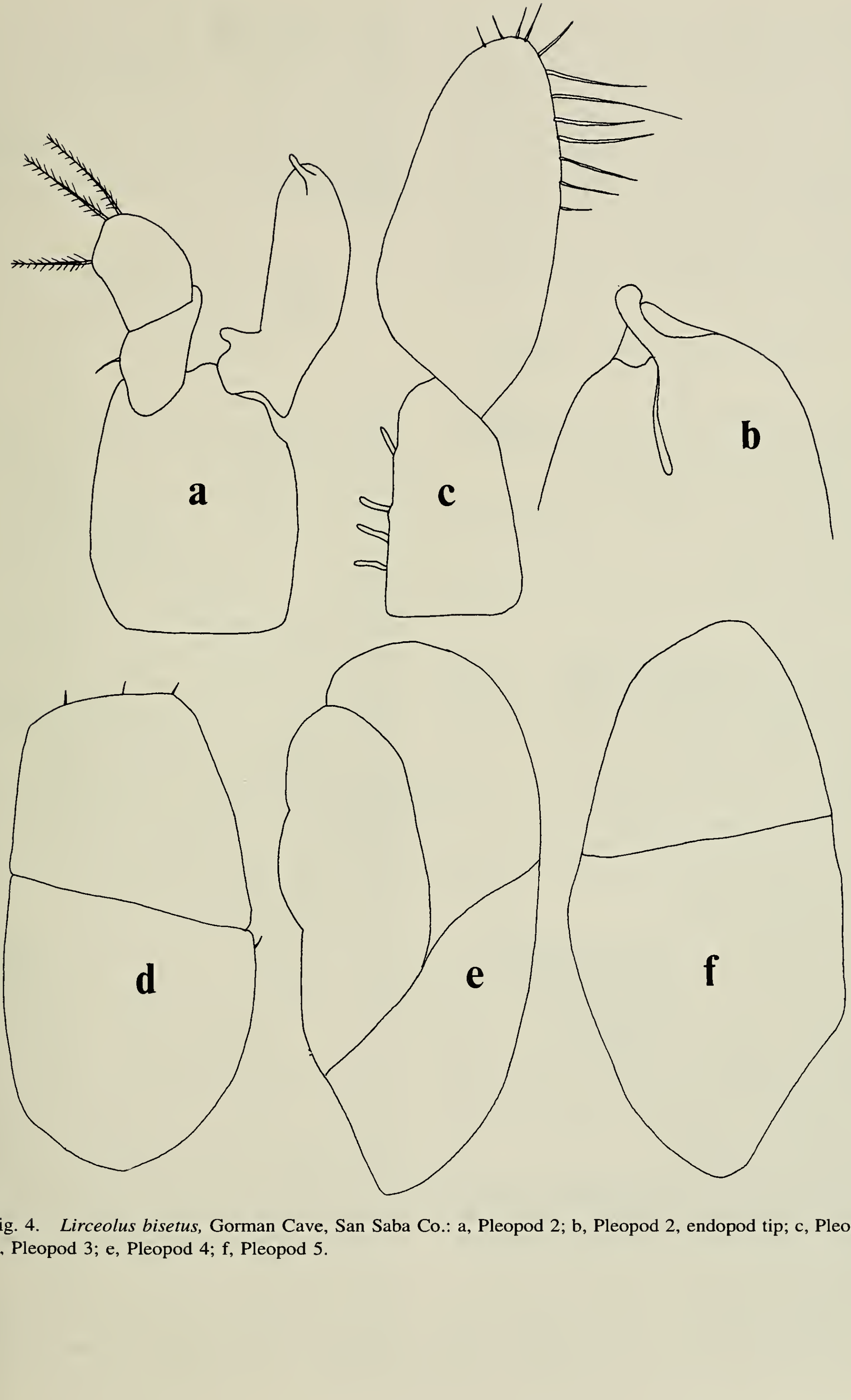

Fig. 4. *Lirceolus bisetus,* Gorman Cave, San Saba Co.: a, Pleopod 2; b, Pleopod 2, endopod tip; c, Pleopod 1; d, Pleopod 3; e, Pleopod 4; f, Pleopod 5.

possesses a cannula consisting of a knob-like process. The caudal process of *L. bisetus* is produced as a subtriangular extension of the endopod, while in *L. hardeni* and *L. smithii* it is more broadly rounded. In *L. bisetus,* pleopod 3 exopod has a transverse suture, while this suture is oblique in *L. smithii* and *L. hardeni.* The fourth pleopod exopod has two sutures in *L. bisetus,* one suture in *L. hardeni,* and is membranous without distinct sutures in *L. smithii.*

Lirceolus pilus (Steeves, 1968)
Figs. 5, 6

Asellus pilus Steeves, 1968:188. Reddell & Mitchell, 1969:8. Reddell, 1970: 396.—Fleming, 1973:295, 297.

Conasellus pilus (Steeves).—Henry & Magniez, 1970:356.—Mitchell & Reddell, 1971:55.

Lirceolus pilus (Steeves).—Lewis, 1983: 145–148.

Material examined.—Texas: Bandera County: Lost Maples State Park, Jun 1986, S. J. Harden, 1♂♂, 2♀♀; Medina County: Valdina Farms Sinkhole, 15 miles north Sabinal, 12 Jan 1963, J. Reddell, D. McKenzie, J. Porter, holotype ♂ (USNM 119593), allotype ♀ (USNM 119594), 1♂, 1♀ paratypes (USNM 119595); same locality, 20 Mar 1971, J. Reddell, S. Wylie, T. Mollhagen, 2♂♂.

Description.—The illustrations of the male pleopod 2 endopod tip by Steeves (1968) and Lewis (1983) show the cannula as a decurved, beak-like process. This is the appearance of the cannula when viewed under the weight of a coverslip. When viewed floating in glycerin the cannula has more of a knob-like appearance, similar to other species of *Lirceolus.*

Distribution.—*Lirceolus pilus* is known from two localities associated with the Balcones Fault Zone. The species was previously known only from the type-locality in Medina County.

Habitat.—Harden (in litt.) reported that the isopods occurred in Valdina Farms Sinkhole at the junction of two streams. They were found in an area of clay substrate on or near rotten wood. The four specimens used by Steeves (1968) for his description were apparently taken from gravel in the same area. A map of Valdina Farms Sinkhole is given by Fieseler et al. (1978).

Caecidotea Packard, 1871
Species Group uncertain
Caecidotea bilineata, new species
Figs. 7, 8, 11

Material examined.—Texas: Bell Co., Tahuaya Springs, Camp Tahuaya, 14 Jun 1985, Mark Mauldin, ♂♂♀♀; same locality/collector 24 Jun 1985, 1♀; 26 Jun 1985, 4♀♀; 3 Jul 1985, 1♂, 5 Jul 1985, 1♀; 8 Jul 1985 2♀♀; 12 Jul 1985, 1♂; 15 Jul 1985, 1♀; 18 Jul 1985, 1♀; 24 Jul 1985, 1♀; Dallas Co., Chinkapin Spring, 15 Aug 1975, A. G. Grubbs, 4♂♂, 14♀♀; same locality/collector, 2 Jun 1976, 1♂, 1♀; Max's Well, 1 m E. Rowlett, 24 May 1975, A. G. Grubbs, 8♂♂, 2♀♀; Salix Spring, Garland, 5 Jun 1976, A. G. Grubbs, 7♂♂, 5♀♀. Type material from Tahuaya Springs consists of the holotype ♂ (USNM 264052), dissected ♂♀ paratypes (USNM 264053), and 4♀ paratypes (USNM 264054), deposited in the National Museum of Natural History, Smithsonian Institution.

Description.—Eyeless, unpigmented, longest ♂ 7.5mm, ♀ 6.5mm; body slender, linear, about 4.5× as long as wide. Head about 1.6× as wide as long. Antenna 1 reaching to midlength of last segment of peduncle of antenna 2, flagellum with up to 6 segments, aesthete formula 3-0. Antenna 2 flagellum to about 44 segments. Mandible with 4-cuspate incisors and lacinia mobilis, palp with dense rows of plumose setae on distal segments. Maxilla 1, inner lobe with 5 plumose setae, outer lobe with 13 stout spines. Maxilliped with 5–6 retinacula.

Coxae visible in dorsal view. Male pereopod 1, palmar margin of propus lacking processes, 2 small proximal spines present;

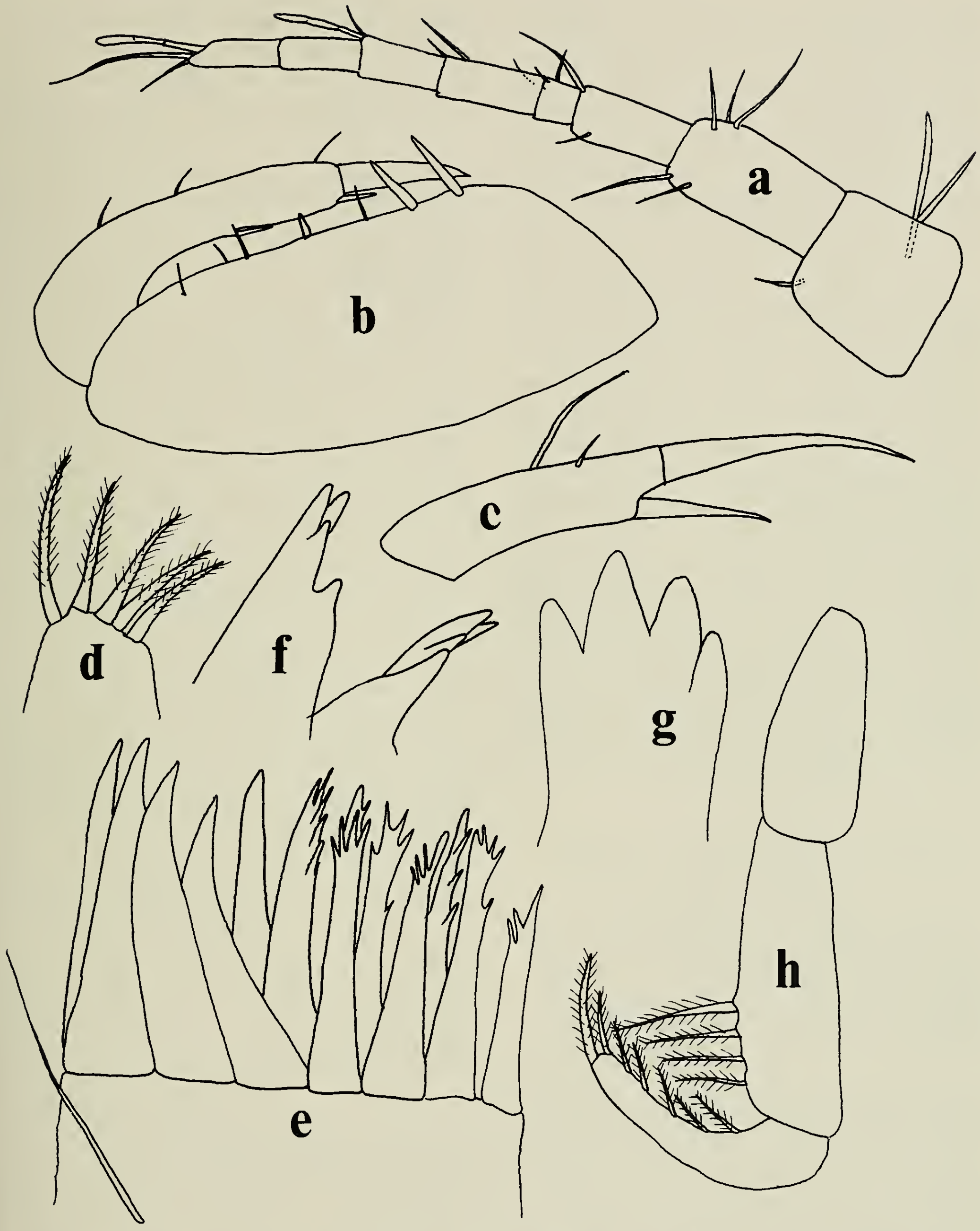

Fig. 5. *Lirceolus pilus,* Valdina Farms Sinkhole, Medina Co.: a, Antenna 1; b, Pereopod 1; c, Pereopod 4, dactyl; d, Maxilla 1, inner lobe; e, Maxilla 1, outer lobe; f, Incisor and lacinia mobilis, left mandible; g, Incisor, right mandible; h, Mandibular palp.

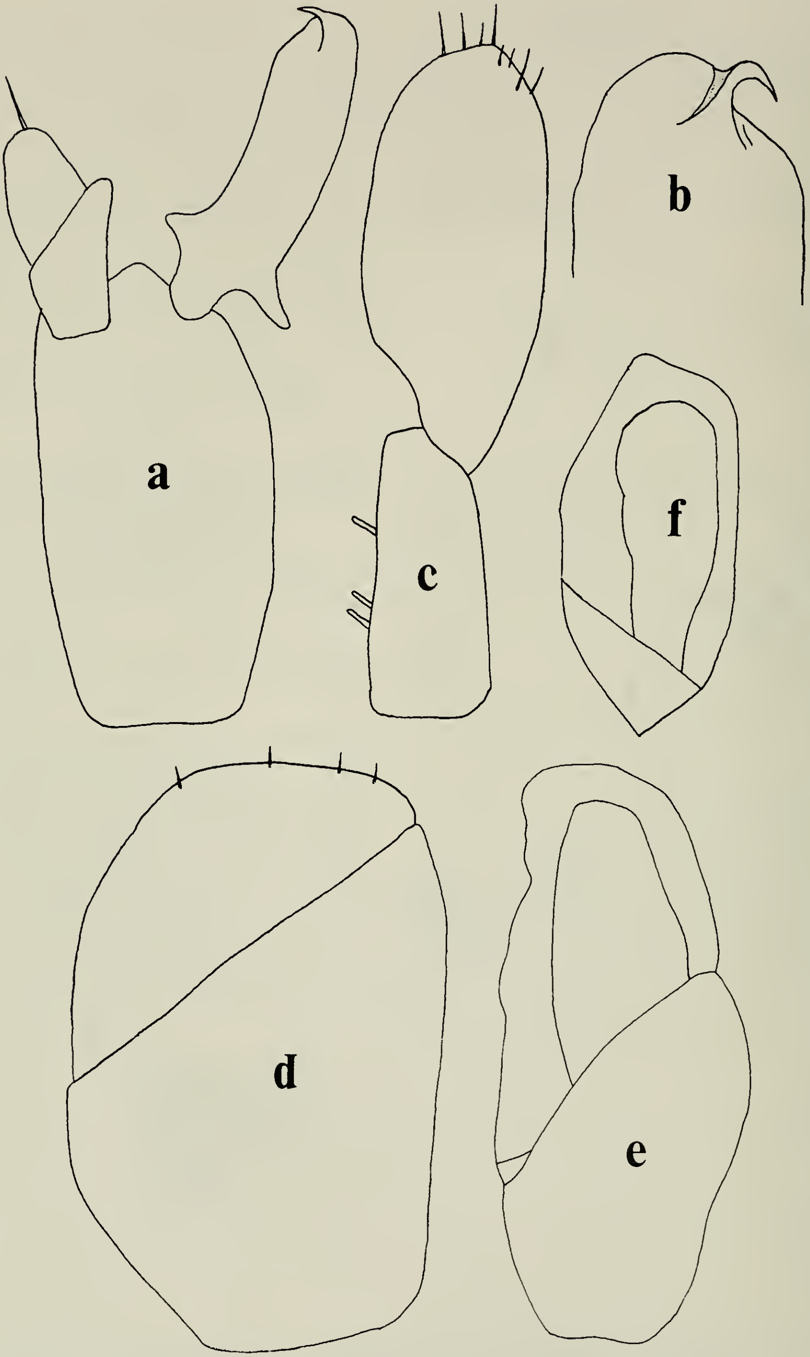

Fig. 6. *Lirceolus pilus,* Valdina Farms Sinkhole, Medina Co.: a, Pleopod 2; b, Pleopod 2, endopod tip; c, Pleopod 1; d, Pleopod 3; e, Pleopod 4; f, Pleopod 5.

propus about 1.9× as long as wide in male and female, sexual dimorphism not apparent. Pereopod 4, carpus of male about 2.7× as long as wide, 3.1× in female, sexual dimorphism slight.

Pleotelson about 1.4× as long as wide, sides subparallel, caudomedial lobe poorly produced. Pleopod 1 longer than pleopod 2, protopod with 7 retinacula, exopod about 1.3× length of protopod, subrectangular, lateral margin slightly concave, about 14 non-plumose setae along distal and distolateral margins. Pleopod 2 exopod, proximal segment with 4 lateral setae (2 of them plumose) and 1 long mesial seta, distal segment with about 17 very long plumose marginal setae. Endopod with pronounced basal apophysis, tip with 4 processes: (1) mesial process subrectangular; (2) lateral process anvil-shaped, produced laterally; (3) cannula conical, base obscured by other processes; and (4) caudal process broadly rounded, extending beyond cannula. Pleopod 3 exopod with transverse suture, distal margin with about 6 long plumose setae. Pleopod 4 exopod with 2 sutures, proximolateral setae present in some specimens. Pleopod 5 exopod with single transverse suture. Uropods quite short, about 0.4× length of pleotelson, endopod and exopod of about equal length.

Etymology.—The name of this species refers to the two suture lines of the fourth pleopod exopod, bi = two, lineata = lines. As first noted by Lewis and Bowman (1981), this morphology is found in many phreatobitic *Caecidotea.*

Habitat.—*Caecidotea bilineata* is known only from non-cave groundwater habitats in deposits of Cretaceous age. It is presumably a phreatobite.

Range.—The range of this species spans about 200 kilometers in northeastern Texas.

Relationships.—The species group assignment of this species is uncertain. *Caecidotea bilineata* shares the following characteristics with the Hobbsi Group: (1) pleopod 1 exopod subrectangular, laterally concave, single seta within proximomesial margin; (2) pleopod 2 exopod distal segment with long plumose setae; (3) pleopod 2 endopod with pronounced basal apophysis; (4) cannula conical, obscured by three other processes; (5) pleopod 3 exopod distal margin with long plumose setae present; (6) pleopod 4 exopod with two sutures, similar to other phreatobitic species of the group.

Caecidotea bilineata is unlike other species of the Hobbsi Group in the lack of both gnathopod processes and long plumose setae on the distal margin of the exopod of the first pleopod. The structure of the gnathopod (the elongate shape and lack of processes along the palmar margin of the propus) is similar to those found in species of the *Lirceolus* or the *Caecidotea* Cannula Group. The very short, cylindrical uropods with equidistant rami are also unusual among subterranean *Caecidotea.* This characteristic is not only interesting, but useful, in that it can be used to quickly separate *Caecidotea bilineata* from *C. reddelli* (which has long, spatulate uropods) in populations where both are present.

Hobbsi Group
Caecidotea reddelli (Steeves, 1968)
Figs. 9, 10, 11

Asellus reddelli Steeves, 1968:185–188.—Reddell & Mitchell, 1969:8.—Reddell, 1970:396.—Elliott & Mitchell, 1973: 171, 178, 181–182, 185, 187.—Fleming, 1973:295, 300.

Conasellus reddelli (Steeves).—Henry & Magniez, 1970:356.—Mitchell & Reddell, 1971:55.

Caecidotea reddelli (Steeves).—Lewis, 1983:145.

Material examined.—Texas: Bell County: Nolan Creek Cave, 4 Oct 1964, D. McKenzie, 4♂♂, 4♀♀; 27 Jan 1990, J. Reddell, M. Reyes, 1♂, 2♀♀; Critchfield Springs, Salada, 8 Jul 1985, M. Maulden, 1♂. Coryell County: Tippitt Cave, 4 Oct 1964, D. McKenzie, 5♂♂, 4♀♀. Dallas County: seeps along Turtle Creek, Dallas,

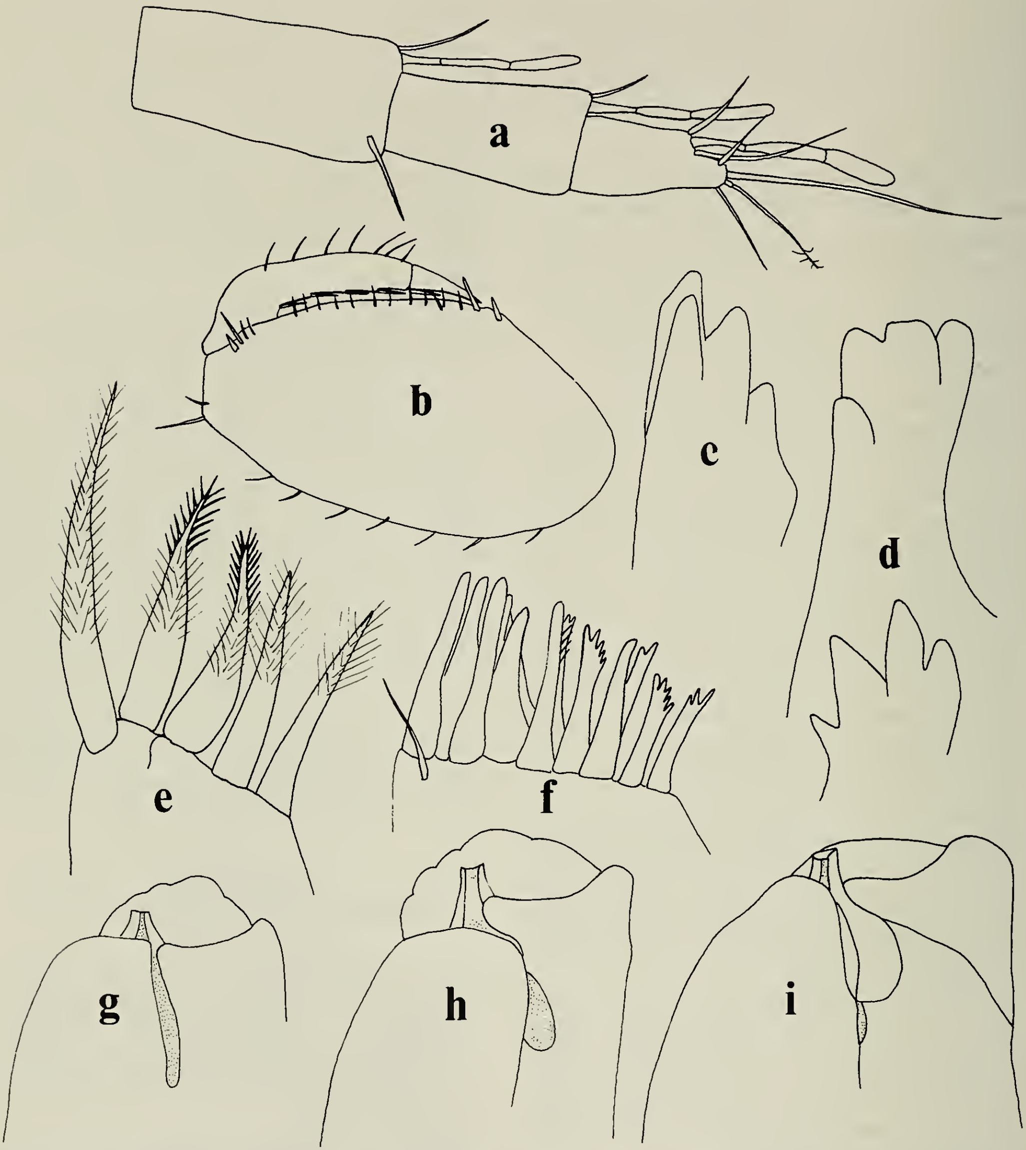

Fig. 7. *Caecidotea bilineata,* a–f, i, Max's Well, Dallas Co.; g, Chinkapin Spring, Dallas Co.; h, Salix Spring, Dallas Co.: a, Antenna 1, apical segments; b, Pereopod 1; c, Incisor, right mandible; d, Incisor and lacinia mobilis, left mandible; e, Maxilla 1, inner lobe; f, Maxilla 1, outer lobe; g, Pleopod 2, endopod tip; h, Pleopod 2, endopod tip; i, Pleopod 2, endopod tip.

15 Feb 1945, Leslie Hubricht, 79♂♀; well water, Dallas, 9 Jun 1920, F. C. Bishop, 1♂, 3♀♀; seeps, 15 miles northwest of Cedar Hill, 29 Feb 1948, Leslie Hubricht, 94♂♀; Salix Spring, Garland, 5 Jun 1976, A. G. Grubbs, 1♂; Henderson County: seep on east bank of Trinity River, above Texas 31 bridge, northeast of Trinidad, 1 Jul 1955, Leslie Hubricht, 51♂♀; Travis County: Armadillo Ranch Sink, 23 Sep 1990, J. Reddell, M. Reyes, C. Sexton, 2♂♂; Kretschnarr Salamander Cave, 6 Apr 1986, J. Reddell, M. Reyes, 2♂♂; 1♀; 21 Apr 1984, J. Reddell, M. Reyes, 8♂♂, 1♀; 4 Jul 1986,

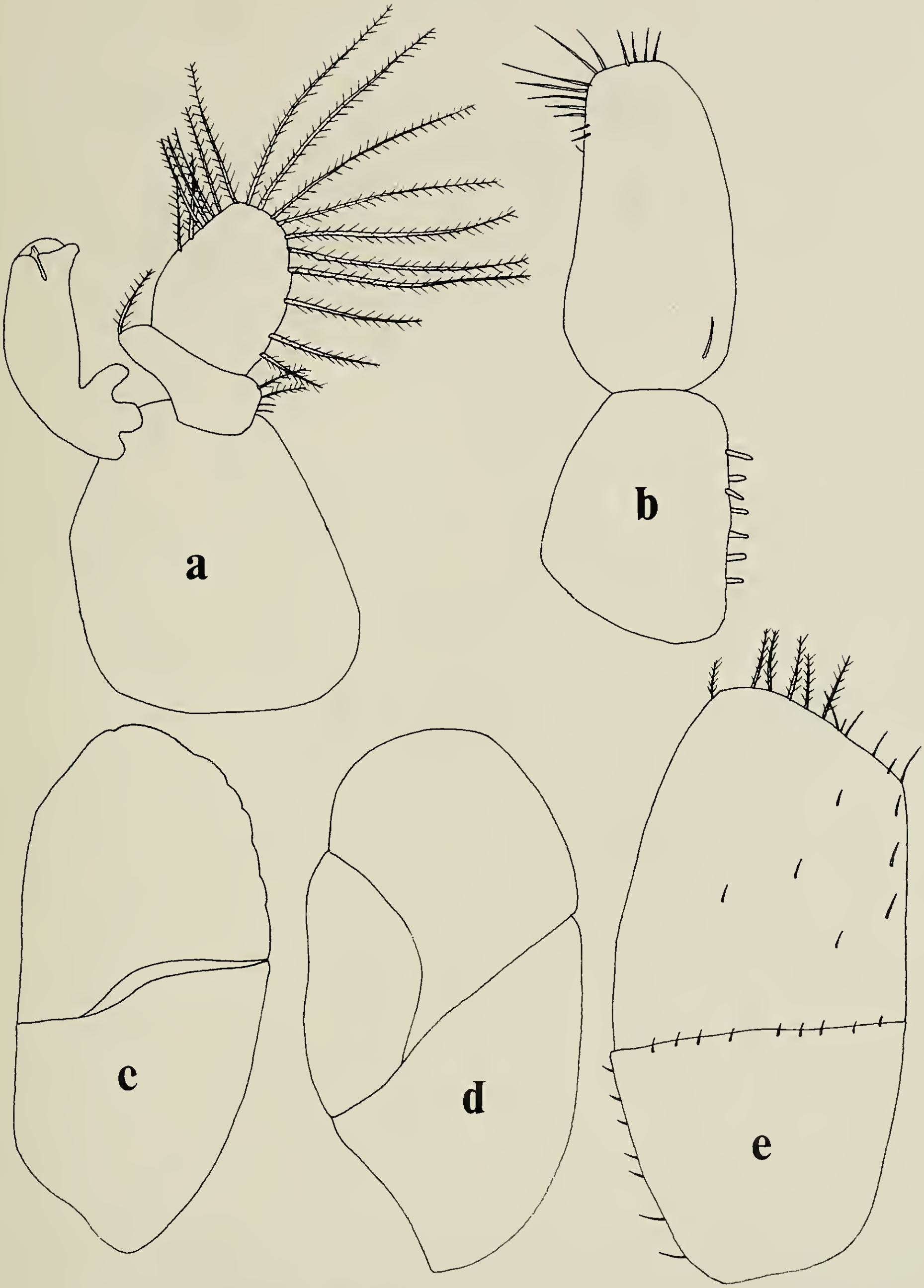

Fig. 8. *Caecidotea bilineata,* Max's Well, Dallas Co.: a, Pleopod 2; b, Pleopod 1; c, Pleopod 5; d, Pleopod 4; e, Pleopod 3.

D. Pate, W. Russell, E. Heinen, M. Standifer 8♂♂, 6♀♀, +juveniles; Buda Boulder Springs, 6 Jun 1975, A. G. Grubbs, 1♂; same locality and collector, 6 Jun 1975, 8♂♂; Spanish Wells Cave, 9 Jun 1967, R. Mitchell, 5♂♂, 5♀♀.

Distribution.—Steeves (1968) gave locations for this species for caves in Wil-

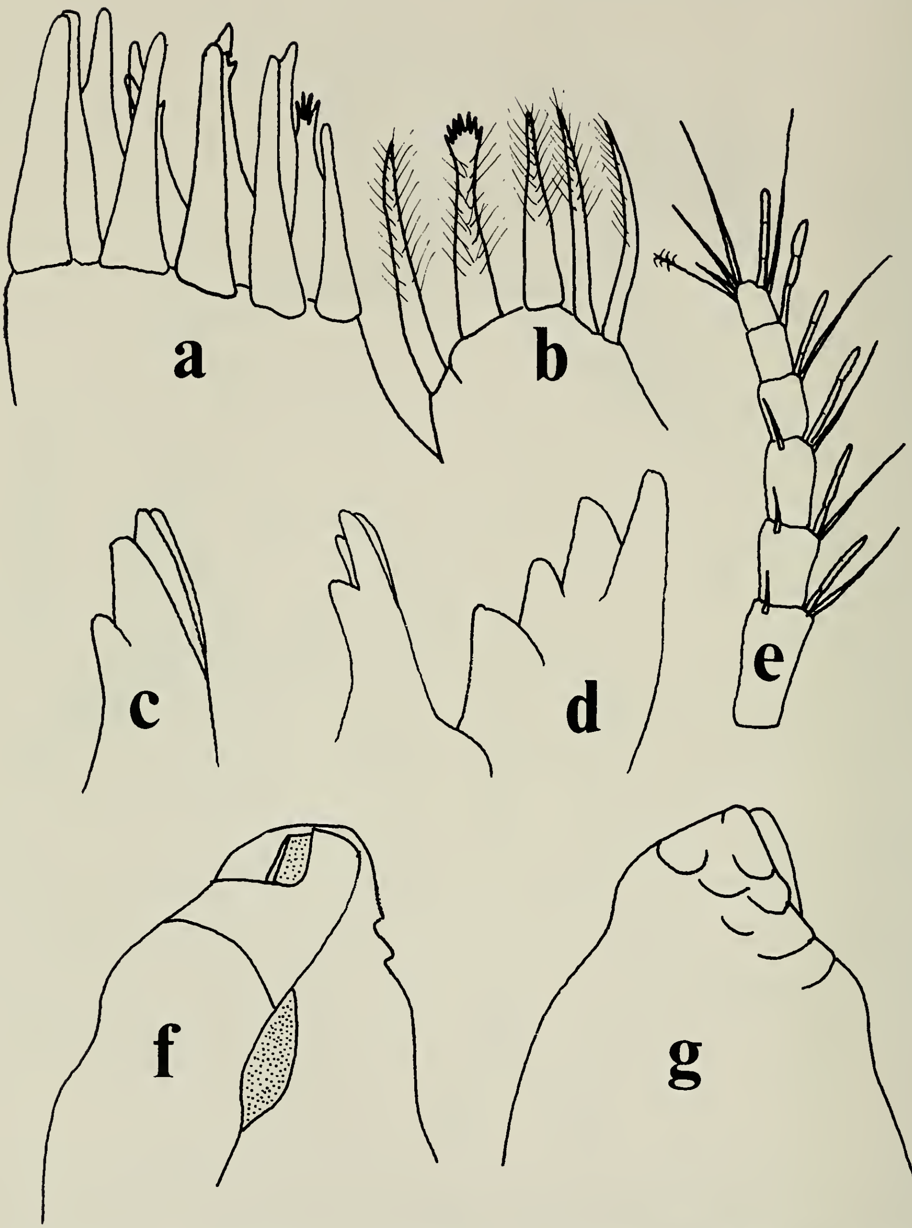

Fig. 9. *Caecidotea reddelli,* Kretschnarr Salamander Cave, Travis Co.: a, Maxilla 1, outer lobe; b, Maxilla 1, inner lobe; c, Incisor, right mandible; d, Incisor and lacinia mobilis, left mandible; e, Antenna 1, apical segments; f, Pleopod 2, endopod tip, anterior; g, Pleopod 2, endopod tip, posterior.

liamson, Travis, Coryell and Bell counties, Texas. Mitchell & Reddell (1971) showed an additional locality in Hays County in the distribution map in their paper. Overall, *C. reddelli* is known from both the North Balcones Fault Zone and the adjacent part of the Gulf Coastal Plain Province directly to the northeast in Dallas and Henderson counties.

Habitat.—Steeves (1968) reported that *Caecidotea reddelli* was taken from small cave streams or pools, typically on gravel

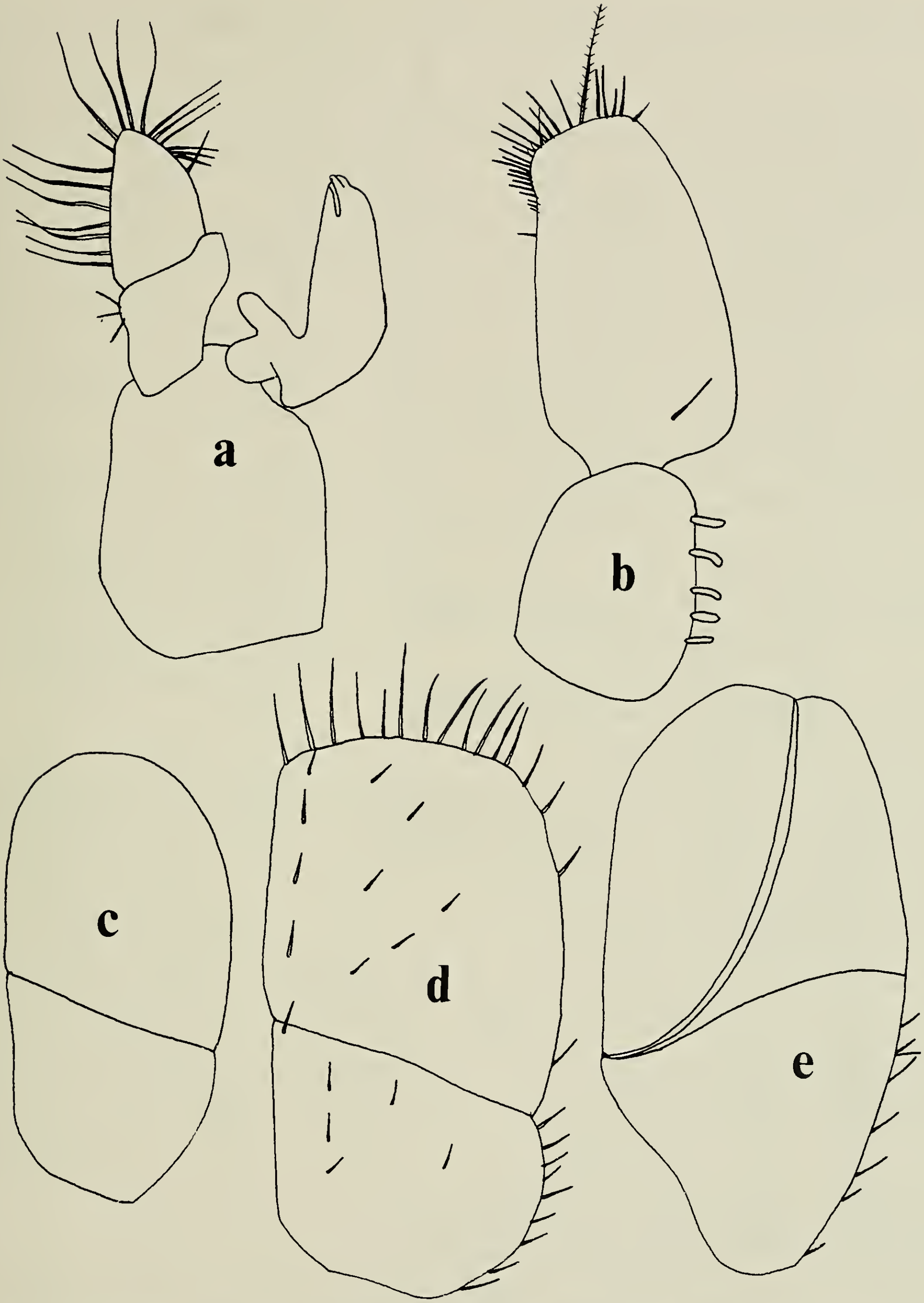

Fig. 10. *Caecidotea reddelli,* Kretschnarr Salamander Cave, Travis Co.: a, Pleopod 2; b, Pleopod 1; c, Pleopod 5; d, Pleopod 3; e, Pleopod 4.

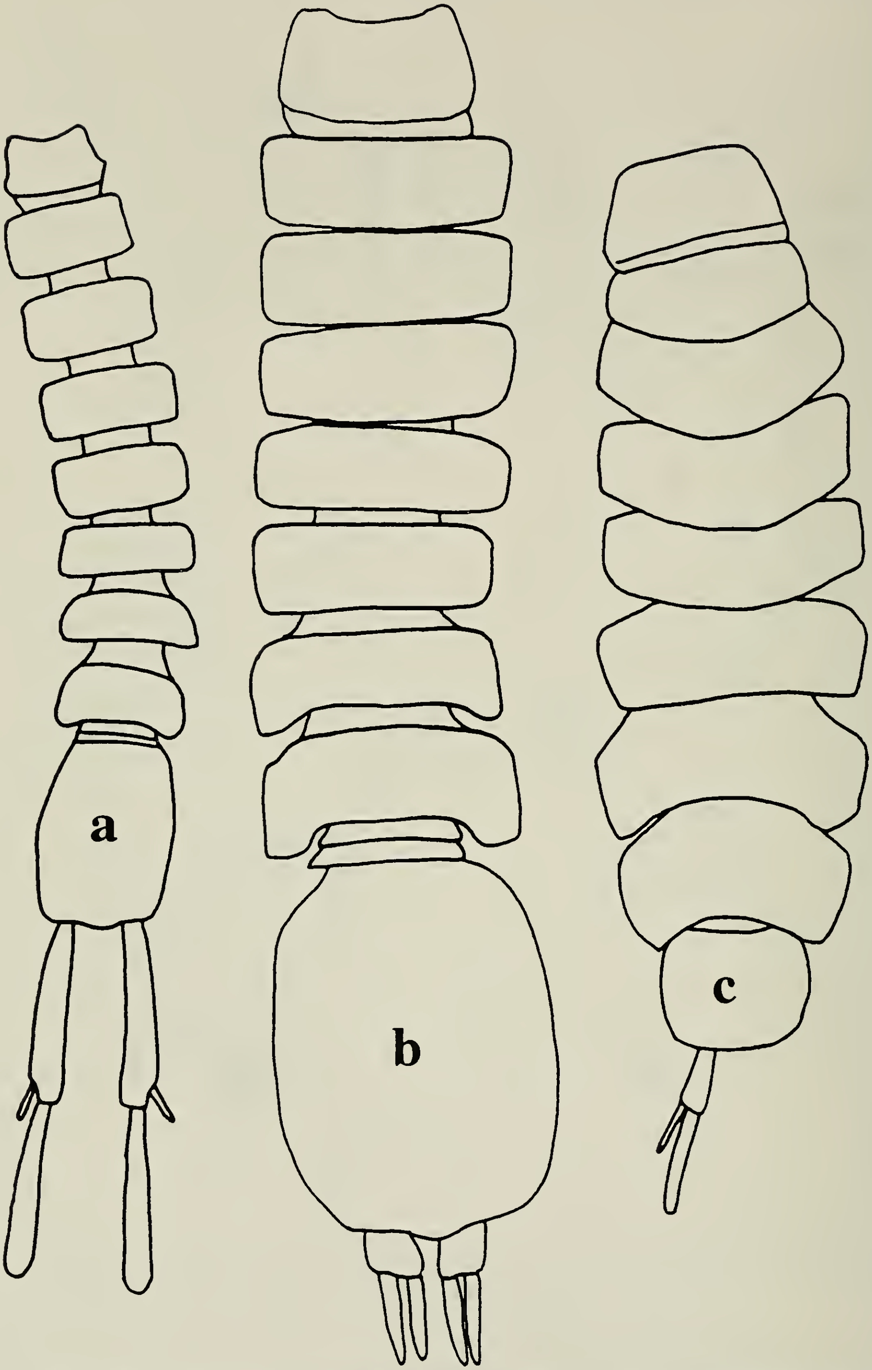

Fig. 11. *Caecidotea reddelli,* Kretschnarr Salamander Cave, Travis Co.: a, habitus and uropods; *Caecidotea bilineata,* Max's Well, Dallas Co.: b, habitus and uropods; *Lirceolus smithii,* artesian well at San Marcos, Hays Co.: c, habitus and uropods (after Bowman & Longley, 1976).

or organic debris. Elliott & Mitchell (1973) conducted a temperature tolerance test on several aquatic troglobites, including *C. reddelli,* and found that this species had no significant temperature preference. They speculated that in some cases troglobites appeared to lose responses to environmental conditions (such as temperature) that remain homogeneous, even though there may be seasonal variation.

Caecidotea reddelli was found to occur syntopically with *C. bilineata* in a collection taken from Salix Spring, in Dallas County. As both Dallas and Henderson counties lie outside of the major cave areas of Texas, *C. reddelli* is presumably phreatobitic, rather than strictly troglobitic. This conclusion is supported by the morphology of the exopod of the fourth pleopod, which has the characteristic 2-suture pattern found almost exclusively in phreatobitic (rather than troglobitic) species of *Caecidotea.*

Caecidotea species

Material examined.—Texas: Culberson County: Border Cave, 4 Jul 1985, Scott J. Harden, C. F. Lindbloom, 2♀♀; same locality, Scott J. Harden, 15 Aug 1986, 1♂, 1♀.

Range.—An undescribed species of the *Hobbsi* Group is known from this cave, but insufficient material was available for description at this time. Its occurrence in Border Cave is the farthest west that any population of subterranean *Caecidotea* has been discovered in North America east of the front range.

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Description of *Neobathymysis japonica,* a new genus and species, and revision of the genus *Bathymysis* with a new species from Japan (Crustacea: Mysidacea: Mysidae)

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Abstract.—A new genus *Neobathymysis* is established for *N. japonica,* collected from Japanese waters. *Neobathymysis* is closely related to the genera *Bathymysis* and *Australomysis* but distinguished from *Bathymysis* by the eye with well-pigmented cornea and definite stalk, the presence of the triangular rostrum and the slender antennal scale, and from *Australomysis* by the expanded second endopod segment of the maxilla and the shape and armature of the telson. *Bathymysis renoculata* Tattersall, 1951, known from the east coast of the United States, is transferred to the present new genus. Differences between *Neobathymysis japonica* and *N. renoculata* are discussed. A new species, *Bathymysis distincta,* and an undecided species, *Bathymysis* sp. are described from specimens from Japanese deep waters. Differences among three species, *Bathymysis helgae* Tattersall, 1907, *B. distincta* new species and *Bathymysis* sp. are discussed. The generic diagnosis of *Bathymysis* is amended.

The genus *Bathymysis* was established by Tattersall in 1907 for a species, *B. helgae,* from North Atlantic waters, based on: (1) the form of the small eyes, set close together apparently without definite eyestalks; (2) the 2nd thoracopod, like ones in *Leptomysis* but more robust; (3) the form of the telson, with deeply serrated cleft, lateral margins and apical lobes armed throughout with spines (Tattersall & Tattersall 1951). It was not until 1951 when another species, *Bathymysis renoculata* Tattersall, from the east coast of the United States was described. For the large and developed eyes with definite eyestalks of *Bathymysis renoculata,* the diagnosis of the genus was amended (Tattersall 1951). Pillai (1963) revised the definition of the genus, and described *Bathymysis varunae* based on a single badly damaged male; later Pillai (1964) described the female of the same species. Subsequently (Pillai 1973) *Bathymysis varunae* was synonymized with *Doxomysis quadrispinosa.*

A comparative study of the two known species of *Bathymysis* with the material in the present work, permits a revised diagnosis of the genus *Bathymysis,* the description of a new species, *B. distincta,* the description of an undecided species, *Bathymysis* sp., and the establishment of a new genus, new species, *Neobathymysis japonica.*

The type specimens are deposited in the National Science Museum, Tokyo (NSMT).

Neobathymysis, new genus

Diagnosis.—Body robust. Carapace short, with rostral projection. Eyes well developed, with reniform cornea and distinct eyestalk. Antenna with scale setose all round and distal suture present, with 2 spines on sympod. Maxilla with distal segment of endopod expanded and armed with barbed spines and plumose setae. Endopod of 1st thoracopod with well-developed lobes on basis, preischium and ischium;

Table 1.—Morphological differences between *Neobathymysis renoculata* (Tattersall, 1951) and *N. japonica,* new species.

	N. renoculata (Tattersall, 1951)	*N. japonica,* new species
Antennal scale	7.5 times as long as broad	6.4 times as long as broad
Maxilla	Distal margin of terminal segment of endopod with about 12 strong barbed setae	Distal margin of terminal segment of endopod with about 10 strong setae, the bigger 4 setae are barbed
Thoracopods	Endopod of 3rd–8th thoracopods with carpopropodus 3-subsegmented	Endopod of 3rd thoracopod with carpopropodus 3-subsegmented Endopod of 4th–8th thoracopods with carpopropodus 4-subsegmented
Endopod of 4th male pleopod	7th segment longer than 6th, 8th very short and armed with 1 long and 1 short setae at apex	6th segment somewhat longer than 7th, 8th very short and armed with 2 long apical setae of almost same length
Endopod of uropod	About 37 spines on inner margin	About 42 spines on inner margin

dactylus with nail. Endopod of 2nd thoracopod slender, with short dactylus. Endopod of 3rd–8th thoracopods with carpopropodus divided to 3 or 4 subsegments; dactylus with slender nail. Male pleopods biramous, exopod of 4th pleopod much longer than endopod, with modified seta on antepenultimate and penultimate segments. Telson cleft, without plumose setae, with spines covering all lateral margins and cleft.

Type species.—Neobathymysis japonica, new genus, new species.

Remarks.—Neobathymysis resembles *Bathymysis* Tattersall, 1907, in many morphological characters except for the eyes. In *Neobathymysis* the eyes are provided with large and well-pigmented corneas and definite eyestalks, while in *Bathymysis* the visual elements are imperfectly developed and the eyestalk is indistinct. In addition to the eyes, *Neobathymysis* differs from *Bathymysis* in the presence of the rostral projection, the elongated antennal scale, and the presence of two spines on the antennal sympod, vs. one in *Bathymysis.*

In agreement of generic characters *Bathymysis renoculata* Tattersall, 1951, should be transferred to *Neobathymysis.*

Neobathymysis also resembles *Australomysis* Tattersall, 1927, but distinguished from the latter genus as follows: (1) in *Neobathymysis* the lateral margins of telson lobes are parallel and have several similar-sized spines on rounded apical margin; while in *Australomysis* the lobes narrow distally and have a long spine on each apex; (2) in *Neobathymysis* the distal endopod segment of the maxilla is expanded distally, while it is elongated in *Australomysis. Neobathymysis* is easily distinguished from *Iimysis, Nouvelia, Tenagomysis, Doxomysis,* and *Afromysis,* by the lack of a pair of plumose setae in the telson cleft.

Neobathymysis japonica, new species
Figs. 1, 2. Table 1

Bathymysis sp.—Murano, 1970:146, figs. 27–30.

Type specimens.—Holotype (NSMT-Cr 11723), male 9.7 mm; allotype (NSMT-Cr 11724), female with well-developed oostegites 9.6 mm; paratypes (NSMT-Cr 11725), 16 males (6.5–8.8 mm), 11 females (6.6–9.4); 22 May 1968, East China Sea (28°40.6′N, 126°48.6′E), 185 m, sledge net.

Other material.—1 immature female (13.5 mm), 23 Apr 1967, Tateyama Bay (about 35°N, 139°50′E), 370-380 m, sledge net. 1 adult male, 13 Apr 1968, Tateyama Bay (35°00.2′N, 139°48.0′E), 220–330 m, sledge net. 1 adult female, 3 Nov 1968, Suruga Bay (34°55.5′N, 138°37.5′E), 0–1150 m oblique tow, ORI-100 net (conical net with 1.6 m mouth diameter).

Body length.—Adult females, 7.7–10 mm; adult males, 7.3–13 mm.

Etymology.—Derived from the locality where the species was collected.

Description.—Body robust. Carapace covering laterally all thoracic somites, and in dorsal view all but 8th and part of 7th thoracic somites; produced in front into well developed, broadly triangular apex (Fig. 1A); eyes and antennular peduncles uncovered; anterolateral corner rounded.

Eyes very large, reniform, reaching distal segment of antennular peduncle, visual area very expanded. Stalk short but distinct (Fig. 1A).

Antennular peduncle of male (Fig. 1B) more robust than in female (Fig. 1C), 1st segment longer than combined length of 2nd and 3rd; a large spine placed dorsally on distal end of 3rd segment, male appendage well developed (Fig. 1B).

Antennal scale narrowly lanceolate, 6.4 times as long as broad, extending beyond distal end of antennular peduncle for almost one-third of its length, setose all round, with well-marked distal suture. Peduncle half as long as scale, with 2nd and 3rd segments about same length, 1st segment short; 2 spines on sympod, 1 at base of scale and another at base of peduncle (Fig. 1D).

Mandible like that described for *Bathymysis renoculata.* Maxillule outer lobe with 14 spines and 5 spine-like setae, inner lobe with 16 setae, 4 of which are at top end of lobe and very large (Fig. 1E). Maxilla with distal segment of endopod expanded, wider than long and bearing about 10 strong setae, of which 4 larger and stronger ones are barbed; exopod large, with 17 setae on margin (3 of them are missing) (Fig. 1F).

First thoracopod with lobes bearing strong barbed setae on basis, preischium, ischium and merus; dactylus with long and slender nail, which is about same length as carpopropodus (Fig. 1G); exopod with flagellum 9-segmented (Fig. 1H). Endopod of 2nd thoracopod slender with long distal nail; basis expanded inwards, ischium twice as long as preischium; merus elongate and longer than carpopropodus; dactylus very short (Fig. 1I); exopod with flagellum 10-segmented (Fig. 1J). Endopod of 3rd thoracopod with carpopropodus divided into 3 subsegments by transverse sutures, 1st subsegment slightly longer than combined length of 2nd and 3rd, 3rd longer than 2nd; distal nail long and well developed; preischium short; ischium and merus about same length; dactylus shortest segment (Fig. 2A). Endopod of 4th–8th thoracopods as in that of 3rd but carpopropodus 4-subsegmented, 1st and 4th subsegments subequal in length and longer than 2nd and 3rd being also about same length (Fig. 2B). Exopod and basis of endopod of 3rd–8th thoracopods like that of 2nd. All exopods with a small blunt process on outer distal corner of basal plates (Fig. 1J).

In both sexes, 6th pleonite about 1.5 times as long as 5th pleonite.

Pleopods in male biramous; 1st with exopod 7-segmented, unsegmented endopod about equal to 1st segment of exopod in length, with well-developed quadrangular pseudobranchial lobe; basal plate bearing about 9 setae arranged longitudinally (Fig. 2C); 4th pleopod with 7-segmented endopod and 8-segmented exopod; endopod not modified, exopod nearly twice as long as endopod (Fig. 2F); 6th segment somewhat longer than 7th, with short seta and very long strong and sigmoidally-curved plumose seta on outer distal corner, 7th segment with plumose seta twice longer than its segment on distal margin, 8th segment very short, armed distally with 2 long setae of almost same length (Fig. 2G); 2nd, 3rd and 5th pleopods with endopod 7-segmented, shorter than 7-segmented exopod (Figs. 2D, E, H); 5th pleopod armed on 1st segment of endopod with process tipped with seta (Fig. 2H). Pleopods in female uniramous and unsegmented.

Endopod of uropod longer than telson, with inner margin armed with continuous row of about 40 spines from proximal side of statocyst to near apex and gradually increasing in size distally (Fig. 2I). Exopod of uropod narrow, setose all round, slightly curved outwards, about 1.3 times as long as endopod, with blunt-end (Fig. 2J).

Telson 1.25 times as long as 6th pleonite and nearly twice as long as broad at base; cleft for 0.25 of its length, sides of cleft with about 25 short spines continuing to spines arming apex; lateral margin and apex with about 40–43 sharp spines throughout entire margin (Fig. 2K)

Remarks.—Murano (1970) described briefly this species as *Bathymysis* sp. from specimens from Tateyama Bay, central Japan. Table 1 shows the morphological differences between *Neobathymysis japonica* new genus, new species, and *N. renoculata* (Tattersall, 1951).

Bathymysis Tattersall, 1907

Bathymysis.—Tattersall, 1907:116; 1911: 53.—Tattersall & Tattersall, 1951:300–301.

Diagnosis.—Carapace short without distinct rostral projection. Eye small and subquadrangular, visual elements imperfectly developed, without definite eyestalk. Antennal scale lanceolate, short, setose all round, distal suture present. Maxilla with distal segment of endopod expanded but longer than broad. Endopod of 1st thoracopod with well-developed gnathobasic lobes on basis, preischium and ischium. Endopod of 2nd thoracopod slender, with short dactylus. Endopod of 3rd–8th thoracopods with carpopropodus 3-segmented, dactylus with spine. Male pleopods biramous and multi-segmented except unsegmented endopod of 1st; exopod of 4th pleopod with modified setae on antepenultimate and penultimate segments. Telson cleft, without plumose setae at apex of cleft, spines covering all or part of lateral margins and cleft.

Remarks.—With the establishment of a new genus, *Neobathymysis,* the original diagnosis (Tattersall 1907) is revised with addition of the present new species.

Bathymysis distincta, new species

Figs. 3, 4. Table 2

Type specimens.—Holotype (NSMT-Cr 11720), adult female 8.9 mm; allotype (NSMT-Cr 11721), adult male in ecdysis of about 7.9 mm; paratype (NSMT-Cr 11722), adult female in ecdysis about 9.1 mm; 1 Mar 1965, Sagami Bay (35°04.1′N, 139°16.9′E), about 1000 m, ORI-net in oblique tow accidentally touched sea bottom.

Other material.—1 mature male (8.8 mm), 15 Oct 1994, off Boso Peninsula (34°49.6′N, 140°39.8′E), 1762 m, sledge net.

Etymology.—From the Latin "distinct", referring to the morphological difference from *Bathymysis helgae.*

Description.—General form robust. Carapace very short, almost 0.25 length of whole body, anterior margin rounded without rostral projection; anterolateral corner pointed; posterior margin leaving last 2 thoracic somites and part of 6th exposed in dorsal view, and laterally covering all thoracic somites and part of 1st pleonite. Abdomen about 1.5 times as long as carapace (Fig. 3A).

Eyes united to form single plate, eyeplate small and subquadrangular with median notch, without definite stalk, not reaching 2nd segment of antennular peduncle, without any kind of armature or ocular process, not pigmented at least in preserved specimens (Fig. 3B).

Antennular peduncle with 1st and 3rd segments subequal in length, 2nd segment about 0.33 length of 1st; 1st segment with outer distal corner produced anteriorly, and with several setae (Fig. 3C).

Antennal scale short, barely 3 times as long as broad, slightly extending beyond antennular peduncle, setose all round, with small terminal joint marked off by distinct suture. Antennal peduncle about same length as antennular peduncle, 3rd segment shorter than 2nd, 1st segment very short.

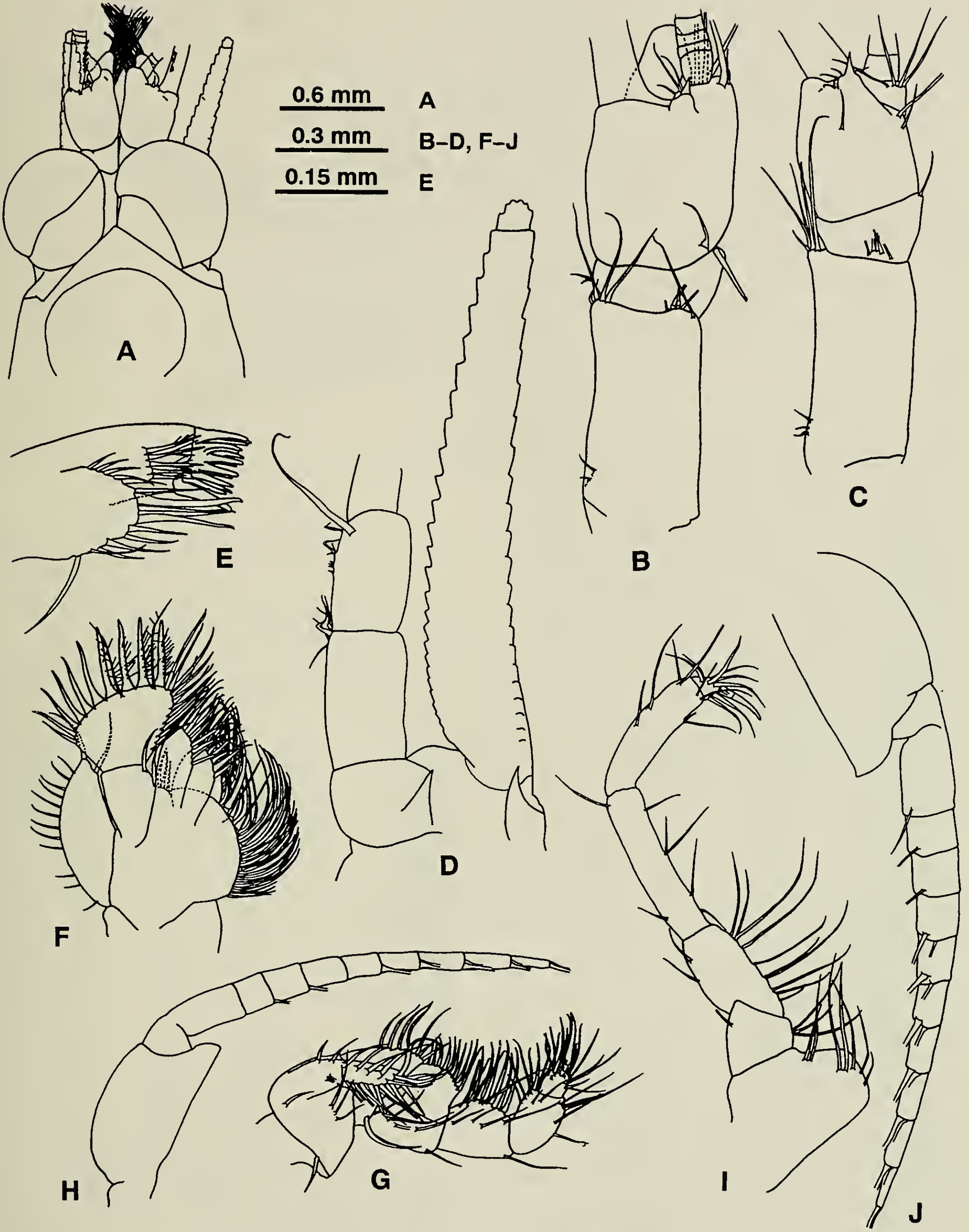

Fig. 1. *Neobathymysis japonica,* new genus, new species. F, allotype; A–E, G–H, I–J, paratypes. A. Anterior part of male in dorsal view. B. Antennular peduncle of male. C. Antennular peduncle of female. D. Antenna. E. Maxillule. F. Maxilla. G. Endopod of 1st thoracopod. H. Exopod of 1st thoracopod. I. Endopod of 2nd thoracopod. J. Exopod of 2nd thoracopod.

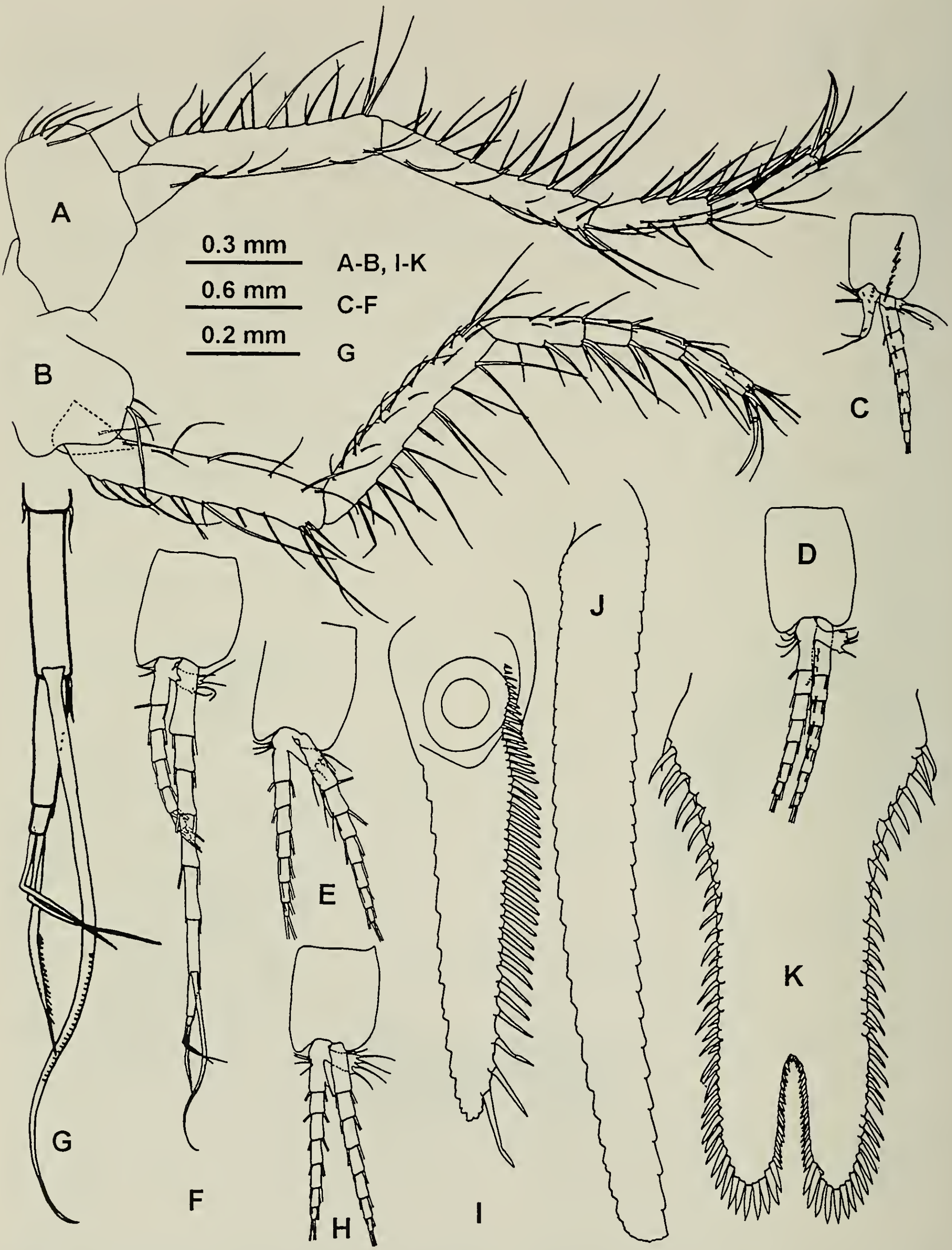

Fig. 2. *Neobathymysis japonica,* new genus, new species. A–C, I–K, paratypes; D–H, holotype. A. Endopod of 3rd thoracopod. B. Endopod of 4th thoracopod. C. 1st male pleopod. D. 2nd male pleopod. E. 3rd male pleopod. F. 4th male pleopod. G. Distal part of 4th male pleopod. H. 5th male pleopod. I. Endopod of uropod. J. Exopod of uropod. K. Telson.

Table 2.—Morphological differences among species in the revised genus *Bathymysis* Tattersall, 1907.

	B. helgae Tattersall, 1907	*B. distincta*, new species	*B.* sp.
Eyes	Not united	United	As in *B. helgae*
Antennal scale	About 4 times as long as broad	Almost 3 times as long as broad	As in *B. helgae*
Endopod of uropod	About 37 unbarbed spines on inner margin	About 15 unbarbed spines on inner margin	Spines barbed, number unknown due to damage
Telson	Equal in length to 6th pleonite. About twice as long as broad at base. Apical cleft 0.33 of telson length. Spines covering all lateral margins. Cleft completely covered with spines	1.3 times as long as 6th pleonite. Slightly less than twice as long as broad at base. Apical cleft 0.25 of telson length. Spines covering distal 0.6 of lateral margins. Cleft spines covering all except small distal portion	As in *B. helgae* except apical cleft which is 0.25 of telson length

Blunt process on distal inner corner of sympod (Fig. 3D).

Maxillule as in *Bathymysis helgae* (Fig. 3E). Maxilla damaged but resembling that of *Bathymysis helgae,* distal segment of endopod expanded and large exopod (Fig. 3F).

Most thoracopods missing except male 1st endopod and 4th–7th exopods, and female 6th–8th exopods. Endopod of 1st thoracopod as in *Bathymysis helgae,* merus expanded and bearing strong barbed setae (Fig. 4A). Eighth thoracopod with flagellum of exopod 8-segmented, endopod damaged, penis tubular and very long, slightly shorter than exopod, bearing slender seta on its distal end (Fig. 4B).

Sixth abdominal somite about twice as long as 5th (Fig. 3A).

Male pleopods missing except for unsegmented endopod of 1st (Fig. 4C).

Endopod of uropod reaching slightly beyond apical spines of telson; inner margin armed with about 15 spines from statocyst region to near apex, spines become progressively longer distally, intervals between them gradually growing also distally (Fig. 4D). Exopod of uropod almost 1.3 times as long as telson, inner and outer margins straight (Fig. 4E).

Telson about 1.3 times longer than 6th pleonite, less than twice as long as broadest basal part, with 10-13 spines on distal 0.6 of lateral margin; spines moderately increasing in length from proximal to distal part. Apical cleft occupying 0.25 of total length of telson, with both sides nearly parallel, without plumose setae and bearing about 14 small spines on each side covering all except small distal portion. Apical lobes with slightly truncate distal margin with 4 large spines each (Fig. 4F).

Remarks.—The telson of one male specimen (Fig. 4G) collected from deep-sea floor at one longitude degree east from the type locality, differs slightly from that of holotype (Fig. 4F) in: (1) small spines covering completely the apical cleft in this specimen, while a small distal portion of apical cleft uncovered in the holotype and (2) sides of cleft divergent distally in this male, but nearly parallel in the holotype. This specimen is in rather bad condition, so we tentatively identify it with *Bathymysis distincta.* Morphological dissimilarities between *Bathymysis distincta* and *B. helgae* are shown in Table 2.

Bathymysis sp.
Fig. 5. Table 2

Material.—1 badly damaged adult male of about 12.2 mm; 25 Oct 1964, Sagami

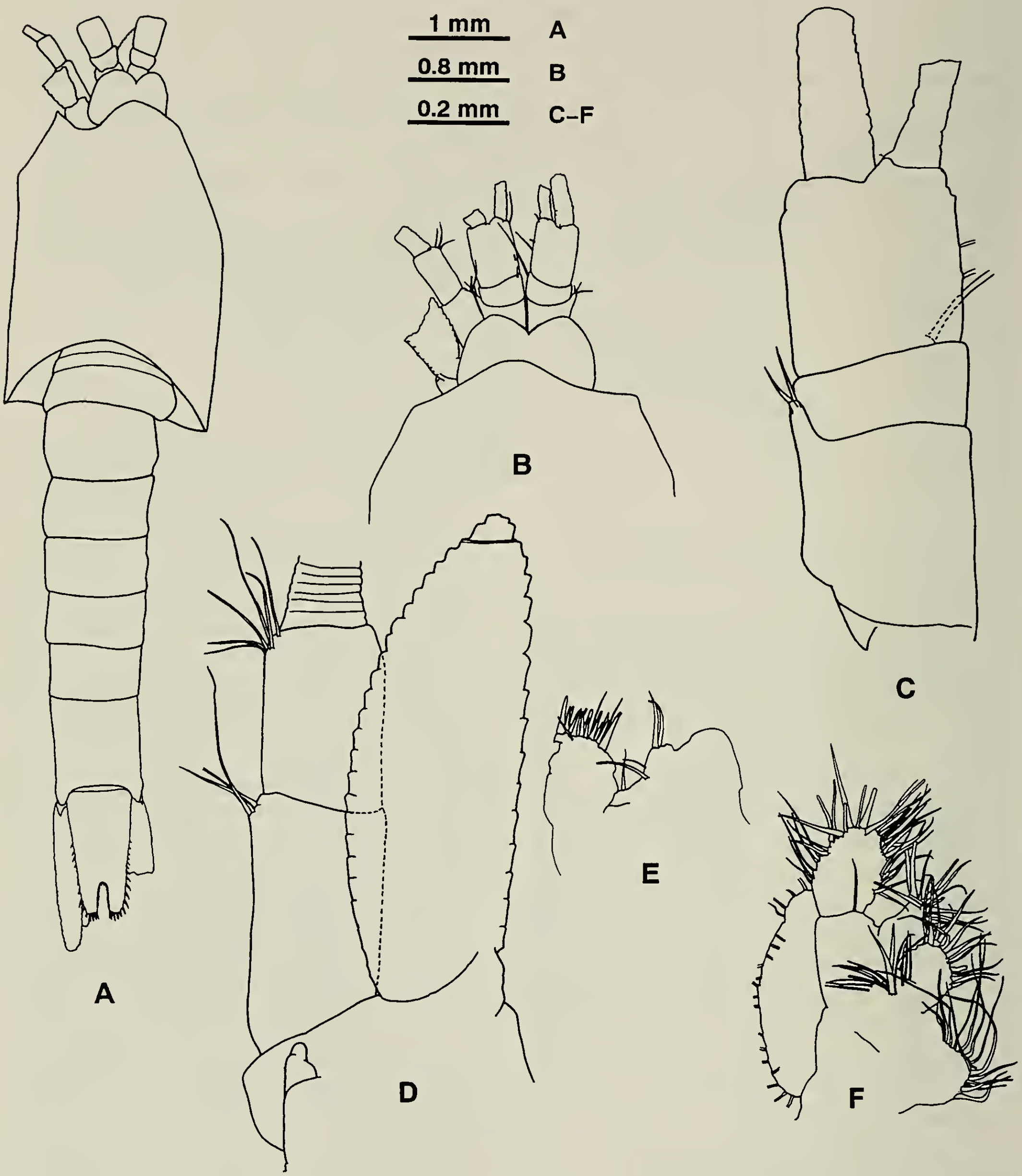

Fig. 3. *Bathymysis distincta,* new species. A–C, holotype; D–F, allotype. A. Female in dorsal view. B. Anterior part of female in dorsal view. C. Antennular peduncle. D. Antenna. E. Maxillule. F. Maxilla.

Bay (35°05.4′N, 139°17.1′E), about 1000 m, ORI-net in oblique tow accidentally touched sea bottom.

Description.—Carapace, eye and antennular peduncle as in *Bathymysis helgae.*

Antennal scale short, narrowly lanceolate, about 4 times as long as broad, setose all round, with small terminal joint marked off by distinct suture, peduncle broken. Bluntly process on distal inner corner of sympod (Fig. 5A).

Maxillule and maxilla as in *Bathymysis helgae.*

First and 2nd thoracopods as in *Bathy-*

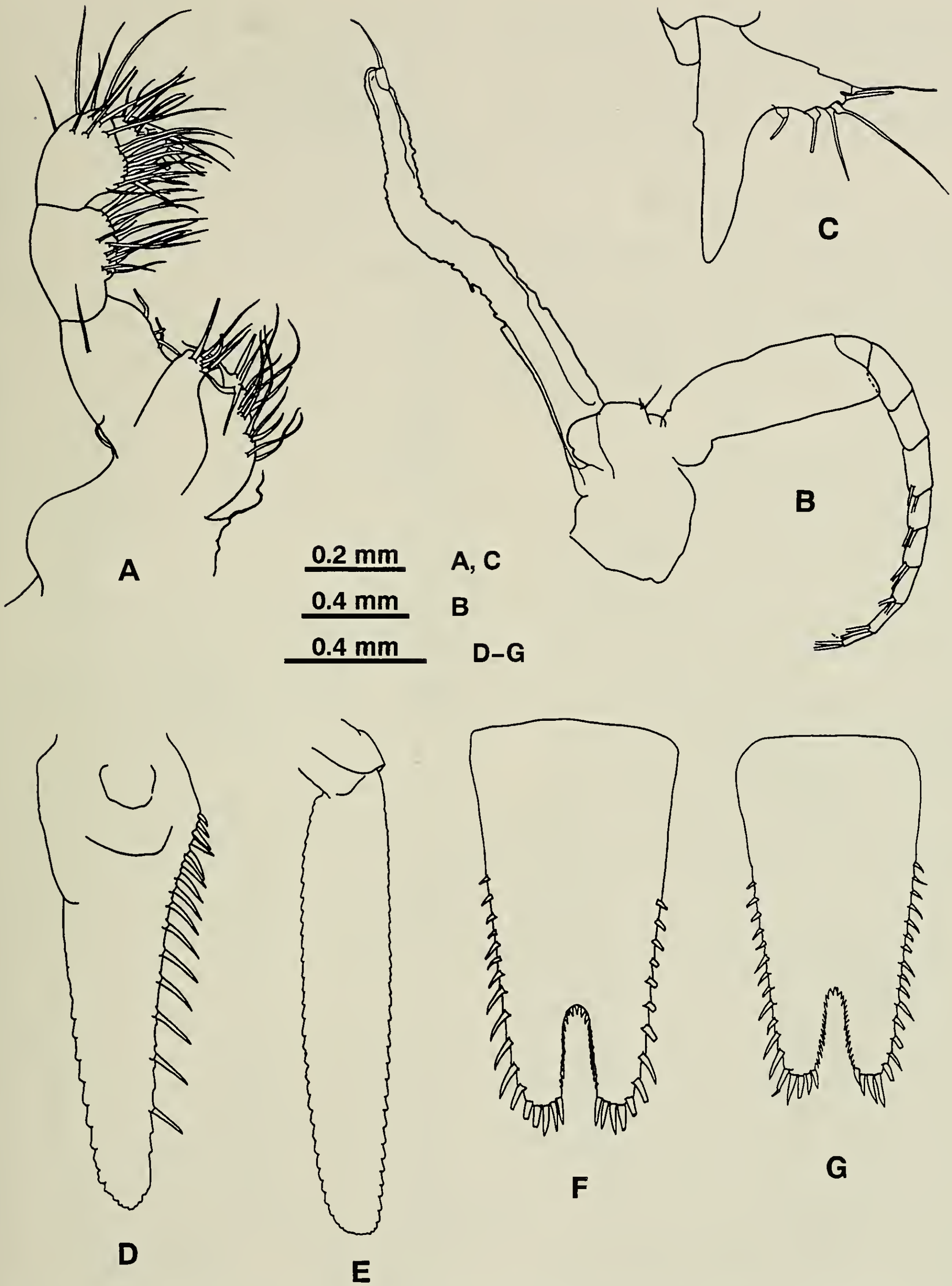

Fig. 4. *Bathymysis distincta,* new species. A–C, allotype; D–F, holotype. A. Endopod of 1st thoracopod. B. 8th thoracopod with penis and exopod, endopod absent. C. 1st male pleopod, exopod absent. D, Endopod of uropod. E, Exopod of uropod. F–G, Telson.

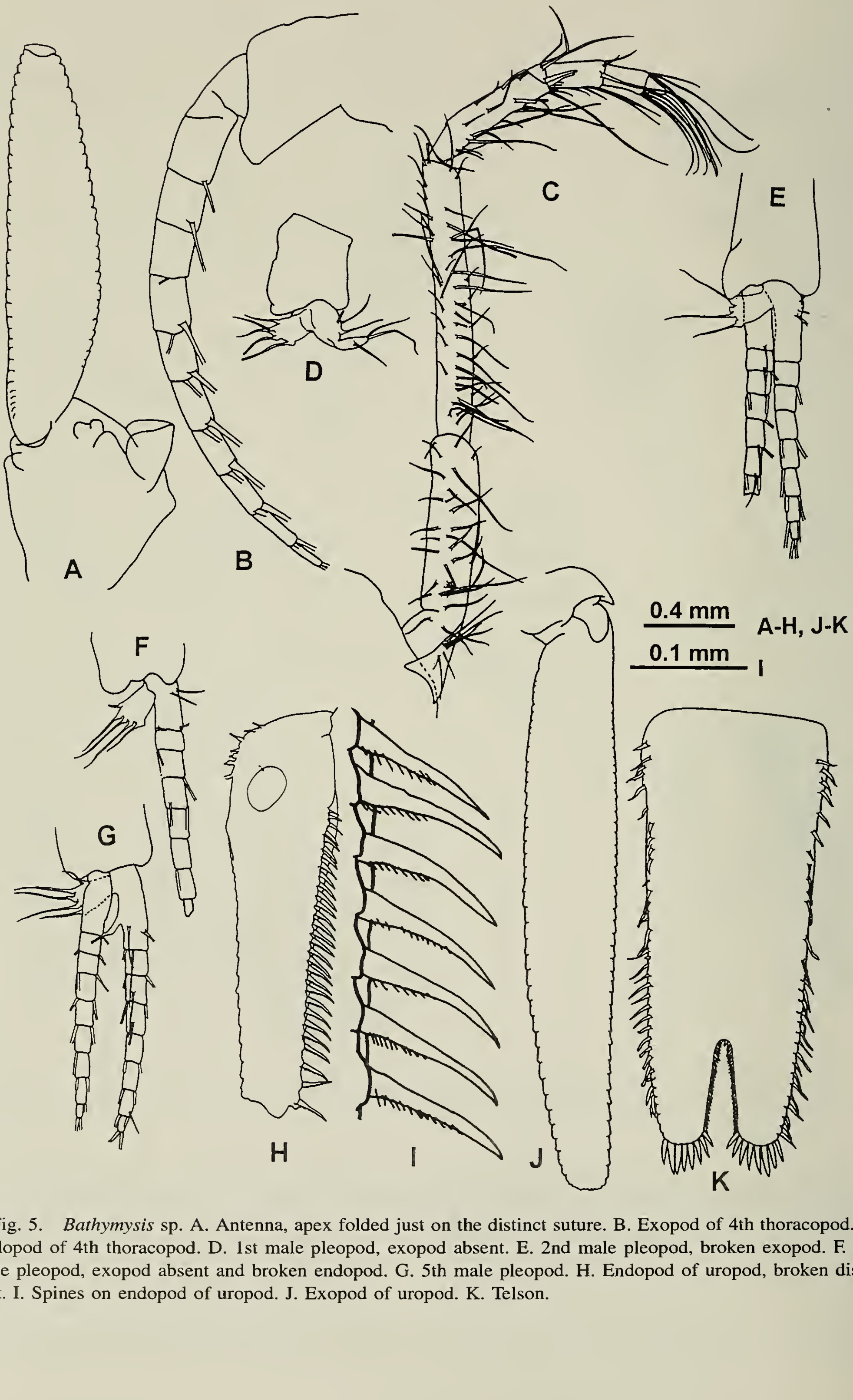

Fig. 5. *Bathymysis* sp. A. Antenna, apex folded just on the distinct suture. B. Exopod of 4th thoracopod. C. Endopod of 4th thoracopod. D. 1st male pleopod, exopod absent. E. 2nd male pleopod, broken exopod. F. 4th male pleopod, exopod absent and broken endopod. G. 5th male pleopod. H. Endopod of uropod, broken distal part. I. Spines on endopod of uropod. J. Exopod of uropod. K. Telson.

mysis helgae. Fourth and 5th thoracopods slender and long, exopod well developed (Fig. 5B), endopod with carpopropodus divided into 3 subsegments by transverse sutures; 1st subsegment longer than combined length of remaining subsegments, 2nd longer than 3rd; distal nail long and slender, preischium short, merus longer than ischium, dactylus shortest (Fig. 5C). Other thoracopods damaged.

Male pleopods biramous. First with unsegmented endopod, exopod missing (Fig. 5D); 2nd with endopod 8-segmented, distal part of exopod broken (Fig. 5E); 4th with broken endopod and exopod missing (Fig. 5F); 5th with 8-segmented endopod slightly longer than 9-segmented exopod and bearing digitiform process on 1st segment (Fig. 5G).

Endopod of uropod damaged distally, inner margin armed with continuous row of barbed spines (Figs. 5H, I). Exopod of uropod with convex inner margin and straight outer margin (Fig. 5J) about 1.3 times longer than telson.

Telson as long as 6th pleonite, about twice as long as broad at base, with about 40–46 spines throughout each lateral margin and apex. Cleft occupying 0.25 of telson length, without plumose setae and bearing about 30 small spines covering all of each side. Sides of cleft somewhat divergent distally (Fig. 5K).

Remarks.—The present specimen, although damaged, closely resembles *Bathymysis helgae* in the carapace, peculiar eyes, antennal scale, maxilla, thoracopods, pleopods and exopod of uropod. Nevertheless, two differences are present between *Bathymysis helgae*: (1) the endopod of uropod has unbarbed spines in *B. helgae* whereas in *Bathymysis* sp. the spines are barbed; (2) the telson of *B. helgae* has an apical cleft 0.33 of telson length instead of 0.25 in *Bathymysis* sp., which suggests that the present male is specifically distinct from *B. helgae.* Morphological differences among *Bathymysis helgae, B. distincta,* and *Bathymysis* sp. are shown in Table 2.

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Siriella tuberculum, a new species (Crustacea: Mysidacea: Mysidae) from Akajima Island, Ryukyu Islands, Japan

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Abstract.—A new species of Mysidae, *Siriella tuberculum*, is described from the Ryukyu Islands. This species is distinguished from other species of the genus *Siriella* by the rounded rostrum and the armature on the uropod and telson in both sexes, and particularly by the presence of a single, medial, dorsal protuberance on the carapace in the adult female.

In the genus *Siriella* sexual dimorphism is frequently observed in the carapace, antennal scale and telson in addition to secondary sexual characters that include marsupium, penis, antennule and pleopods. During a study of Mysidacea in vicinity of the Ryukyu Islands, an undescribed species which shows sexual dimorphism in the carapace was collected from Akajima Island. Females of this mysid have a dorsal tubercle just anterior to the cervical sulcus which is lacking in male specimens. The only other species with a similar character is *Siriella nodosa,* the females of which have two tubercles compared to only one in the undescribed species. In this paper we present the description of this new species of *Siriella.*

The type specimens are deposited in the National Science Museum, Tokyo (NSMT).

Siriella tuberculum, new species
Figs. 1–2

Type series.—Holotype (NSMT-Cr 11747), adult male (6.9 mm); allotype (NSMT-Cr 11748), adult female (6.3 mm); paratypes (NSMT-Cr 11749), adult male (6.8 mm) and adult ovigerous female (6.4 mm); Aka Harbor, Akajima Island, Ryukyu Islands, 8 m, bottom trap, 24 Jun 1990.

Other material: 1 immature male (4.6 mm), 1 immature female (4.5 mm) and 3 juveniles (2.2–3.6 mm); Aka Harbor, surface towing, 23 Jun 1990, collected by M. Murano, T. Ishimaru, K. Koike and K. Koike.

Description.—Carapace anteriorly produced into low triangular rostral plate with narrowly rounded apex, not extending to base of antennular peduncles, lateral margin of rostrum slightly concave (Fig. 1A, B); posterior margin of carapace emarginate, leaving last 3 thoracic somites exposed dorsally; female, small, with an obtusely angled pre-cervical protuberance present on median dorsal surface (Fig. 1C).

Eye short, expanded, as long as broad, cornea occupying half of eye, globular, wider than eyestalk; eyestalk without papilliform process (Fig. 1A, B).

Antennular peduncle of male more robust than that of female, first segment as long as third, third segment armed with 1 seta on inner margin and 2 setae at inner distal corner (Fig. 1A); female, first segment 1.2 times longer than third, second segment armed with 1 long seta at inner distal corner, third segment armed with 1 long seta on inner margin and 2 long setae at inner distal corner (Fig. 1B).

Antennal scale of male extending to middle of third segment of antennular peduncle,

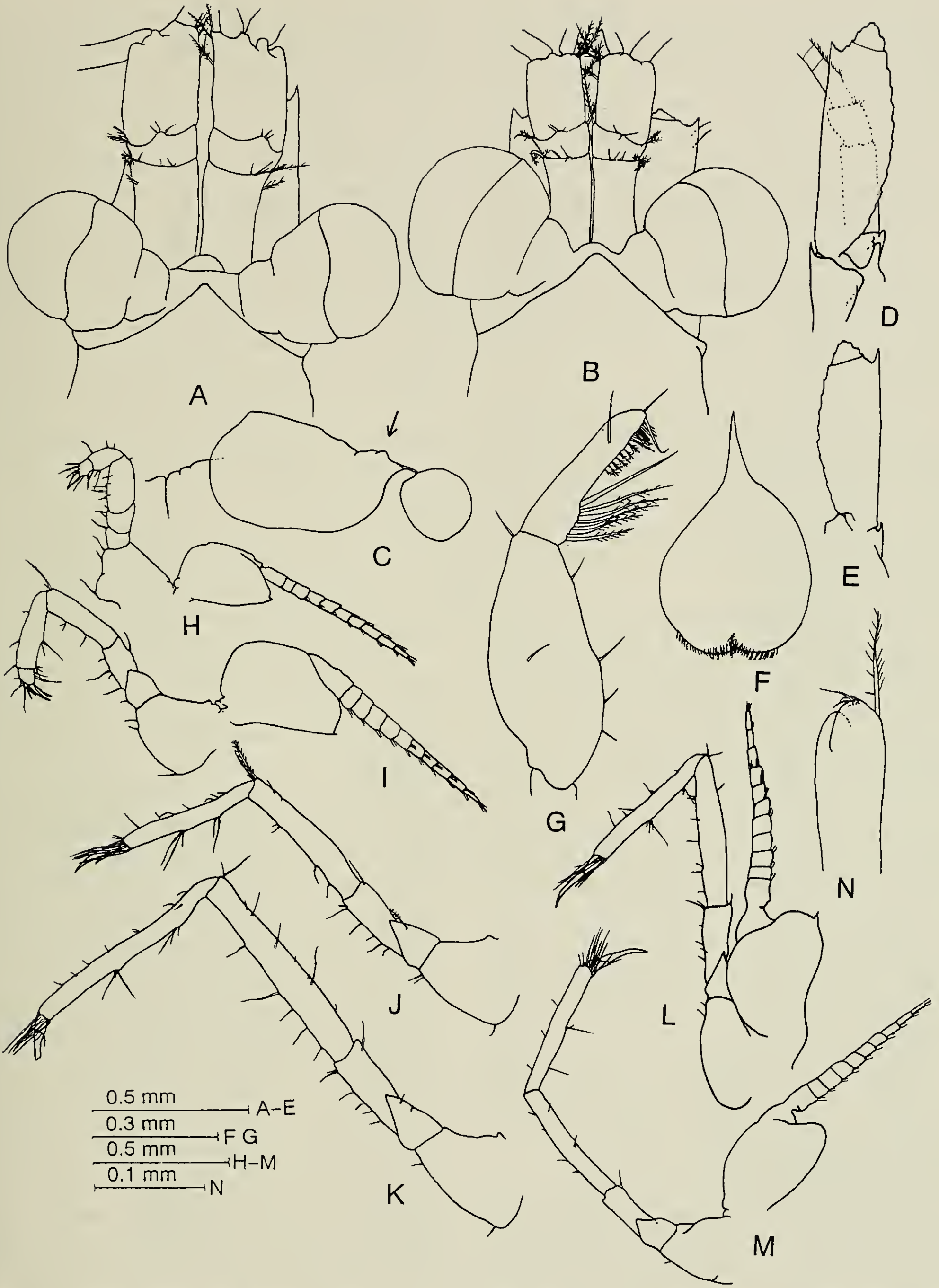

Fig. 1. *Siriella tuberculum,* new species. A, D, F–N: holotype; B, C, E: allotype. A, Anterior end, dorsal view; B, anterior end, dorsal view; C, carapace, lateral view; D, antenna; E, antennal scale; F, labrum; G, mandibular palp; H, first thoracic limb; I, second thoracic limb; J, endopod of third thoracic limb; K, endopod of fourth thoracic limb; L, seventh thoracic limb; M, eighth thoracic limb; N, penis.

3.4 times as long as broad, with indistinct suture near distal end, distal segment as long as broad, lateral margin naked and straight, distal lobe 4 times as long as spinous process terminating external margin (Fig. 1D); female scale nearly 3 times longer than broad, distal lobe only slightly longer than terminal spinous process of external margin (Fig. 1E). Antennal peduncle extending to distal fourth of scale, second segment longest, about twice as long as broad and twice as long as third segment (Fig. 1D).

Labrum with forwardly directed long spine (Fig. 1F). Mandibular palp with second segment about twice as long as broad, third segment ⅔ as long as second segment (Fig. 1G). Maxilla with second segment of endopod more than 3 times as long as broad.

First and second thoracic endopods short, terminating in a strong nail. Third to eighth thoracic endopods slender, carpopropodus undivided; third limb with merus armed with long plumose seta at outer distal corner, fourth to eighth limbs without such seta on merus. Thoracic exopods 10-segmented in first and eighth limbs, 11-segmented in second to seventh limbs; basal plates of first to seventh exopods with small tooth on outer distal corner (Fig. 1H–M).

Penis 2.6 times as long as broad, distal margin rounded, armed with 1 long plumose seta at anterior corner and 3 naked setae on apex (Fig. 1N).

Abdomen consisting of 6 somites, first somite ⅚ length of second somite, second to fifth somites subequal, sixth somite 1.5 times longer than fifth.

Male pleopods developed; first pleopod with 10-segmented exopod, endopod present as bilobed and straight pseudobranchial process; second to fifth pleopods with 11-segmented exopods, endopods subequal in length to exopod, 11-segmented, with bilobed pseudobranchial rami which are spirally coiled in second to fourth pairs and straight in fifth pair; no modified setae on all pleopods (Fig. 2A–E).

Endopod of uropod extending beyond telson for ⅓ of its length, tapering, armed on inner ventral margin from statocyst region to apex with 23 prominent barbed spines, which are increasing regularly in size towards apex and not arranged in series; exopod of uropod longer than endopod of uropod, divided by obscure suture at distal third, proximal segment with external margin naked except for distal ⅛ armed with 4 spines, distal segment 1.7 times as long as broad, setose all round (Fig. 2F, G).

Telson 1.2 times longer than sixth abdominal somite, about 2.5 times as long as broad, not reaching articulation of exopod of uropod; lateral margin armed with 2 large spines near base, followed by unarmed section which occupies ¼ of the margin, distal half armed with continuous row of 16–18 spines increasing in length distally; distal margin armed with pair of long stout spines between which 3 tiny spines and pair of plumose setae are present (Fig. 2G).

Marsupium composed of 3 pairs of brood laminae.

Remarks.—Siriella tuberculum clearly belongs to the *thompsoni* subgroup (Ii 1964) because the pseudobranchial rami on the second to fourth male pleopods are spirally coiled, the male pleopods are without modified setae, and the exopod of the uropod has spines confined to the distal part of the outer margin of the proximal joint.

Siriella tuberculum shows prominent sexual dimorphism in the carapace. Adult females have a small protuberance just anterior to the cervical groove. This character is not present in males and relates *S. tuberculum* to *S. nodosa* Hansen, 1910. In the latter species, however, adult females contain two protuberances, pre-cervical and post-cervical, along the median line of the carapace. In immature specimens of *S. nodosa* only a single protuberance is found, but its position is posterior to the cervical groove (Hansen 1910, Tattersall 1936). Furthermore, *S. tuberculum* is distinguished from *S. nodosa* in the following points: The

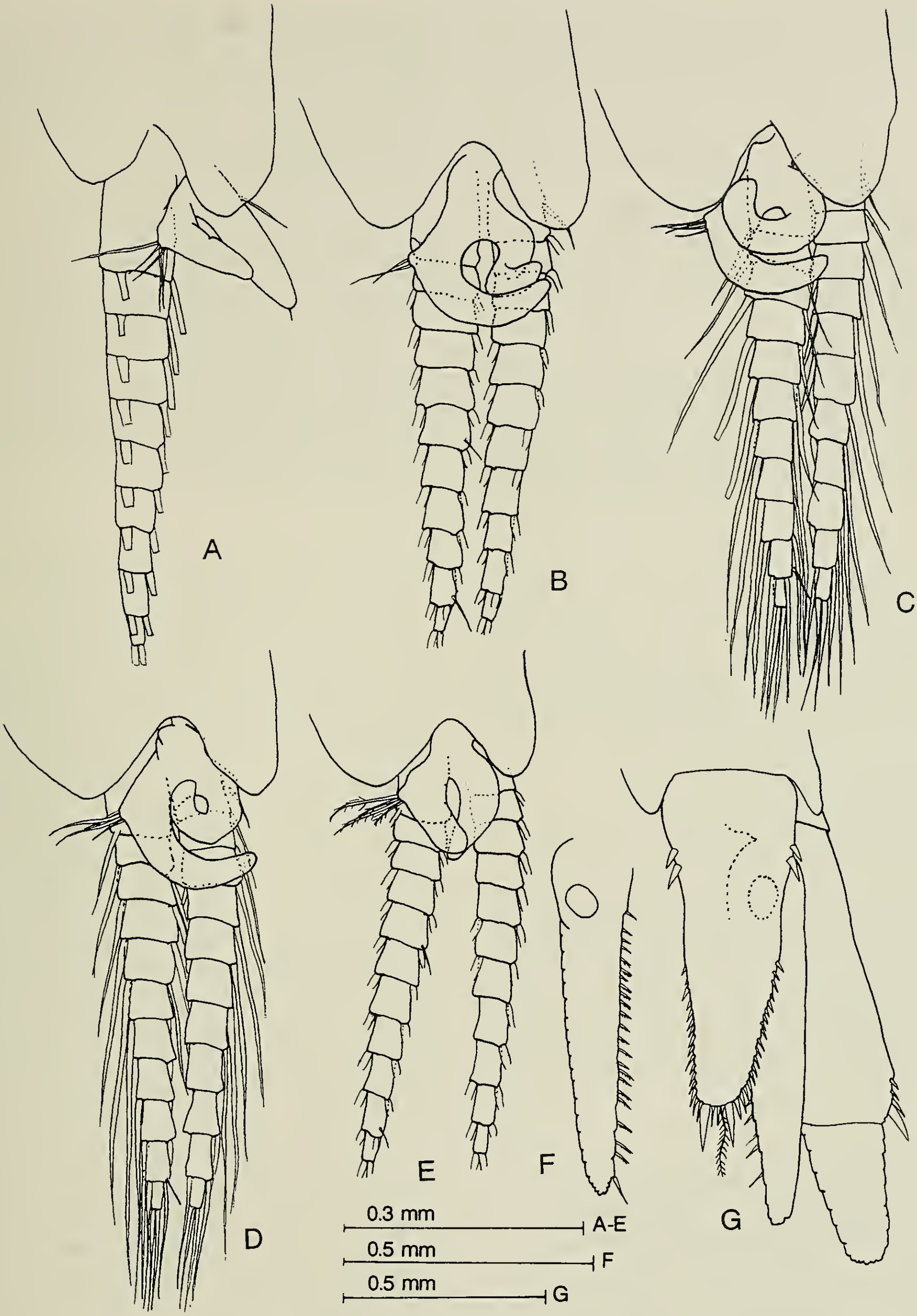

Fig. 2. *Siriella tuberculum,* new species. A–G: holotype. A, First pleopod; B, second pleopod; C, third pleopod; D, fourth pleopod; E, fifth pleopod; F, endopod of uropod, ventral view; G, uropod and telson, dorsal view.

telson has two spines on the lateral margin near the base as opposed to one in *S. nodosa*; and, the median margin of the endopod of the uropod is furnished with spines that become longer distally, while these spines are arranged in a series of longer and shorter ones in *S. nodosa.*

Etymology.—Siriella tuberculum is named after the presence of a small tubercle just anterior to the cervical groove of the carapace.

Acknowledgments

The authors wish to express our sincere thanks to Dr. T. Ishimaru, Tokyo University of Fisheries, Mr. K. Koike, Kitazato University, and Mrs. K. Koike for their cooperation in collecting the present material. We also thank Dr. Richard F. Modlin, University of Alabama in Huntsville, for his critical reading the manuscript.

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The adult male of the myodocopid ostracode *Philomedes cubitum* Kornicker, 1975, from the Strait of Magellan (Crustacea: Ostracoda: Myodocopina)

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Abstract.—The carapace and appendages of the adult male of *Philomedes cubitum* Kornicker, 1975, are described and illustrated from a specimen collected in the Strait of Magellan, which is the type locality. Observed sexual dimorphism is normal for the genus.

The Philomedidae contains two subfamilies, 11 genera, and about 75 species, and live in all oceans from intertidal to abyssal depths (Cohen 1982:183). Species of *Philomedes* are cosmopolitan, ranging from the Arctic to Antarctic, and have a known depth range of intertidal to 3480 m (Kornicker 1989:67). Most members of the genus, including *P. cubitum,* have juveniles that are not capable of swimming and are restricted to the bottom where they either crawl on the substrate or burrow into it. When they become adult, both sexes become capable of swimming and rise in the water to couple. After mating, the female either rubs or breaks off its swimming bristles and is again restricted to the bottom. Adult males die soon after coupling and as a result are less abundant than adult females.

The species *Philomedes cubitum* was described by Kornicker (1975:289) from 29 specimens (2 non-ovigerous adult females, and 27 juveniles) collected in 1969 at 2 stations at depths of 21.3–28 m in the Strait of Magellan. The adult male described herein was the only specimen of this species collected in the Strait by the Italian National Scientific Commission for Antarctica, Magellan Cruise, February–March 1991. Further collections were made in 1994, but only about 6 of more than 200 samples have been examined so far without recovering more specimens of *P. cubitum.* The junior author was a member of the scientific unit working with planktonic Ostracoda. The specimen was noted in McKenzie et al. (1996); a comprehensive description follows.

In the figures, arabic numerals indicate limbs 1–7, as well as individual joints of each limb (the location of the numeral indicating whether a limb or joint is indicated). Roman numerals I–III indicate the endites. For definition of lettering system for appendage bristles see Skogsberg (1920:188) and Kornicker (1985:2). Letters used in identifying sclerites of the protopodite of the 2nd antenna are explained in Kornicker (1994:189).

Suborder Myodocopina Sars, 1866
Philomedidae Müller, 1906
Philomedinae Müller, 1906
Genus *Philomedes* Liljeborg, 1853

Philomedes Liljeborg, 1853:175.
Bradycinetus Sars:109 [preprint 1865].

Type species.—*Philomedes longicornis* Liljeborg, 1853:176 [= *Cypridina brenda* Baird, 1850].

Fig. 1. *Philomedes cubitum* USNM 194145, adult, male, length 1.56 mm: Complete carapace, ov. Abbreviations are: ant: antenna; am: central adductor muscle attachments; ap: anterior process; Bo: Bellonci organ; co: copulatory organ; cop: copepod; cx: coxale; end: endopodite; ex: exopodite; epip: epipodite; fu: furca; gird: girdle; hrt: heart; im: inner margin of infold; iv: inside view; le: lateral eye; lv: lateral view; me: medial eye; mls: medial longitudinal sclerite of protopodite of 2nd antenna; mnd: mandible; mv: medial view; mx: maxilla; nabs: not all bristles shown; ov: outside view; prot: protopodite; sens: sensory bristle of 5th joint of 1st antenna; ul: upper lip; Y-scl: Y-sclerite. Arrows on illustrations of the carapace indicate anterior.

Philomedes cubitum Kornicker, 1975
Figs. 1–7

Philomedes cubitum.—Kornicker, 1975:289, figs. 178, 179; McKenzie et al., 1996.

Holotype.—USNM 138656, adult female.

Type locality.—*Hero* Cruise 69-5, station 48, 53°41′40″S, 72°0′45″W, depth 21.3 m, Strait of Magellan, 20 Oct 1969.

Material.—USNM 194145, adult male.

Collection data.—Strait of Magellan. Italian National Scientific Commission for Antarctica, Magellan Cruise, MV *Cariboo,* Feb–Mar 1991; station 21 (plankton sampling began at 53°52.07′S, 70°30.00′W (1303 h) and ended at 52°52.70′S, 70°29.60′W (1331 h), 1 Mar 1991. Depth to bottom 46 m; sampling depth 20–42 m. The mouth area of the plankton net is 0.25 square meters, mesh size 250 micrometers.

Distribution.—Strait of Magellan: females and juveniles in substrate at depth of 21.3–28 m; adult male in plankton at depth of 20–42 m.

Description of adult male.—Carapace elongate, oval, with prominent rostrum and broad incisur, and with small projecting caudal process not projecting posteriorly past posterior margin of valve, which extends laterally past tip of caudal process (Figs. 1, 3a–c, 4a–c); without small protuberance at ventral corner of rostrum present on female shell (Kornicker 1975:290). Ornamentation (Figs. 1, 3b, c): Carapace smooth, with relatively few long and short bristles scattered on valve surface; long bristles more numerous along edge of rostrum and posterior valve margin.

Infold: Infold broad along anterior, anteroventral, and posteroventral margin; rostral infold with 17 bristles (Fig. 4a); 1 small bristle just ventral to inner end of incisur (not shown); anterior part of ventral infold with 5 bristles; remaining infold of ventral margin

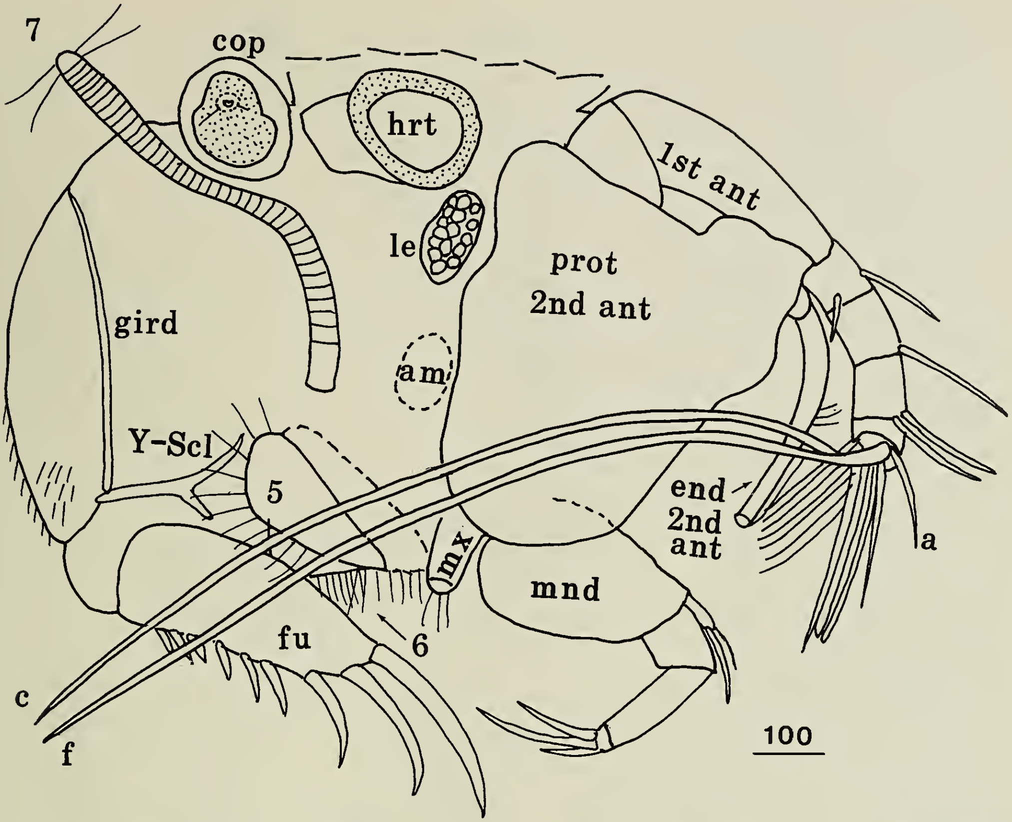

Fig. 2. *Philomedes cubitum* USNM 194145, adult male: Camera lucida drawing of body (nabs). Note parasitic copepod attached to body near 7th limb. Scale in microns. (For abbreviations, see Fig. 1.)

and posterior infold bare; list paralleling inner margin of posteroventral and posterior infold with about 17 bristles in groups of 1 to 3 bristles (not all shown in Fig. 4b, c). Shell edge forming high angle at posteroventral corner of each valve and resulting in small projecting caudal process (Fig. 4b, c); posterior end of process with 3 short bristles (Fig. 4b, c).

Selvage: Lamellar prolongation of selvage broadly striated and fringed in area of rostrum and incisur (Fig. 3c); prolongation divided at inner end of incisur; anteroventral infold with few long hairs at midwidth of lateral side. Ventral prolongation not striated, and with short marginal fringe; posterior prolongation broad and fringed but absent along caudal process.

Central adductor muscle attachments (Fig. 3a, d): Comprising about 16 oval and elongate attachments.

Carapace size: USNM 194145, length 1.56 mm, height 0.88 mm.

First antenna (Figs. 2, 5a): 1st joint with few medial spines. 2nd joint with few ventral and dorsal spines, and 3 bristles (1 ventral with long spines, 1 dorsal, 1 lateral). 3rd joint with 3 bristles (1 ventral, 2 dorsal). Fourth joint with 6 bristles (4 ventral, 2 dorsal). Sensory bristle of 5th joint with numerous long slender proximal filaments and 3 long subterminal filaments excluding stem (not all shown). Medial bristle of 6th joint near dorsal margin and with long spines near midlength. 7th joint: a-bristle short spinous; b-bristle with 3 proximal and 5 terminal filaments including stem; c-bristle very long with 12 marginal filaments. 8th joint: d- and

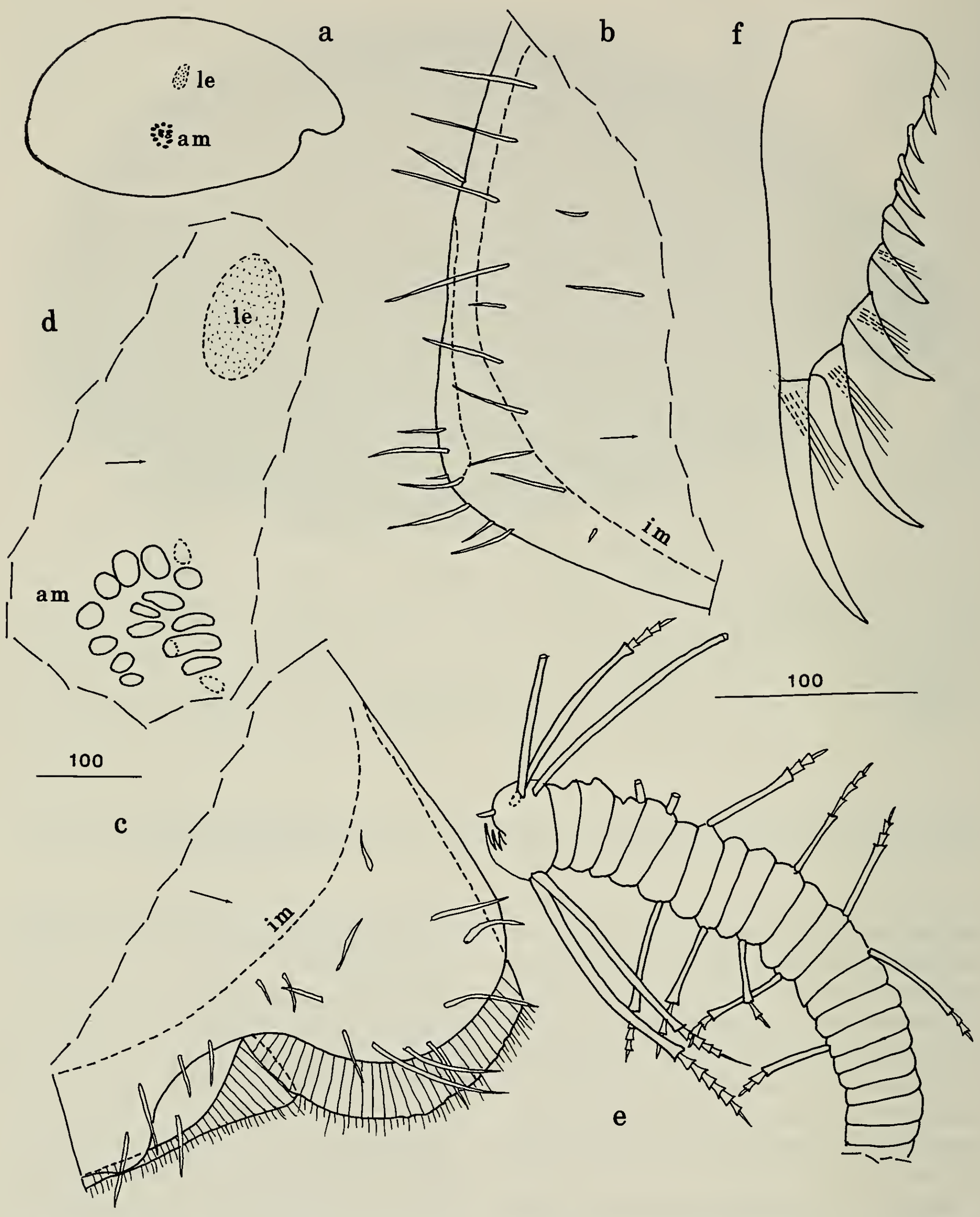

Fig. 3. *Philomedes cubitum* USNM 194145, adult male: a, Outline of complete carapace from right side, ov; b, Detail of posteroventral corner shown in a; c, Detail of rostrum and incisur in a; d, detail of lateral eye (stippled) and central adductor muscle attachments shown in a; e, 7th limb; f, left lamella of furca, lv. Scale in microns; same magnification: b, c, f; d, e. (For abbreviations, see Fig. 1.)

e-bristles about same length as b- and g-bristles, bare with blunt tips; f-bristle very long with 10 marginal filaments; g-bristle with 3 proximal and 4 terminal filaments including stem. (Filaments of c- and f-bristles not shown.).

Second antenna (Figs. 2, 5c–e): Protopodite bare with e-sclerite. Endopodite 3-joint-

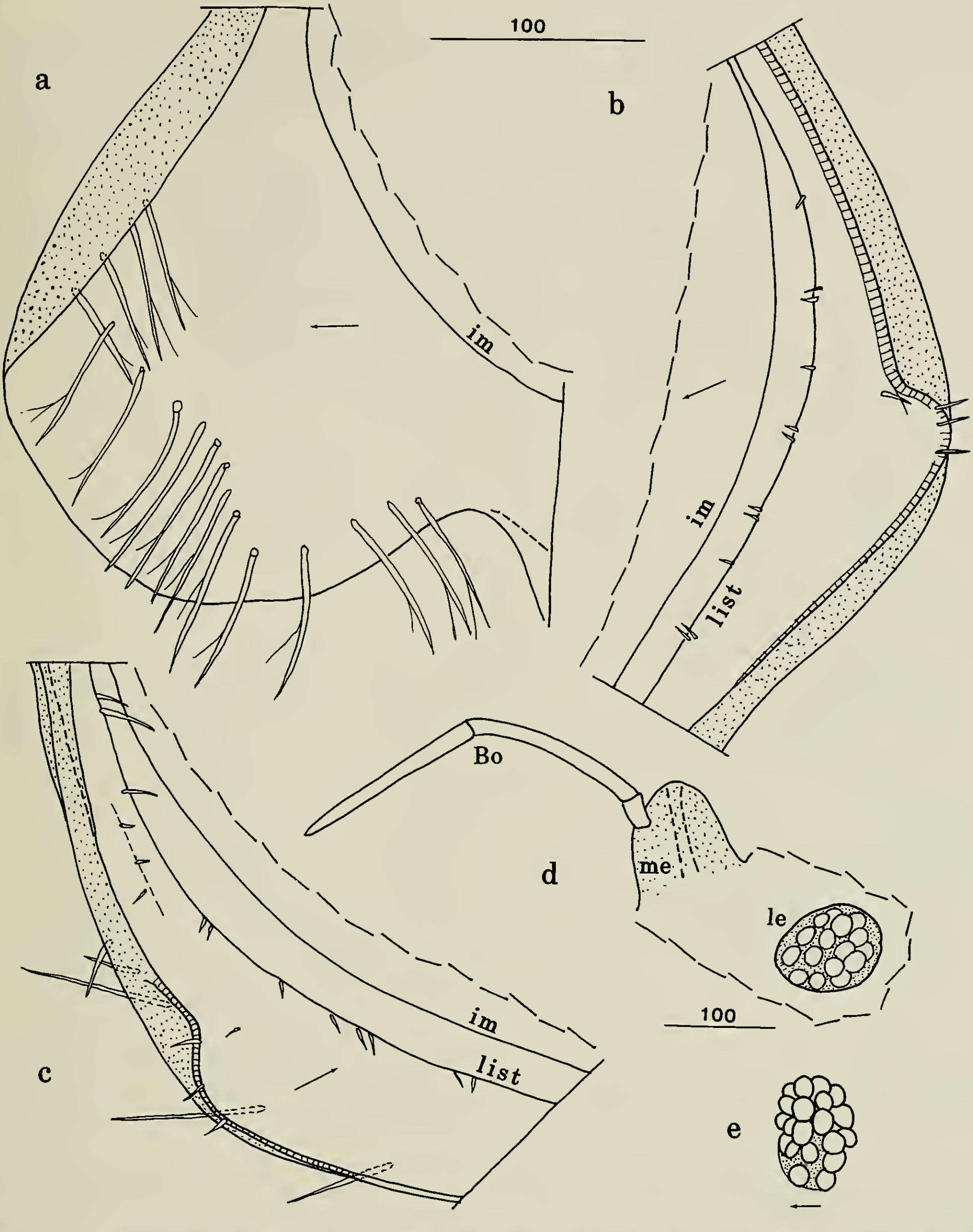

Fig. 4. *Philomedes cubitum* USNM 194145, adult male: a, rostrum right valve, iv; b, c, caudal processes right and left valve, respectively, iv; d, lateral eye, medial eye, and Bellonci organ, stippling indicates pigment; e, left lateral eye. Scale in microns; same magnification: a–c; d, e. (For abbreviations, see Fig. 1.)

ed: 1st joint with 6 bristles (5 proximal and 1 distal); 2nd joint elongate with 3 short bristles near midlength; 3rd joint reflexed on 2nd, with 1 long proximal and 2 short terminal bristles. Exopodite: 1st joint with small distomedial spine; 3rd joint longer than 2nd joint; 2nd joint with bristle with row of stout ventral spines at midlength; bristles of joints 3–8 long with natatory hairs; 9th joint with 7 unbroken bristles; joints 3–8 with stout basal spines; joints 2–8 with terminal row of minute spines.

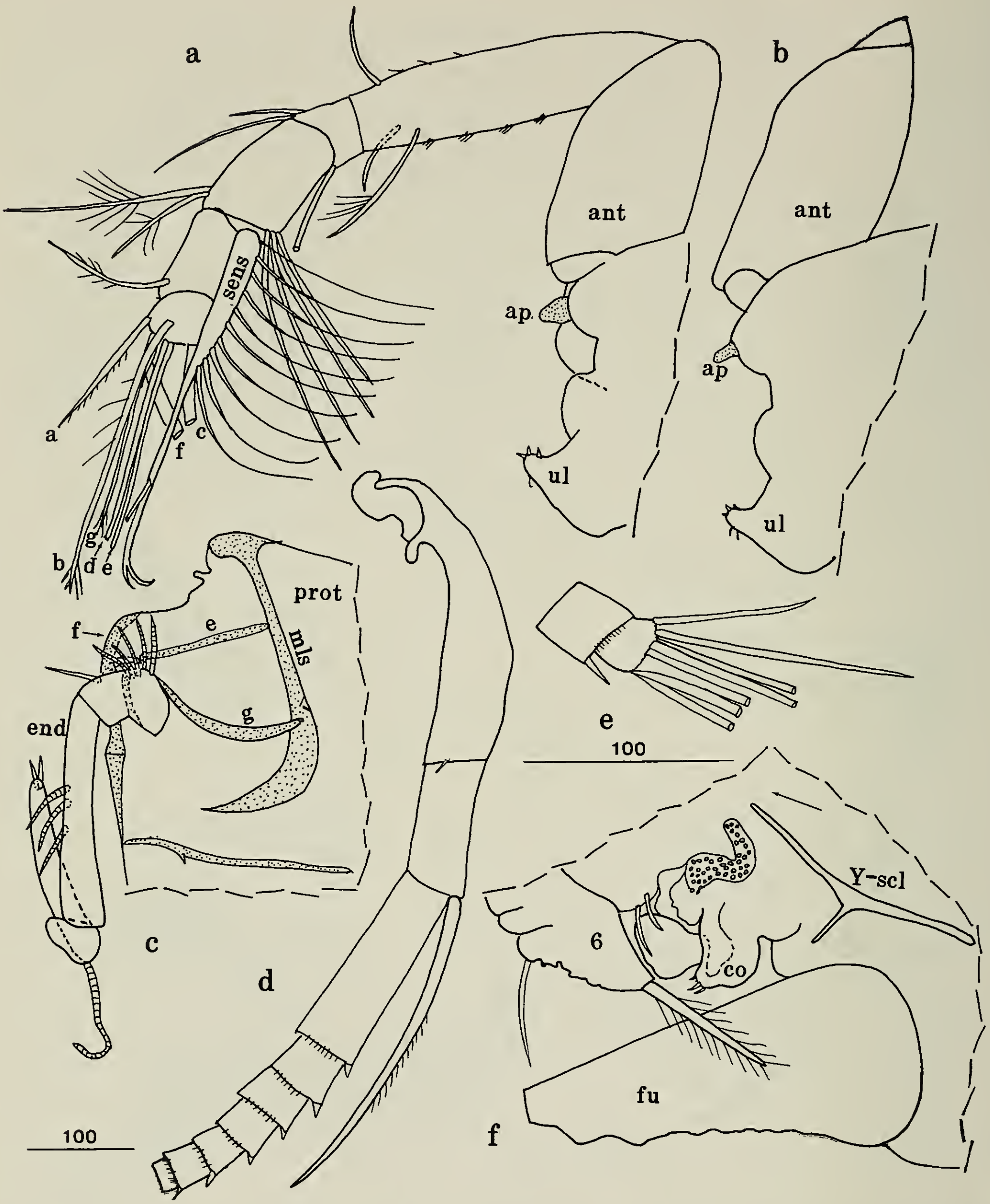

Fig. 5. *Philomedes cubitum* USNM 194145, adult male: a, profile of anterior of body from left side and right 1st antenna, mv; b, profile of anterior of body from left side and joint 1 of left 1st antenna, lv; c, part of protopodite (sclerites stippled) and endopodite right 2nd antenna, mv; d, exopodite left 2nd antenna, mv, nabs; e, joints 8 and 9 exopodite left 2nd antenna, lv; f, part of posterior of body from left side. Scale in microns; same magnification: a–d, f; e. (For abbreviations, see Fig. 1.)

Mandible (Figs. 2, 6a): Coxale endite absent. Basale: dorsal margin with 3 bristles (1 short bare near midlength, 2 terminal (1 long with long spines near midlength, 1 short bare)); medial surface with rows of spines in dorsal half (not shown) and 5 bristles (4 proximal and 1 at about ¼ length of joint) either bare or with short spines; ventral mar-

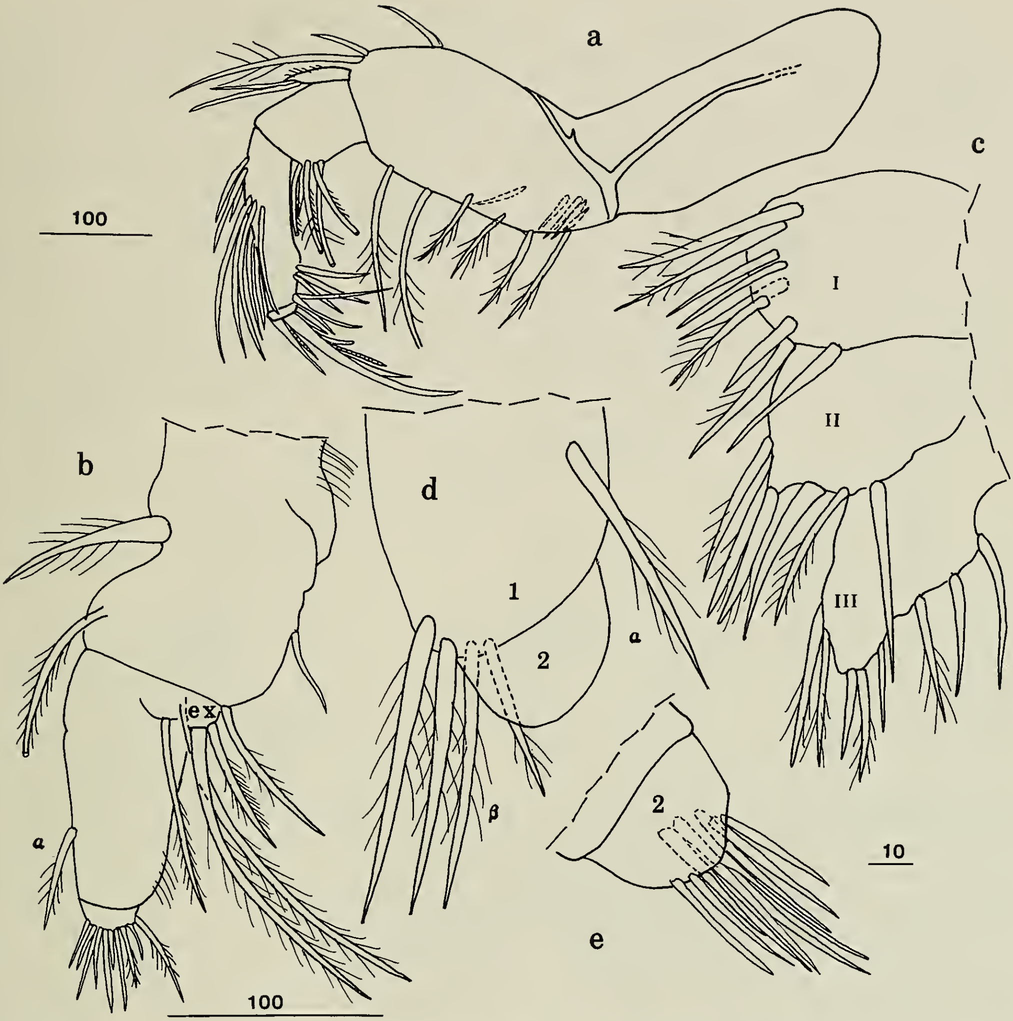

Fig. 6. *Philomedes cubitum* USNM 194145, adult male: a, left mandible, lv; b, right maxilla, mv, nabs; c, endites right maxilla, lv; d, alpha- and beta-bristles of 1st endopodial joint left maxilla, mv; e, bristles of 2nd endopodial joint left maxilla, mv. Scale in microns; same magnification: a; b; c–e. (For abbreviations, see Fig. 1.)

gin with 6 bristles (middle with base slightly lateral). Exopodite with hirsute tip reaching midlength of dorsal margin of 1st endopodial joint, with 2 bare subterminal bristles. 1st endopodial joint with 5 ventral bristles (2 longest with long spines, others with short spines) and short terminal dorsal spines. 2nd endopodial joint: ventral margin with 3 bristles in both subterminal and terminal groups; dorsal margin with 3 bristles in proximal group and 6 in distal group; medial surface with rows of spines. 3rd endopodial joint with 3 stout claws with ventral teeth along middle part (teeth not shown), and 4 ringed bristles.

Maxilla (Figs. 2, 6b–e): Limb reduced. Endite I with 9 bristles, endite II with 6 bristles; endite III with 8 bristles. Coxale with stout hirsute dorsal bristle. Exopodite with 3 bristles with long hairs. Basale with 3 long bristles along distal margin. 1st endopodial joint with 1 alpha-bristle and 4 beta-bristles. 2nd endopodial joint with about 10 bristles.

Fifth limb (Figs. 2, 7a–c): Limb reduced.

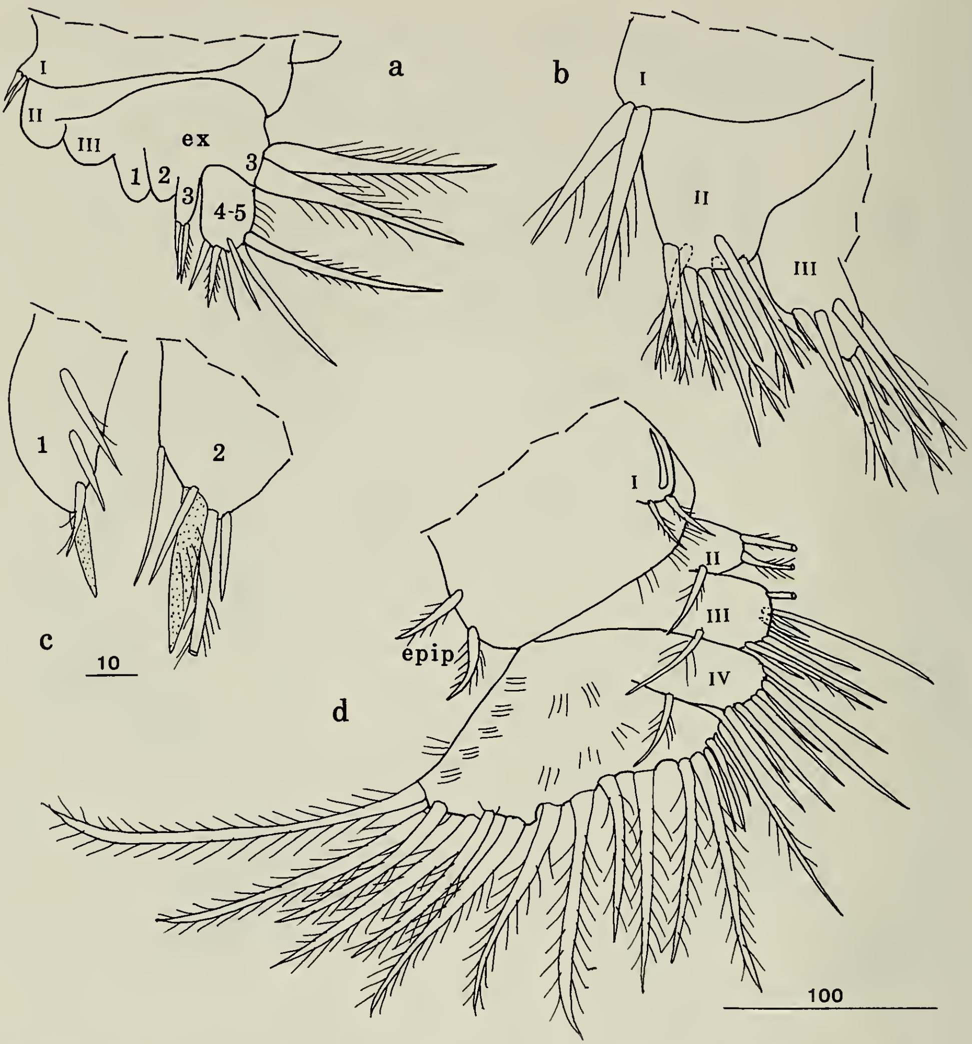

Fig. 7. *Philomedes cubitum* USNM 194145, adult male: a, 5th limb, nabs; b, endites of 5th limb shown in a; c, bristles of exopodial joints 1 and 2 of 5th limb shown in a; d, left 6th limb, mv. Scale in microns; same magnification: a, d; b, c. (For abbreviations, see Fig. 1.)

Endite I with 2 bristles; endites II and III each with 8 bristles. Exopodite: 1st and 2nd joints each with 1 broad bristle and several slender bristles; 3rd joint with 3 short bristles on inner lobe (nabs) and 2 stout hirsute bristles on outer lobe; 4th and 5th joints fused, with total of 6 slender bristles.

Sixth limb (Figs. 2, 5f, 7d): With 2 spinous epipodial bristles; endite I with 3 spinous bristles; endite II with 4 spinous bristles (1 medial, 3 terminal) (nabs); endite III with 9 spinous bristles (1 medial, 8 terminal); endite IV with 8 spinous bristles (1 medial, 7 terminal); end joint with 16 spinous bristles and medial and lateral hairs.

Seventh limb (Figs. 2, 3e): Limb with 16 bristles, 5 in distal group (3 on peg side, 2 on comb side), 11 proximal (6 on peg side, 5 on comb side). Terminal comb with about 7 alate teeth; 1 long and 1 short peg (not shown) opposite comb. Only 1 limb examined, other fragmented.

Furca (Figs. 2, 3f, 5f): Each lamella with 9 claws decreasing in length and width along lamellae; anterior 5 claws stout; all claws with teeth along posterior edges; tips of claws pointed; hairs present at bases of claws and following last claw.

Bellonci organ (Fig. 4d): Elongate with 2 sutures, 1 proximal and 1 at midlength; tip broadly pointed.

Eyes (Figs. 2, 3a, d, 4d, e): Lateral eye well developed with 16–20 ommatidia and black pigment between them. Medial eye about same size as lateral eye, amber-colored, bare.

Upper lip (Fig. 5a, b): With anterior projection with small processes at tip; ventral surface with few anterior hairs.

Genitalia (Fig. 5f): Lobate with few bristles.

Anterior of body (Fig. 5a, b): With elongate anterior process.

Posterior of body (Fig. 2): Evenly rounded with hairs in ventral third.

Y-sclerite (Figs. 2, 5f): With ventral branch typical for genus.

Heart (Fig. 2): Well developed.

Gut content: With minute unrecognizable amber-colored particles.

Ectozoa (Fig. 2): USNM 194145 with female choniostomatid on dorsal part of body.

Discussion.—Observed sexual dimorphism in this species is common to members of the genus. Choniostomatid copepods are generally sparser in males than females (Kornicker 1975:56), which suggests that they are probably present in many adult female *P. cubitum,* although they have not yet been reported.

The right-angle bend in the selvage at the posteroventral corner of each valve clearly shows that the male described above is conspecific with the previously described female in Kornicker (1975:289), which had been collected in the same area. The right-angle bend has not been reported in other species of *Philomedes.* Additional congeneric comparisons may be found in the original description of the species (Kornicker 1975: 289).

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Additions to the Pycnogonida fauna of Carrie Bow Cay, Belize, middle America

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Abstract.—Five additional species are added to the 31 species in 14 genera known to inhabit reefs in the vicinity of Carry Bow Cay, Belize. Four of these species are known from other localities while one is new; *Ascorhynchus petilus,* new species. The new species is described, illustrated, and its morphology compared with related species in this genus. Additional illustrations are provided for another species, *Parapallene bermudensis* Lebour, from an adult specimen where the species was known previously only from juveniles.

There is only one previous report on the pycnogonida of Belize (Child 1982a), listing known species and describing new species collected up to that time. Five additional species from the vicinity of Carrie Bow Cay, Belize, were collected during ongoing studies of the Caribbean reef system at that locality. The study has been continued each year since 1972, and many collectors have contributed specimens taken fortuitously with general benthic material. The present report brings the species count up to date and describes and illustrates a new species; *Ascorhynchus petilus,* and compares it with related species. Four other known species are listed as new to Belize, and parts of one additional species, *Parapallene bermudensis* Lebour, are illustrated to contribute knowledge of adult morphology where only juveniles had previously been known.

Systematics

Class Pycnogonida
Family Ammotheidae
Genus *Achelia* Hodge, 1864
Achelia gracilis Verrill

Achelia (?) *gracilis* Verrill, 1900:582, fig. 4, pl. 70, fig. 10.

Ammothea gracilis.—Cole, 1904:317–323, pl. 21, figs. 4–14.

Ammothea (*Achelia*) *gracilis.*—Giltay, 1934:5.

Achelia gracilis.—Marcus, 1940:79 [key].—Hedgpeth, 1948:244, fig. 38f–g.—Sawaya, 1951:274 [key].—Stock, 1954: 117.—Bourdillon, 1955:597.—Stock, 1975:983; 1979:10; 1986:416; 1992b: 118.—Müller, 1992:43, fig. 1.

Material examined.—Carrie Bow Cay, on *Madracis* sp. in five separate places along the forereef crest in 15 m, 16°48.2′N, 088°04.5′W, 19 April 1988 (2 males, 2 females, 1 juvenile, 2 damaged specimens).

Distribution.—Found in many localities from Bermuda to the Caribbean and the northeast coast of South America in Brazil, in depths to 44 m.

Remarks.—It is no surprise to find this infrequently collected species at Belize although it is not nearly so common as its congener, *Achelia sawayai* Marcus. It has been reported in many papers from Florida and the northeast Caribbean Sea, but not as often in the western Caribbean.

Genus *Ascorhynchus* Sars, 1877
Ascorhynchus petilus, new species
Fig. 1A–F

Material examined.—Curlew Cay Bank, among coral, sponge, and *Halimeda* in 21.3

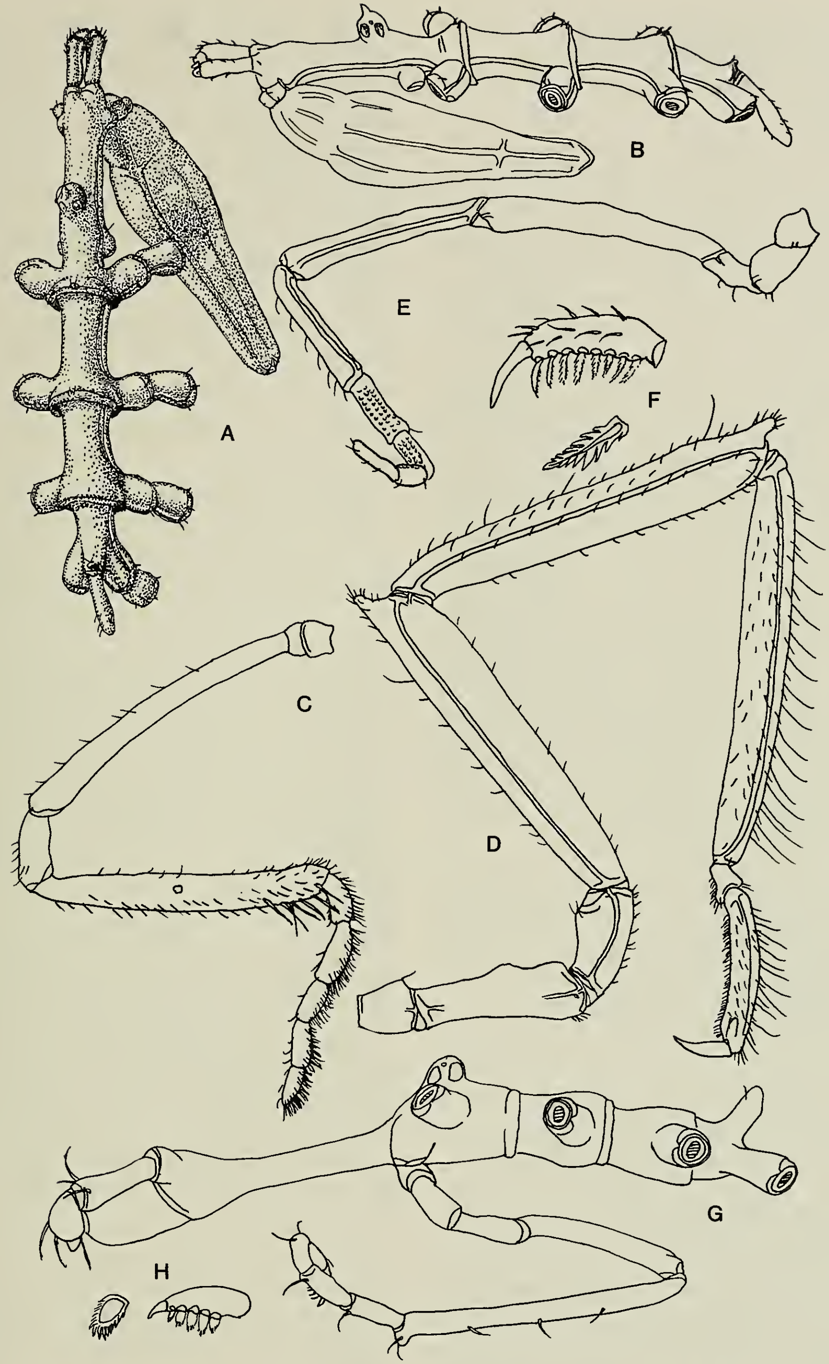

Fig. 1. *Ascorhynchus petilus,* holotype female: A, trunk, dorsal view; B, trunk, lateral view; C, palp; D, third leg; E, oviger; F, oviger terminal segment and one spine, enlarged. *Parapallene bermudensis* Lebour: G, adult male trunk, lateral view with oviger; H, oviger terminal segment with one spine, enlarged.

m, 16°47′N, 088°04′W, 8 Apr 1986 (1 female, holotype, USNM 234709).

Distribution.—Known only from the type locality.

Description.—Species moderately small for genus, leg span 36.2 mm. Trunk long, slender, fully segmented, lateral suture lines conspicuous, segments of equal diameter with neck, small swelling at posterior of each segment, with tiny dorsomedian tubercle bearing 1–2 short setae. Lateral processes extremely short, widely separated, length equal to or shorter than adjacent trunk diameter, with 2–3 short dorsodistal setae, without tubercles. Neck long, oviger implantation bulges to posterior but separated from first lateral processes. Ocular tubercle low, rounded, with tiny apical tubercle, eyes prominent, tubercle situated anterior to oviger implants, almost at midpoint of neck. Proboscis long, 0.6 of trunk length, slender, with proximal constriction only, distal tip narrow, lips rounded. Abdomen short, downcurved, extending only to distal rim of first coxae, armed with few short dorsal and distal setae, suture and tiny tubercle on trunk at abdomen base.

Chelifores very short, scape 1-segmented, almost cylindric, with few short dorsal and distal setae. Chela reduced to short rounded bud with tiny papilla representing finger, armed with 2–3 short setae.

Palps typical, long, slender, fifth segment almost as long as third, armed with many short setae increasing in numbers distally, and few distal setae longer than segment diameter. Distal 5 segments short, subequal, each armed with many ventral setae only as long as segment diameters.

Oviger (female) fourth segment longest, fifth almost as long as fourth, sixth about 0.7 length of fifth, armed with few short lateral setae. Strigilis segment 7 about 0.7 length of subequal distal 3, all armed with two lateral rows of short setae and 1 major and 2 minor rows of denticulate spines, spines with 5–6 lateral serrations. Terminal claw very slender, slightly curved, short, only half length of terminal segment.

Legs robust, major segments slightly swollen. Coxae typical, third coxae about 0.6 length of second. Femur with few tiny setae, femur and first tibia with small dorsodistal tubercles extending only slightly beyond distal suture. Tibiae with many short dorsal and lateral setae and row of longer dorsal setae increasing in numbers distally. Tarsus very short, subtriangular, with few short dorsal and many ventral setae. Propodus moderately short, slightly curved, with rows of tiny lateral setae, many very short sole setae, and row of dorsal setae, some longer than propodal diameter. Claw robust, short, about 0.3 length of propodus, only curved distally.

Male diagnostic characters unknown.

Measurements of female holotype in mm.—Trunk length (chelifore insertion to tip 4th lateral processes), 2.81; trunk width (across 2nd lateral processes), 0.76; proboscis length, 1.91; abdomen length, 0.41; third leg, coxa 1, 0.6; coxa 2, 1.6; coxa 3, 1.0; femur, 3.85; tibia 1, 3.96; tibia 2, 4.14; tarsus, 0.42; propodus, 1.56; claw, 0.59.

Etymology.—The name (Latin: *petilus,* meaning thin or slender) refers to the very slender appearance of the trunk with its short lateral processes.

Remarks.—A member of the largest single group of *Ascorhynchus* species, those which have one scape segment and a short tarsus (the brevitarsal group with tarsus half or less of the propodal length), this species closely resembles several known species with these characters and which have either tiny dorsomedian trunk and lateral process tubercles or none in these locations. Among these species are: *Ascorhynchus antipodum* Child, 1987; *A. foresti* Stock, 1991; *A. tenuirostrum* Carpenter, 1892; *A. pudicum* Stock, 1970; and remotely, *A. fusticulum* Nakamura and Child, 1983.

The new species is perhaps closest in trunk morphology to *A. antipodum.* The latter species has very short lateral processes on an elongate trunk, a long neck with oviger implantations well in advance of the first lateral processes, a similar slender proboscis with a single proximal constriction, and similar ovigers. There are many differences between these two species: *A. antipodum* is a blind deep-water species with anterolateral trunk tubercles; a much longer abdomen, a much shorter second tibia with far fewer setae; a tarsus half the propodal length; and very much longer chelifore scapes.

The next close relation in this category is *A. tenuirostrum.* It has a similar long slender trunk but with somewhat longer lateral processes bearing small dorsodistal tubercles. Its chelifore scape is very short but its legs are much more slender and only the femur has a long dorsodistal tubercle. The abdomen is equally short but the proboscis has a long tubular distal part like the neck of a flask.

The new species is only distantly related to the other members of this category. Both *A. foresti* and *A. pudicum* have a short tarsus and claw but their lateral processes are longer and closer together than those of *A. petilus.* Their ovigers are similar and they have short scapes but both species have dorsomedian and lateral process tubercles and their ocular tubercle is longer than that of *A. petilus.* The similarities between *A. petilus* and *A. fusticulum* are more tenuous. The Japanese species has the short tarsus and single scape segment but has longer lateral processes more closely spaced and armed with many lateral spine bearing tubercles, a tall ocular tubercle, and longer abdomen, along with several oviger and leg differences.

There are other *Ascorhynchus* species with a long slender trunk having short lateral processes, but they have a tarsus more than half the propodal length or two scape segments, or both, among other differences.

In agreement with Stock (1993:352, footnote), and the third edition of Zoological Nomenclature, the generic suffix is recognized as masculine with species names following this rule.

Family Callipallenidae
Genus *Callipallene* Flynn, 1929
Callipallene brevirostris (Johnston)

Pallene brevirostris Johnston, 1837:380, pl. 12, figs. 7–8.

Callipallene brevirostris.—Hedgpeth, 1948: 202–203, fig. 18a [early literature].—Stock, 1979:14; 1986:424; 1987:512–513.

Callipallene brevirostrum.—Stock, 1975: 1010–1011.

Material examined.—Twin Cays, from mangrove roots and *Caulerpa* in 0–2 m, 16°49.8′N, 088°05.9′W, 17 Apr 1981 (1 ♂). Several other damaged specimens from Carrie Bow Cay may be this species, but all are without legs and some have lost other appendages.

Distribution.—This most common of all amphi-Atlantic species is listed in almost all reports on North Atlantic shallow fauna. It has one record from Meteor Bank, West Africa, and a maximum known depth record of 316 m. It is known more often in North Atlantic shore areas in much shallower depths. It has also been captured in the Mediterranean and Black Seas.

Remarks.—It is probably the result of a collecting artifact that this common species had not been taken in Belize until this record. For a comparison of the differences between this species and *C. belizae* see Child (1982:365).

Genus *Parapallene* Carpenter, 1892
Parapallene bermudensis Lebour
Fig. 1G–H

Parapallene bermudensis Lebour, 1949: 930–932, figs. 2–3.—Child, 1982a:366–367, fig. 165; 1992:61–62, fig. 28.

Material examined.—Carrie Bow Cay, 16°48.2′N, 088°04.5′W, 36 m with scuba, 29 Mar 1980 (1 ♀, without legs). Carrie Bow Cay, fore reef crest among dead coral rubble in 16.8 m, 2 Apr 1986 (1 ♂ with eggs, 1 damaged specimen).

Distribution.—As its name implies, the species was first collected in the Bermudas in about 33 m. It was later taken as a juvenile in Belize in about the same depth. The above captures of adults confirm the juvenile record from the same place. The depth range for this species is now extended to 16.8–33 m.

Remarks.—The adult male oviger has never been illustrated and a lateral figure of a male is included with oviger attached and an enlarged figure of the terminal oviger segment and a spine (Fig. 1G–H).

Family Phoxichilidiidae
Genus *Anoplodactylus* Wilson, 1878
Anoplodactylus glandulifer Stock

Anoplodactylus glandulifer Stock, 1954: 80–84, fig. 36.—Arnaud, 1973:955.—Stock, 1974:16–17.—Child, 1982b:273–274; 1988a:58–59.—Nakamura & Child, 1988:813.—Müller, 1990:74; 1992:166, figs. 27–30.—Child, 1990:331.—Stock, 1992a:94–95; 1994:18 [list], 59.—Bamber, 1992:193–194.

Anoplodactylus multiclavus Child, 1977: 593–596, fig. 4; 1979:58, fig. 19d; 1982b: 272.—Müller, 1992:166.

Material examined.—Carrie Bow Cay, reef crest rubble, Feb 1978 (1 ♂ with eggs).

Distribution.—This species was thought to have an Indo-Pacific distribution and has been taken in many localities from the Red Sea and Oman to Australia, Hong Kong, and the Marshall Islands in very shallow waters. The second named species, *A. multiclavus,* was thought to be the Atlantic counterpart of Stock's species with a few differences in diagnostic characters. Müller (1992:166) was first to point out that the two are the same. As *A. multiclavus,* this species was collected and described from the U.S. Virgin Islands, and subsequently collected in Panama, Belize, and St. Vincent Island.

Remarks.—There appears to be a consistent difference among various populations of this species in numbers of cribriform cement gland cups; from two to five. This specimen has three on all legs except for the fourth or posterior pair which have four cups each.

Family Rhynchothoracidae
Genus *Rhynchothorax* Costa, 1861
Rhynchothorax mediterraneus? Costa

Rhynchothorax mediterraneus Costa, 1861: 8–9, pl. 1.—Child, 1988a:56 [literature].—Arnaud & Krapp, 1990:4, tab. 1.—Stock, 1992b:135–136; 1994:41.—Miyazaki & Stock, 1995:325–327, figs. 1–2.

Rhynchothorax crenatus Child, 1982a:374–376, fig. 167 [new synonymy].

Material examined.—Carrie Bow Cay, reef front, 15 m, 2 Apr 1980 (1 spec.).

Distribution.—The distribution of this species is extended north from several places in Brazil to Belize. It is also found in North and East Africa, the Mediterranean, Madagascar, Aldabra Atoll, and Papua New Guinea and Indonesia. It is usually found in moderately shallow water form the littoral to 200 m, but Stock (1992b:135) lists one capture depth as 1100 m, which may possibly be an error.

Remarks.—This specimen is only provisionally placed with this species. It could be *R. orientalis* Child (1988b:28–29, fig. 12), from the Philippine Islands. Both species have tall dorsomedian tubercles. The single observable difference between this subadult specimen and *R. orientalis* appears to be in the shape of these dorsal trunk tubercles and the minor difference of no tubercles on the fourth lateral processes, which are present on the Philippines species. The dorsal trunk tubercles have a single anterior-pointing curved tip in this specimen while they have an anterior and posterior double tip on tubercles in *R. orientalis.*

In *R. crenatus* adult specimens, the ocular tubercle assumes a long anterior projection. Also, the adult palp adds a tiny fourth terminal segment, the juvenile loses its dorsomedian proboscis tubercle, and the lateral processes develop small low dorsodistal tubercles. All of these adult characters agree very well with *R. mediterraneus.*

Rhynchothorax philopsammum Hedgpeth

Rhynchothorax philopsammum Hedgpeth, 1951:111–115, pl. 3.—Arnaud & Krapp, 1990:6 [literature].—Müller, 1991:155–157, fig. 6.
Rhynchothorax anophthalmus Arnaud, 1972:405–409, figs. 1–7.
Rhynchothorax vallatus Child, 1990:333–334, fig. 7.

Material examined.—Carrie Bow Cay, reef crest, on *Porites* sp., 1–2 m, 26 Apr 1981 (1 spec.).

Distribution.—This species has recently received two groups of specimens as synonyms which greatly extend its known distribution. It has been collected from the Mediterranean and Azores, California and Mexico, Chile and the Great Barrier Reefs, Australia, and the Society Islands. It is a member of the interstitial fauna, coming from habitats in as much as 15 cm in sand. It has also been recorded from 0–2 m on the substrate surface. This is its first record from the Caribbean.

Remarks.—This is the second species without eyes or an ocular tubercle to be collected from Caribbean waters. The other is, *R. architectus* Child (1979:68–72, figs. 23, 24a–g, 25a–e), a species which has an extremely variable set of dorsomedian tubercles on the trunk and proboscis. What was originally described an ocular tubercle is actually a group of small tubercles in place of an otherwise lacking ocular tubercle.

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Pycnogonida of the western Pacific islands, XII. A recent diving survey of Okinawa, Ryukyu Islands

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Abstract.—Seven known pycnogonid species are reported from the Ryukyu Islands at Okinawa, five of them found here for the first time and one new species. The new species, *Parapallene virgosa,* is described, illustrated, compared with others in its genus and with several species in other genera displaying a few similar characteristics. Previous Okinawan pycnogonid literature is discussed in light of these additional species and distribution of all species is included.

Thirteen pycnogonid species in ten genera were previously known from the Ryukyu Archipelago prior to this report. These thirteen came from the Island of Okinawa itself and the Sakishima Islands Group at the southern end of the Archipelago (Ohshima 1935, Hedgpeth 1949, Nakamura & Child 1988). There have been no pycnogonids reported from other Ryukyu Islands. The small collection of eight species reported below increases this number to eighteen species now known in a total of fifteen genera with the addition of five genera and five species previously unknown in Okinawa. One bizarre attenuated species, *Parapallene virgosa,* is described as new, illustrated, and compared with all similarly attenuated species of this and other genera.

The collection was made over the course of several years by R. F. Bolland with the use of scuba while collecting bottom samples for a faunal survey.

Key to the Families of Pycnogonida (discussed in this report)

1). Chelifores and palps both present or one lacking 2
Both chelifores and palps lacking . . . . Pycnogonidae

2). Palps present, chelifores and chelae present or lacking 3
Palps lacking, chelifores and chelae present . . . . Callipallenidae

3). Chelifores lacking 4
Chelifores present, chelae atrophied or lacking . . . . Ammotheidae

4). Proboscis short, with ventral and lateral swelling, mouth a vertical slit; ocular tubercle short . . . . Rhynchothoracidae
Proboscis long, tubular, with annulations, downcurved, mouth a tube; ocular tubercle long . . . . Austrodecidae

Systematics

Family Ammotheidae Dohrn, 1881

Genus *Achelia* Hodge, 1864

Achelia nana (Loman, 1908)

Ammothea nana Loman, 1908:60–61, pl. 1, figs. 1–13.

Achelia nana.—Child, 1983:699 [literature]; 1988a:50–51.—Stock, 1991:161; 1992:89 [text], fig. 6; 1994:35–36.

Material examined.—Okinawa, 26°30.0′N, 127°50.9′E, sta. RFB 1972, 6.1 m, 27 Aug 1988 (1 female). Same locality, sta. RFB 2001, 67.1 m, 23 Oct 1988 (1 male).

Distribution.—This long-known species has a very wide Indo-West Pacific distribution from Durban, South Africa to Australia and Japan. It has usually been collected in intertidal depths to about 25 m. The second station above is deeper than usual for the species, although there is one record of a capture at 435 m. This species has been taken in the Philippines and on Kyushu, Japan, and would thus be expected to occur on Okinawa.

Genus *Ammothella* (Verrill, 1990)
Ammothella biunguiculata (Dohrn, 1881)

Ammothea bi-unguiculata Dohrn, 1881: 158, pl. 8, figs. 1–3.
Ammothella biunguiculata.—Stock, 1974: 12–13, fig. 1 (early literature).—Nakamura & Child, 1991:6–7 (recent literature).—Munilla, 1993:1993.—Chimenz et al., 1993:340.

Material examined.—Okinawa, 26°30.4′N, 127°52.6′E, sta. RFB 1204, 3 m, 29 Jun 1984 (1 male). Same locality, sta. RFB 1223, 3 m, 18 Jul 1984 (1 female).

Distribution.—This is one of the several common species with a "Tethyan distribution": from Spain and the Mediterranean to Japan and Korea. It has been collected from the intertidal to 45 m. It is new to Okinawan shores.

Genus *Tanystylum* Miers, 1879
Tanystylum rehderi Child, 1970

Tanystylum rehderi Child, 1970:302–306, fig. 5; 1983:705; 1988a:53–54.—Müller, 1989:126, figs. 22–39.—Child, 1991: 142.—Stock, 1994:38–39.

Material examined.—Okinawa, 26°30.0′N, 127°50.9′E, sta. RFB 1210, 0–3 m, 3 Jul 1984 (1 male, 1 female).

Distribution.—There are several scattered localities in the Indo-Pacific where this species has been collected, from Aldabra Atoll to Indonesia, Guam, the Palau Islands, and the Society Islands, its type locality. It has, like most *Tanystylum* species, a shallow-water distribution in 0–18 m.

Remarks.—No *Tanystylum* species has been reported from Okinawa or other Ryukyu Islands until this record. There are only three known species of *Tanystylum,* a predominantly temperate and tropical genus, reported from Japanese islands; *T. scrutator* Stock, *T. grossifemorum* (Hilton), and *T. ulreungum* Kim (synonym: *T. nabetensis* Nakamura & Child). This species is quite different from all three.

The nearest known non-Japanese species comes from the central and northern Philippines, *T. philippinensis* Child (1988b:10–12, fig. 4). This species has a tall, erect abdomen like a post or peg, has no male seventh oviger segment apophysis, and has much more tuberculate legs than *T. rehderi.* It is known from as near the Ryukyus as Guam, but this species has up to now been collected in more southern Indo-Pacific localities.

Family Callipallenidae Hilton, 1942
Genus *Callipallenidae* Flynn, 1929
Callipallene novaezealandiae (Thomson, 1884)

Pallene novae-zealandiae Thomson, 1884: 246–247, pl. 14, figs. 1–4.
Callipallene novaezealandiae.—Child, 1982: 277 [literature]; 1983:708; 1988a:27; 1991: 145.—Nakamura & Child, 1988:664; 1991:38.—Stock, 1994:48.

Material examined.—Okinawa, Tengam Pier, 3 km SSE of Ishikawa City, 26°24.0′N, 127°51.5′E, sta. RFB 1124, 12.2 m, 17 Mar 1984 (1 male). Okinawa, 26°30.4′N, 127°52.6′E, sta. RFB 1205, 51.8 m, 30 Jun 1984 (1 male). Same locality, sta. RFB 1232, 45.7 m, 30 Jul 1984 (1 juvenile). Okinawa, Buckner Bay, 26°17.8′N, 127°51.0′E, sta. RFB 1798, unknown depth, 16 Mar 1987 (1 juvenile).

Distribution.—This long-known species has broad Indo-Pacific distribution which includes Japan, and the Sakishima Islands of the Ryukyus. Its usual depth is littoral although it has been taken in as great as 275 m.

Genus *Parapallene* Carpenter, 1892

Parapallene virgosa, new species

Fig. 1

Material examined.—Okinawa, 26°30.4′N, 127°52.6′E, sta. RFB 1227, 54.9 m, 20 Jul 1984 (1 female, holotype, USNM 234710).

Distribution.—Only known from its type locality.

Description.—Habitus extremely slender, leg span abut 83 mm. Trunk cylindrical, fully segmented, no wider than slender lateral processes. Lateral processes cylindrical, slightly inflated distally, separated by 5–6 times their diameters, each with dorsodistal seta shorter than segment diameter. Neck extremely long, slender, oviger bases at posterior, not touching first lateral processes. Neck crop with chelifore and proboscis attachment very slender. Ocular tubercle at anterior of first lateral processes which are at extreme posterior of first segment. Ocular base broad, containing eyes, anterior pair larger than posterior pair, little pigment. Ocular tubercle apex with bulbous extension as tall as basal part, with sensory papillae at distal sides well above eyes. Proboscis moderately short, slightly upcurved, with distal constriction, armed with few short curved median and distal spines, lips flat, without oral setae field. Abdomen very short, erect, glabrous.

Chelifores very slender, with few robust lateral spines as long or longer than segment diameters. Chelae palms with 3 long, broad, distal spines and several shorter proximal setae. Chelae fingers very long, delicate, without teeth, overlap distally.

Oviger slender, segments four and five subequal, segment six only slightly shorter, with few short lateral and distal setae. Strigilis segments seven–nine each slightly narrower than tenth, armed with two or three short ectal setae and endal denticulate spines in formula 6:7:6:6; straight terminal claw with 12 tiny teeth. Denticulate spines with two or three pairs of lateral teeth.

Legs very slender, long, armed with few setae on tibia, of two sizes, neither longer than segment diameter. Second tibia the longest segments, armed with two or three longer ventral spines with serrate inner edges. Femur longer than short first tibia, neither with serrate ventral spines. Tarsus very short, armed with few tiny ventral setae and one serrate sole spine shorter than terminal serrate spine of second tibia. Propodus moderately short, very slightly curved. Propodal heel with four spines, increasing in size distally, two distal spines with serrations, sole with eight or nine short spines, proximal first and second with hint of serrations. Claw almost half propodal length, moderately curved, auxiliaries slightly more than half main claw length.

Male unknown.

Measurements of female holotype in mm.—Trunk length (chelifore insertion to tip 4th lateral processes), 10.64; 1st segment length, 3.57; posterior 3 segments, 7.07; trunk width (across 2nd lateral processes), 6.1; proboscis length, 1.92; abdomen length, 0.76; third leg, coxa 1, 0.86, coxa 2, 3.82; coxa 3, 1.28; femur, 9.78; tibia 1, 8.88; tibia 2, 11.42; tarsus, 0.28; propodus, 1.39; claw, 0.67.

Etymology.—The species name (Latin: *virgosus,* meaning full of twigs) refers to the twig-like appearance of the trunk and appendages on this extremely slender species. Its habitus is very similar to and brings to mind the extreme slenderness of a walking-stick insect.

Remarks.—The bizarre "stretched" trunk and lateral processes of this species fit uneasily in couplet two of Stock's (1991a:191, 193) key to members of this genus, next to *P. parviunguicularis* Stock. That is a species to which *P. virgosa* is not closely related, since the latter has longer auxiliary claws and a long terminal oviger claw. It has no close relations in this genus and only morphologically resembles species in other genera by coincidence. It most notably resembles *Anoplodactylus tenuicorpus* Child, 1988b, from the Philippines, Guam, and the Seychelles, and *A. exagger-*

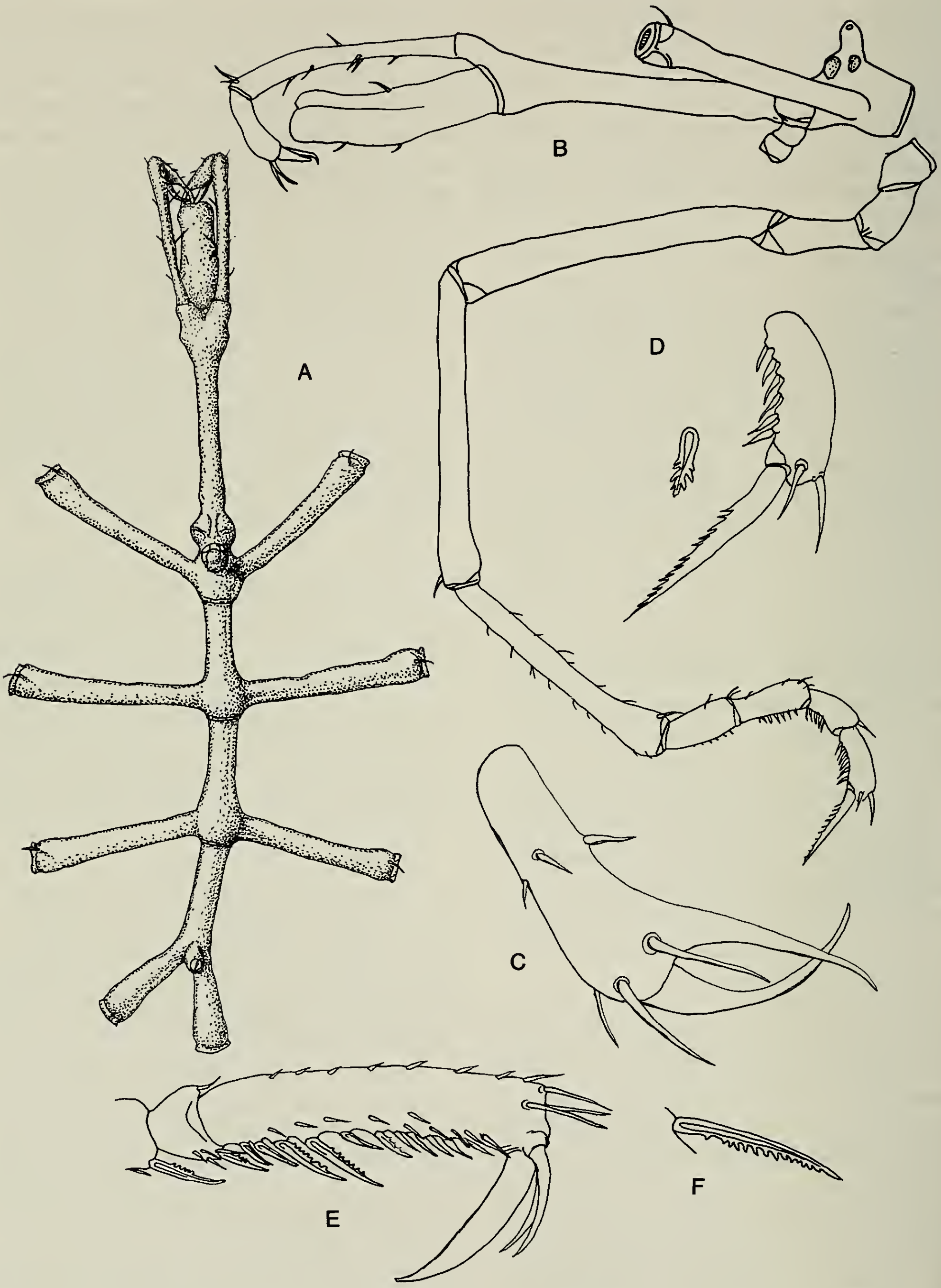

Fig. 1. *Parapallene virgosa,* new species, female holotype: A, Trunk, dorsal view; B, trunk anterior segments, lateral view; C, chela; D, oviger, with terminal segment and denticulate spine, enlarged; E, third leg distal segments, enlarged; F, Second tibia median leg spine, enlarged.

atus Stock, 1994, from Indonesia and Singapore. It should be noted that all three of these slender tenuous species have one or more serrate heel spines. There are other slender species having serrate heel spines, such as *Pseudopallene* sp. (Stock 1994:49) and *Anoplodactylus pectinus* Hedgpeth, 1948. In Hedgpeth's species, the trunk and lateral processes are much less attenuated but the propodus has one or more serrate heel spines as does Stock's *Pseudopallene* sp. It is far from clear whether or not the 2 characters of attenuation and serrate heel spines are in any way related other than by coincidence. Four otherwise unrelated species sharing these characters seems to be too much of a coincidence.

Almost all 18 species of this genus, except for two in Bermuda, Florida and the Caribbean, have been described from Indo-West Pacific localities, principally from southern Africa to Australia, New Zealand and the East Indies. This is the second species to be collected (the first being *P. nierstraszi* Loman) at what is apparently the northern extremes for this genus. Its capture strengthens the idea of a post-Tethyan north-south corridor brought about by northerly currents which continued to flow as circumtropical currents after the closure of the Tethys Sea.

Family Austrodecidae Stock, 1954
Genus *Austrodecus* Hodgson, 1907
Austrodecus tubiferum Stock, 1954

Austrodecus gordonae Stock, 1954:153 (part), fig. 76e.

Austrodecus tubiferum Stock, 1957:75–77, fig. 43.—Nakamura & Child, 1988:669; 1991:35.—Child, 1994:51 (list), 53 (text).—Stock, 1994:43–44, fig. 14b.

Material examined.—Okinawa, 26°30.4′N, 127°52.6′E, sta. RFB 1212, 6.1 m, 4 Jul 1984 (1 spec.).

Distribution.—This species was known only from Japan and Okinawa, in sublittoral depths (37–184 m), and more recently from Mauritius and Rodriguez Islands in the Indian Ocean. This is the only known species to be collected as far north in the Pacific as Japan. Almost all of its congeners are known only from further south and Antarctic localities.

Remarks.—There is only one species of this tiny genus known in northwest Pacific waters, making it quite easy to identify.

Family Rhynchothoracidae Thompson, 1909
Genus *Rhynchothorax* Costa, 1861
Rhynchothorax orientalis Child, 1988

Rhynchothorax orientalis Child, 1988b:28–29, fig. 12.—Stock, 1991:227.

Material examined.—Okinawa, 26°30.4′N, 127°52.6′E, sta. RFB 1222, 42.7 m, 18 Jul 1984 (1 male).

Distribution.—Known previously only from two Philippine localities; the type was captured in 1–3 m, and the second was found in 92–97 m. Its distribution is herein extended to Okinawa and to the intermediate depth of 43 m.

Remarks.—The bifurcate tubercles of the trunk and ocular tubercles and the tubercles of the first coxae are all slightly larger than those of the type which is apparently a female. This could be expected in a male. The anterior ocular tubercle extension or projection is apparently a common character in several *Rhynchothorax* species. This character is shared with *R. mediterraneus* Costa, and *R. percivali* Clark. The shorter posterior and longer anterior legs are an even more common phenomenon among species of this genus.

Family Pycnogonidae Wilson, 1878
Genus *Pycnogonum* Brünnich, 1764
Pycnogonum benokianum Ohshima, 1935

Pycnogonum benokianum Ohshima, 1935:137–139.—Ohshima & Kishida, 1947:1010, fig. 2866.—Hedgpeth, 1949:304–307, fig. 49.—Utinomi, 1971:327.—Nakamura & Child, 1988:662 [text].

Material examined.—Okinawa, 26°30.

0′N, 127°50.9′E, sta. RFB 1973, 3 m, 27 Aug 1988 (1 male).

Distribution.—This is the second known record for this species and it is known only from Okinawa. Hedgpeth (1949) redescribed and illustrated the types while subsequent records only repeated the type information.

Remarks.—This male reveals almost no variation from Hedgpeth's (1949:305, fig. 49) figures of the male type. The ovigers of this specimen are slightly shorter but that may be due to the angle at which the type's oviger was drawn. The trunk tubercles are slightly less conspicuous and lower than those of the type, but the proboscis is barrel-shaped like that of the type figured by Hedgpeth.

Acknowledgments

I wish to extend my gratitude to the collector, R. F. Bolland, for depositing his collections with the National Museum of Natural History and to the personnel of the Smithsonian Oceanographic Sorting Center for sorting the pycnogonids for my examination.

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Pycnogonida of the western Pacific islands, XIII. Collections from Indonesia, Melanesia, and Micronesia

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Abstract.—Twenty nine species are reported in collections from Java and Sunda Strait in Indonesia, Papua New Guinea and Fiji in Melanesia, and from three island groups in the Caroline Islands, Micronesia. Current distribution for each species is given along with remarks on the specimens where pertinent. Three new species are described: *Achelia bullosa, Tanystylum papuensis,* and *Anoplodactylus brochus.* Each new species is illustrated and compared with congeners.

This report on the little known pycnogonids of western Pacific islands contains specimens from several collecting efforts made on the shores of Indonesia in the Sunda Straits and Java, in Melanesia at Papua New Guinea (PNG), and the Fiji Islands, and from Yap, Chuuk (Truk), and Pohnpei (Ponape) Islands of the Carolines in Micronesia. Collections of marine specimens of any kind from these localities are scarce because many of the best collecting areas in these islands and many of the islands themselves are difficult to reach. Collections are often more difficult to make and assemble because of lack of transport to and within the islands. Because of their often rough terrain or widely scattered localities, some of these collecting sites can only be approached by boat which contributes to the difficulties of collecting.

These small collections include 29 species, most known from surrounding localities, some known from within the island groups themselves, and 3 new species. The new species are: *Achelia bullosa, Tanystylum papuensis,* and *Anoplodactylus brochus,* all from the shores of Papua New Guinea. Distributions are given for all species and the new species are described, illustrated, and compared with others having similar characters.

There are no reports which treat exclusively shallow-water pycnogonids of any of these islands groups. There are a few short reports which include one or a few species from these islands and several monographs treating deep-sea species from surrounding waters. A few reports include some pycnogonid fauna of New Guinea but only as part of a broader geographic context, an expedition's results, or a set of discrete collections presented together as a geographic unit. These are Stock (1968) on the collections of the International Indian Ocean Expeditions, Stock's (1961) single new species report, and his (Stock 1994) recent paper on the geographic area treated in part by this report. Others include the benchmark monograph by Loman (1908) on the Siboga Expedition collections of Indonesia, and the species from the nearby Torres Straits enumerated by Carpenter (1892, 1893). Müller (1990b) greatly expanded our knowledge of Fijiian pycnogonida and his (1992a) Malaysian report contributed to knowledge of the fauna in that little known region. These vast island groups are otherwise rarely mentioned in other pycnogonid literature.

Systematics

Family Ammotheidae Dohrn, 1881
Genus *Achelia* Hodge, 1864
Achelia assimilis (Haswell, 1885)

Ammothea assimilis Haswell, 1885:1026–1027, pl. LIV, figs. 5–9.

Achelia assimilis.—Child, 1988b:2; 1990: 312–313; 1991:138.–Stock, 1994:32–33 [literature].

Material examined.—Indonesia: Sunda Strait, W Java, Pulau Sebuko 05°53′S, 105°31′E, on shallow algae, coll. Taylor, 19 Oct 1938 (1 ♂, 1 ♀ ovig., 2 ♀, 1 Juv.).

Papua New Guinea (PNG): Bismarck Sea: Madang, NW margin of Paddock Reef, rubble in 3 m, coll. Thomas & Clark, 14 Jan 1989 (1 ♀). Same locality, landward side of Yazi Reef, rubble in 1 m, coll. Thomas & Clark, 15 Jan 1989 (1 ♂).

Fiji: SW Viti Levu Island, rubble and calcareous algae off Votualailai Village beach in 1 m, coll. Child, 28 Jul 1978 (1 ♀).

Distribution.—This extremely variable species is found at an increasing number of localities according to recent literature. It has been collected in shallow habitats from the Australian Great Barrier Reef to as far north as the Philippine Islands. Most captures have been in the southwest Pacific Ocean and the southern tip of South America.

Achelia bullosa, new species
Fig. 1

Material examined.—PNG, Bismark Sea: Madang, patch reef between Gosem Island and Jais Aben Resort, broken coral in 1 m, coll. Thomas & Clark, 13 Jan 1989 (1 ♂ with eggs, holotype, USNM 234711, 1 ♀, paratype, USNM 234712).

Description.—Size tiny, leg span 5.25 mm. Trunk extremely compact, almost circular in dorsal outline, integument papillose over most surfaces, anterior two segmentation lines complete, posterior line missing, several other suture lines conspicuous on cephalic segment. Lateral processes contiguous over their lengths, armed with anterodistal and posterodistal tubercles consisting of low papillose mounds, broader than their height and armed with tiny distal seta each. Trunk anterior corners each with similar low setose mound. Ocular tubercle slightly broader at base than tall, conspicuously papillose, eyes small, anterior pair slightly larger than posterior pair, all darkly pigmented. Abdomen moderately short, extending only to half length of first coxae of fourth leg pair, carried horizontally with slight dorsal curve distally, armed with few short distal setae.

Proboscis moderately short, a swollen truncate cone half length of trunk, oral surface flat, lips moderately large, not protruding.

Chelifores slender, only about three times longer than maximum diameters. Scape with large dorsodistal mound tubercle equal to width of segment, armed with four–five distal setae. Chela tiny, bulbous, without trace of fingers but with distal cleft, armed with single distal seta.

Palps eight-segmented, short, only slightly longer than proboscis, massive and tuberculate. First segment extremely broad, wider than twice its length. Second segment only as long as its width, armed with dorsolateral ectal tubercle bearing distal seta. Third segment almost twice as broad as its length, armed with similar tubercle as that of second segment but larger, armed with two distal setae. Fourth segment longest, twice its diameter, armed with low laterodistal tubercle bearing two distal setae. Terminal four segments each increasingly smaller and narrower, each armed with few short ventrodistal and laterodistal setae.

Ovigers typical of genus, fourth and fifth segments subequal, armed with few short ectal setae. Strigilis sixth segment with several recurved spines and two–three setae, seventh and eighth segments with two ectal setae and two endal denticulate spines each, ninth and tenth segments without setae but with two denticulate spines each. Denticu-

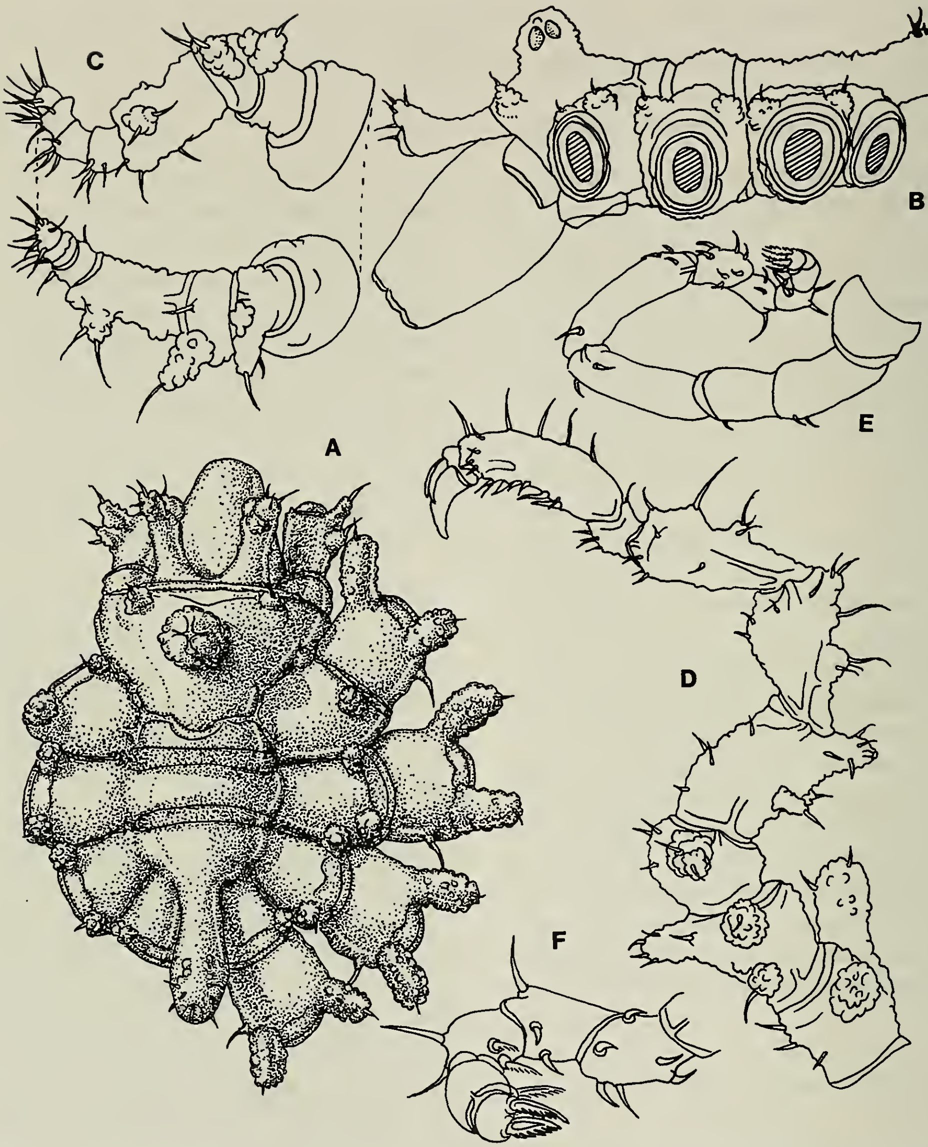

Fig. 1. *Achelia bullosa,* new species. A, trunk, dorsal view; B, trunk, lateral view; C, palp, lateral view above, dorsal view below; D, third leg; E, oviger; F, oviger tip, enlarged.

late spines with eight–nine serrations per side.

Leg segments very short, tuberculate, moderately setose. First coxae the longest segments (measured to tubercle tips) bearing pair of large laterodistal tubercles almost as long as segment diameter, conspicuously papillose, armed with one–two distal setae each. Second coxae with paired short lateral tubercles bearing single short setae and single ventrodistal tubercle not as long as segment diameter, bearing sex pore on third and fourth legs, armed with several short setae. Third coxae shorter, with single laterodistal tubercles bearing 2–3 short distal setae. Femora the longest major segments, with slender mediolateral tubercles half as long as segment diameter, armed with single short seta each, and larger dorsodistal tubercle bearing several short setae and tip of cement gland tube. Tibiae of almost equal length, each bearing two dorsal bumps with one–three moderately long setae, also armed with few laterodistal and ventrodistal short setae. Tarsus short, with one ectal and four–five endal setae. Propodus inflated, moderately curved, armed with two moderately long heel spines plus a single distal spine and several sole setae, five–six dorsal setae and several short distal setae. Claw moderately short, robust, auxiliaries 0.6 as long as main claw.

Female: slightly larger in all measurements than the male except for smaller oviger. Oviger bearing single denticulate spines on all except terminal segment which bears two. Leg and lateral process tubercles slightly smaller than those of male. Sex pores on all second coxae.

Measurements of holotype in mm.—Trunk length (chelifore insertion to tip 4th lateral processes), 0.84; trunk width (across 2nd lateral processes), 0.72; proboscis length, 0.42; abdomen length, 0.27; 3rd leg (to tubercle tips), coxa 1, 0.37; coxa 2, 0.3; coxa 3, 0.19; femur, 0.32; tibia 1, 0.29; tibia 2, 0.3; tarsus, 0.08; propodus, 0.31; claw, 0.12.

Distribution.—Known only from the type-locality, a patch reef off Gosem Island, Madang, Papua New Guinea, in 1 m.

Etymology.—The name given to this species (Latin: *bulla*; a knob, boss, or bubble, with the suffix *osa*; very) refers to the extremely tuberculate and knobby morphology of these specimens.

Remarks.—No other known species of *Achelia* has the blunt lateral tuberculation of this species, particularly those of the palps which are unique in their placement. There are several species which have the short major leg segments of this species and tuberculation which is similar to this, but none have the multiple lateral tubercles of the palps found in this species. A species such as *A. shepherdi* Stock, 1973, fits the description of one of the several species above. Its tuberculation is somewhat similar to that of this species, but its palps have no lateral tubercles and its proboscis is barrel-shaped and much larger than that of *A. bullosa.*

Achelia deodata Müller, 1990

Achelia deodata Müller, 1990b:103–105, figs. 1–6.—Stock, 1994:33.

Material examined.—Caroline Islands: Pohnpei (Ponape) Island, E side near Mant Passage, 07°01′N, 158°18′E, rubble with algae in 0–1 m, coll. Child, Barnard & Child, Jr., 5 Jul 1986 (1 ♂, 1 Juv.).

Distribution.—This recently described species had been known only from the western Indian Ocean in 0–8 m. The two above specimens greatly extend its range into the Pacific for the first time.

Remarks.—These specimens are more like Müller's species than any other Indo-Pacific species in this confusingly variable group. The tubercles of its lateral processes and appendages seem to be the key toward differentiating several of these closely related species. Those of this male are closest to Müller's type figures and description, with a low to tiny tubercle on each lateral process and larger dorsolateral tubercles on the first coxae. The tubercles of this male are placed in the same lateral position but are narrower and longer than those of the type. The legs of this male are slightly longer and appear narrower than those of Müller's type but the femoral cement gland is exactly the same in this male and the type male.

Genus *Ammothella* Verrill, 1900

Ammothella alcalai Child, 1988

Ammothella alcalai Child, 1988a:2–4, fig. 1.—Stock, 1994:26–27.

Material examined.—PNG: Madang, Paddock Reef near Gosem Island, sponge, rubble and algae in 3 m, coll. Thomas & Clark, 8 Jan 1989 (1 Juv). Madang, Paddock Reef, second reef past Gosem, sponges, ascidians and rubble in 2 m, coll. Thomas & Clark, 9 Jan 1989 (1 ♀).

Distribution.—This species was recently described from localities in the southern Philippines, in 0–3 meters. It has been taken more recently in Indonesia in 0.5 m. It is new to Papua New Guinea.

Remarks.—Juveniles of several genera, in this family where many species bear dorsal tubercles, have generally larger tubercles than adults of the same species. This fact also holds true with this species where the lateral process tubercles are as slender but longer than in the adult. I therefore have little hesitation in assigning the juvenile above to *A. alcalai.* Also, there are no lateral tubercles on the anterior rim of the cephalic segment of the juvenile or the adult while most of the better known species from this vicinity have these rather typical rim tubercles.

Ammothella indica Stock, 1954

Ammothella indica Stock, 1954b:113–119, figs. 54–55, 56c, 57a–57c.—Utinomi, 1971:331 [literature].—Nakamura & Child, 1983: 18–19.—Kim, 1986:5, fig. 3.—Kim & Hong, 1986:48.—Nakamura, 1987:26–27, pls. 22–23.—Hong & Kim, 1987:143–144.—Child, 1988a:5; 1988b: 51.—Nakamura & Child, 1991:7.—Müller, 1992a:156.—Stock, 1994:27.

Material examined.—Indonesia: Java, Pulau Kelor, 06°02′S, 108°45′E, algae on rubble, coll. Taylor, 26 Sep 1938 (1 ♂, 1 ♀, 1 juv.). Java, Kepulauan Seribu, 05°36′S, 106°33′E, rubble and algae, coll. Taylor, 5 Oct 1938 (1 Juv.). Java, W end. Ujung Kulon, Menandjung Peninsula, 06°45′S, 105°20′E, algae, coll. Taylor, 18 Oct 1938 (1 ♂).

Distribution.—This is a moderately common Indo-West Pacific species collected in 0–30 m. It was previously known from near the above localities of Java in the Sunda Strait.

Ammothella stauromata Child, 1982

Ammothella stauromata Child, 1982b:271–273, fig. 1; 1988a:5, 7.—Nakamura & Child, 1988b: 809–810.—Müller, 1989: 125; 1990a:66; 1990b:106.—Child, 1990:316.—Stock, 1994:29.

Material examined.—PNG: Madang, reef slope below seawall next to ship channel at Madang Hotel, rubble and calcareous algae in 1–1.5 m, coll. Child, 30 Jul 1980 (1 Juv, 1 larva).

Distribution.—As more collecting records are reported from the western Pacific, this species is found to have a wide distribution which increases as the fauna of many far flung localities are reported. The species has been taken from the Great Barrier Reef of Australia, the Philippines, Samoa, Society Islands, Fiji Islands, and the Marshall Islands. It has never been reported from depths below 6 m. This record marks its first capture in Papua New Guinea.

Remarks.—There is only one other species known in the western Pacific, *Ammothella thetidis* Clark (1963), which has dorsomedian trunk tubercles, and it has many characters which differ from this species. These differences were previously discussed by Child (1990:316).

Ammothella species indeterminate

Material examined.—Indonesia: Bali, Sanur Beach, near Cape Serangan, 08°42.3′S, 115°15.8′E, 0.3 m, coll. Barnard, 12 Jul 1976 (1 juv.).

PNG: Madang, Hansa Bay, Laing Island, coral rubble, lagoon reef in 1.0–1.5 m, coll. Child, 31 Jul 1980 (1 juv.).

Genus *Ascorhynchus* Sars, 1877

Ascorhynchus melwardi Flynn, 1929

Ascorhynchus melwardi Flynn, 1929:252–256, figs. 1–3.—Stock, 1953b:304 [key]; 1954b:128–132, figs. 64–65; 1968:8.

Material examined.—Indonesia: Arafura Sea, Aru Archipelago, W of Wasir Island, sand & rubble in 33–40 m, coll. Western Australian Museum, 15 May 1970 (1 ♀).

Distribution.—This shallow water species is restricted to an area from Singapore and the Greater Sunda Islands to Cape York in Northern Queensland, Australia, from intertidal depths to 40 m. There have been relatively few specimens collected anywhere.

Ascorhynchus minutum Hoek, 1881

Ascorhynchus minutum Hoek, 1881:55–57, pl. VI, figs. 10–16.—Loman, 1908:33.—Stock, 1953b:305 [key]; 1954b:121–124, figs. 57d–57h.—Clark, 1963:61.—Child, 1975:26.

Ascorhynchus auchenicus.—Calman, 1922: 199–203 (part).

Material examined.—Indonesia: Banda Sea, Haruku Island, E of Ambon, sand and rubble, 03°36′S, 128°24′E, 144–157 m, coll. Western Australian Museum, 30 May 1970 (1 chelate juvenile).

Distribution.—This is another fairly rare species. It has been taken in New South Wales and Queensland along with Western Australia, and previously in the Banda Sea in 4–157 m.

Remarks.—This juvenile agrees with figures of the type specimen except in the following characters. Tubercles are lacking middorsally as could be expected in a juvenile, and a bulge replaces the tubercle on the second coxae. The lateral process and first coxae tubercles are as long as their segment diameters and the abdomen is slightly longer, extending to the tip of the fourth coxae. These differences are attributable to this being a juvenile specimen.

Ascorhynchus ramipes (Böhm, 1879)

Gnamptorhynchus ramipes Böhm, 1879b: 56–59.

Ascorhynchus ramipes.—Utinomi, 1971: 332–333 [literature].—Nakamura & Child, 1983:29.—Kim, 1986:7, fig. 4.—Kim & Hong, 1986:50.—Nakamura, 1987:31–32, pl. 28.—Hong & Kim, 1987:146.—Nakamura & Child, 1991:8.—Miyazaki & Hirose, 1993:18–21.

Ascorhynchus latus Calman, 1923:270, figs. 2–3.—Stock, 1953b:304–305 [key].

Ascorhynchus latum.—Stock, 1954b:128, figs. 63a–63c.—Müller, 1990b:106.

Material examined.—Indonesia: E Java, N of Bantenan Peninsula, W of Bali, 08°34′S, 114°36′E, depth unrecorded, coll. U.N.F.A.O. survey, 27 Jun 1971 (1 ♂, 1 ♀). (Hydrographic chart depths at these coordinates are about 165–183 m).

Distribution.—Specimens of this species have been found predominantly at Kyushu and Honshu, Japan, and Korea, but they have also been taken in the Gulf of Thailand and the Gulf of Manaar between India and Sri Lanka. It has the rather wide but shallow depth range of 3–200 m.

Remarks.—These specimens are remarkable for their size and on first superficial examination, were almost identified as a new species. These two are much longer (3–4 times) than the usual *A. ramipes* and it is possible that they could be a new species except that almost all characters agree with those of *A. ramipes.* The male leg span is 91 mm and the female's almost 100 mm, and they can be compared with either *A. ramipes* or *A. auchenicum* in a number of characters.

The conspicuous lateral process and first coxae tubercles differ from either of the two species: they are proportionally larger in diameter, more robust, and those of the first coxae are curved in a distal direction. The trunk and coxae tubercles are much more reduced in proportion to specimen size in northern Pacific specimens. The ocular tubercle is also much taller than the typical *A. ramipes,* and there are many more cement gland pores per leg. The femora have 18–24 dorsolateral pores and the first tibiae, usually without a cement gland, have 9–11 pores over a proximal gland. In general, the diagnostic characters used to describe *A. ramipes* are all present in these specimens, but it appears as though geographic separation is placing this population of a common species in position to become a much larger new species in the future.

These specimens have some similarities to *A. auchenicum* (Slater), an endemic Japanese species. They are at least 3 times larger than any specimen of *A. auchenicum* whose size is given in literature or that I have examined. But, the lateral process and first coxae tubercles are more like those of *A. auchenicum* than those of *A. ramipes.* Many other characters of these two specimens such as abdomen and chelifore length, placement of ocular tubercle in relation to oviger bases, and lack of a dorsal tubercle on the second coxae are more like *A. ramipes.* The greatest difference is in the distal segments of the first pair of legs which are quite different from those of *A. auchenicum.* There is no claw on the first leg pair in *A. ramipes* and in these specimens, and the tarsus is much longer than those of the posterior six legs. There is no explanation for the giant size of these specimens except that the two suggest a possible new species or at least a subspecies in the making.

Genus *Eurycyde* Schiödte, 1857
Eurycyde setosa Child, 1988

Eurycyde setosa Child, 1988a:8–10, fig. 3; 1990:316–317.—Müller, 1992a:156, figs. 1–5.—Stock, 1994:21.

Material examined.—PNG: Madang, Paddock Reef, rubble in 3 m, coll. Thomas & Clark, 10 Jan 1989 (1 ♂). Madang, patch reef between Gosem Island and Jais Aben Resort, broken coral rubble in 1 m, coll. Thomas & Clark, 13 Jan 1989 (1 ♂).

Distribution.—This is another species with a growing distributional knowledge from the literature. It was described from shallows of the northern Philippines, and has been found on the northern end of the Great Barrier Reef, Australia, the Gulf of Siam, Malaysia, and near Port Moresby on the south side of Papua New Guinea. This record extends it to the north side of PNG in equally shallow water.

Remarks.—These specimens are very close to the type, also a male. They appear to bear fewer setae on the first coxae tubercles than the type specimen but the first coxae tubercles of the male collected on 13 Jan are longer than those of the type and are curved, unlike those of the type. The lateral process tubercles of the 10 Jan specimen are smaller and decrease in size from anterior to posterior but those of the 14 Jan specimen are larger than those of the type and the lateral processes of this specimen are farther apart. These variations appear to be age-related and well within the moderate variation known among species in this closely allied genus. The distinguishing character of this species is that of the setose first coxae tubercles which on most species in this genus bear long spines with setules or, in a few instances, no spines at all.

Genus *Tanystylum* Miers, 1877
Tanystylum bredini Child, 1970

Tanystylum bredini Child, 1970:296–299, fig. 3; 1977:441; 1988b:52.—Müller, 1989:125, figs. 11–21; 1990a:67, figs. 7–15; 1992a:156, 159, figs. 6–11.—Stock, 1992:92–93; 1994:36–37.

Material examined.—Indonesia: W Java, Udjung Kulon, Menang Jung, 06°45′S, 105°20′E, on algae, coll. Taylor, 18 Oct 1938 (1 ♂, 2 ♀, 1 juv.).

Distribution.—Another widely distributed Indo-Pacific species, these tiny specimens have been found in tropical localities from Kenya to the Society Islands in 0–7 m. They have been collected previously in Malaysia and Indonesia.

Tanystylum papuensis, new species
Fig. 2

Material examined.—PNG: Madang, Paddock Reef, 2nd reef past Gosem Island, sponges & rubble in 2 m, coll. Thomas & Clark, 9 Jan 1989 (1 ♂ with eggs, holotype,

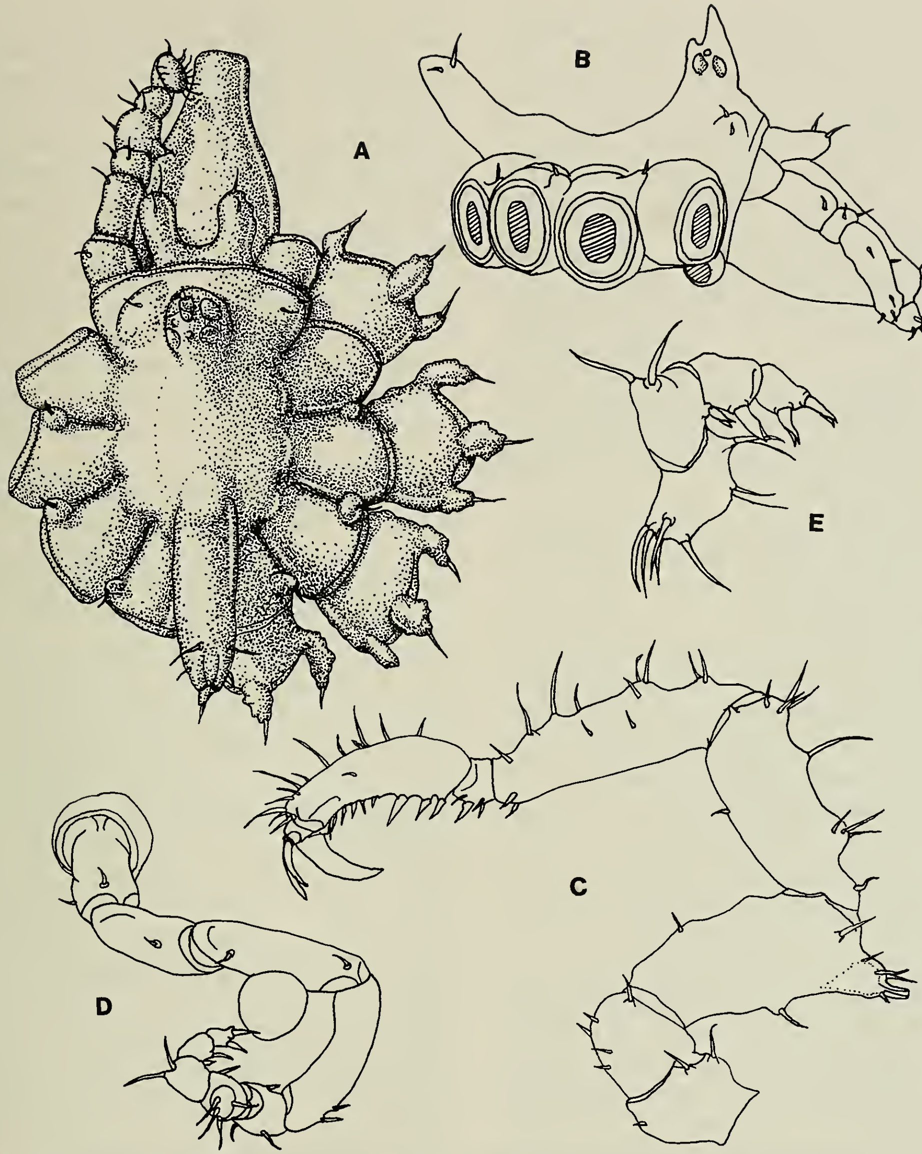

Fig. 2. *Tanystylum papuensis,* new species. A, trunk, dorsal view; B, trunk, lateral view; C, third leg; D, oviger; E, oviger tip, enlarged.

USNM 234714, 2 juv., paratypes, USNM 234715). Madang, Paddock Reef, 40 m off Gosem Island, rubble in 3 m, coll. Thomas & Clark, 7 Jan 1989 (1 ♀, paratype, USNM 234716). Madang, patch reef between Gosem Island and Jais Aben Resort, coral rubble in 1 m, coll. Thomas & Clark, 13 Jan 1989 (1 ♂ with eggs, 1 ♀, 1 Juv, paratypes, USNM 234717).

Other material.—PNG: Madang, Yazi Reef, rubble from landward side in 1 m, coll. Thomas & Clark, 15 Jan 1989 (2 ♂ with eggs, 1 ♀).

Distribution.—Known only from the vicinity of Madang, PNG.

Description.—Size typical or slightly smaller than average; leg span about 7 mm. Trunk circular, unsegmented, glabrous, lateral processes contiguous, armed with short anterodistal tubercle on posterior six legs, each with tiny seta, tubercle missing on first pair. Cephalic segment extending only slightly beyond circular trunk, armed laterally with one–two short setae on swellings. Ocular tubercle on elevated mound, about as tall as wide, eyes small, darkly pigmented, with tall anterior and short posterior apical cones. Proboscis moderately short, inflated in proximal third in lateral view, tapering distally to cylindrical mouth area. Abdomen extending obliquely from basal mound or hump, armed with two pairs of distal setae, the more dorsal pair longer than lateral pair.

Chelifores inflated cylinders, moderately slender, about three times longer than median diameters, armed with two distal setae. Chelae entirely lacking.

Palp of six segments. First and third wider than their length, second only twice as long as diameter, fourth three times longer, second through fourth armed with two–three lateral setae, fourth with fringe of ventrodistal setae. Fifth as long as wide, sixth about three times longer than its diameter, both armed lightly with ventral setae. First to fifth segments combined only as long as proboscis.

Ovigers with lateral seventh segment apophysis armed with four long setae. Second through sixth segments armed with four–five randomly placed short setae. Strigilis seventh with recurved endal spine, eighth with two ectal setae and one endal distally bifurcate spine, ninth with similar bifurcate spine, and tenth tiny segment with two similar spines.

Legs typical, robust, with dorsal setose swellings on main segments. Femoral cement gland in broad dorsodistal tubercle with short tube at tip. Femur with tiny middorsal tubercle bearing seta. Femur and first tibia subequal, second tibia slightly longer. Tarsus very short, with one sole spine and few setae. Propodus moderately curved, broader proximally, tapering distally, with three major heel spines, the largest spine distally, 5–6 short sole spines, and few short and long setae dorsally. Claw robust, well curved, with stout auxiliaries measuring about 0.6 length of main claw.

Female characters: oviger of ten segments, much smaller than that of male, strigilis spines plain. First coxae tubercles smaller, posterior tubercle only a bump.

Measurements of male holotype in mm.—Trunk length, 0.84; trunk width, 0.82; proboscis length, 0.51; abdomen length, 0.29; third leg, coxa 1, 0.21; coxa 2, 0.25; coxa 3, 0.21; femur, 0.56; tibia 1, 0.57; tibia 2, 0.6; tarsus, 0.1; propodus, 0.45; claw, 0.19.

Etymology.—The name refers to the collecting locality for this new species.

Remarks.—This species resembles a species from the Caribbean, *T. isthmiacum* Stock (1955), and a Pacific Species *T. oculospinosum* Hilton, 1942. With *T. isthmiacum,* it shares a male seventh oviger segment apophysis, the tall ocular tubercle apex and tall abdomen, and the strong tarsal spine. It differs by having six palp segments rather than five, oviger spines without denticulations, taller first coxal tubercles, and smaller lateral process tubercles. The new species differs more from *T. oculospinosum. T. papuensis* has a broader proboscis, particularly the distal part, which in *T. oculospinosum* is quite narrow, giving its proboscis a conical shape. The chelifore scapes and first coxae tubercles are much longer in *T. papuensis,* the legs have longer and fewer setae, the propodus is longer and less robust, and the terminal palp segment is longer in relation to its penultimate segment.

Family Austrodecidae Stock, 1954
Genus *Austrodecus* Hodgson, 1907
Austrodecus stocki Child, 1988

Austrodecus stocki Child, 1988b:54–55, fig. 1.—Stock, 1994:42–43, fig. 15.

Material examined.—PNG, Bismark Sea, Madang, reef slope below seawall on deep ship channel, in rubble and calcareous algae in 1–2 m, coll. Child, 30 Jul 1980 (1 subadult ♀).

Distribution.—The female holotype was collected on Aldabra Atoll, Indian Ocean. Stock listed another female from the Mozambique Channel in 62 m. This is the third known specimen and the first collected from southwestern Pacific waters. This species is widely distributed but apparently rare or elusive.

Remarks.—The male characters of this species remain unknown.

Family Rhynchothoracidae, Thompson, 1909

Genus *Rhynchothorax* Costa, 1864

Rhynchothorax orientalis Child, 1988

Rhynchothorax orientalis Child, 1988a:28–29, fig. 12.—Stock, 1991:227.

Material examined.—PNG: Madang, Kranket Island, seaward reef crest, rubble in 4 m, coll. Thomas & Clark, 11 Jan 1989 (1 chelate juvenile).

Distribution.—This species was only known from two places in the Philippines in 1–3 m ad 92–97 m. Its distribution is herein extended to Papua New Guinea, and to 4 m.

Remarks.—This specimen has the three-segmented slender chelifores typical of other species in the juvenile stage. The chelae are tiny scissor-shaped appendages and are apparently not functional. The bifurcate dorsomedian trunk tubercles of the adult are found here in the juvenile, but the anterior tubercle of the ocular segment is not nearly so long. This is probably typical of juveniles. The specimen otherwise agrees well with the type.

Family Phoxichilidiidae, Sars, 1891

Genus *Anoplodactylus* Wilson, 1878

Anoplodactylus batangensis (Helfer, 1938)

Pycnosoma batangense Helfer, 1938:174–176, fig. 6a–c.

Anoplodactylus batangensis.—Stock, 1968: 54 [older literature].—Child, 1992:41–42 [recent literature], fig. 18.—Müller, 1992b:47.—Stock, 1994:54.

Material examined.—PNG: Bootless Inlet, near Port Moresby, Manunouha (Lion) Island reef, rubble with algae in 1–2 m, coll. Child, 26 Jul 1980 (2 ♀).

Distribution.—This easily recognized species has a pantropical distribution in shallow depths. It has been found in Indonesia and eastern Australia and could be expected in PNG.

Remarks.—The extreme taper and upcurve of this species' proboscis help to differentiate it from any other member of this unwieldy genus of more than 120 species.

Anoplodactylus brochus, new species

Fig. 3

Material examined.—PNG: Madang, Paddock Reef, rubble from NW margin in 3 m, coll. Thomas & Clark, 14 Jan 1989 (1 ♂ with eggs, holotype, USNM 234713, 3 ♂ with eggs, paratypes, USNM 234714).

Distribution.—Known only from the type locality, Madang, Papua New Guinea, in 3 m.

Description.—Extremely tiny species, leg span only 3.8 mm. Trunk unsegmented, lateral processes separated by as much as their diameters distally, 1.5 times as long as their diameters, each armed with small low dorosdistal tubercle bearing seta on anterior 6 processes, lacking seta on posterior pair. Palp buds conspicuous broad tubercles in dorsal view. Neck well elevated above proboscis, bearing tall ocular tubercle at extreme anterior. Eyes large, forming distal bulge in ocular tubercle, with low rounded apical tubercle distally. Proboscis cylindrical, slightly constricted at median circumference and upcurved just distal to base, lips rounded. Abdomen moderately tall, erect, straight, with 4 tiny distal setae.

Chelifore scapes slender, not as long as proboscis, slightly downcurved distally, armed with single lateral seta and single dorsodistal seta. Chelae small, overhang proboscis. Palm almost cylindrical, only slightly in-

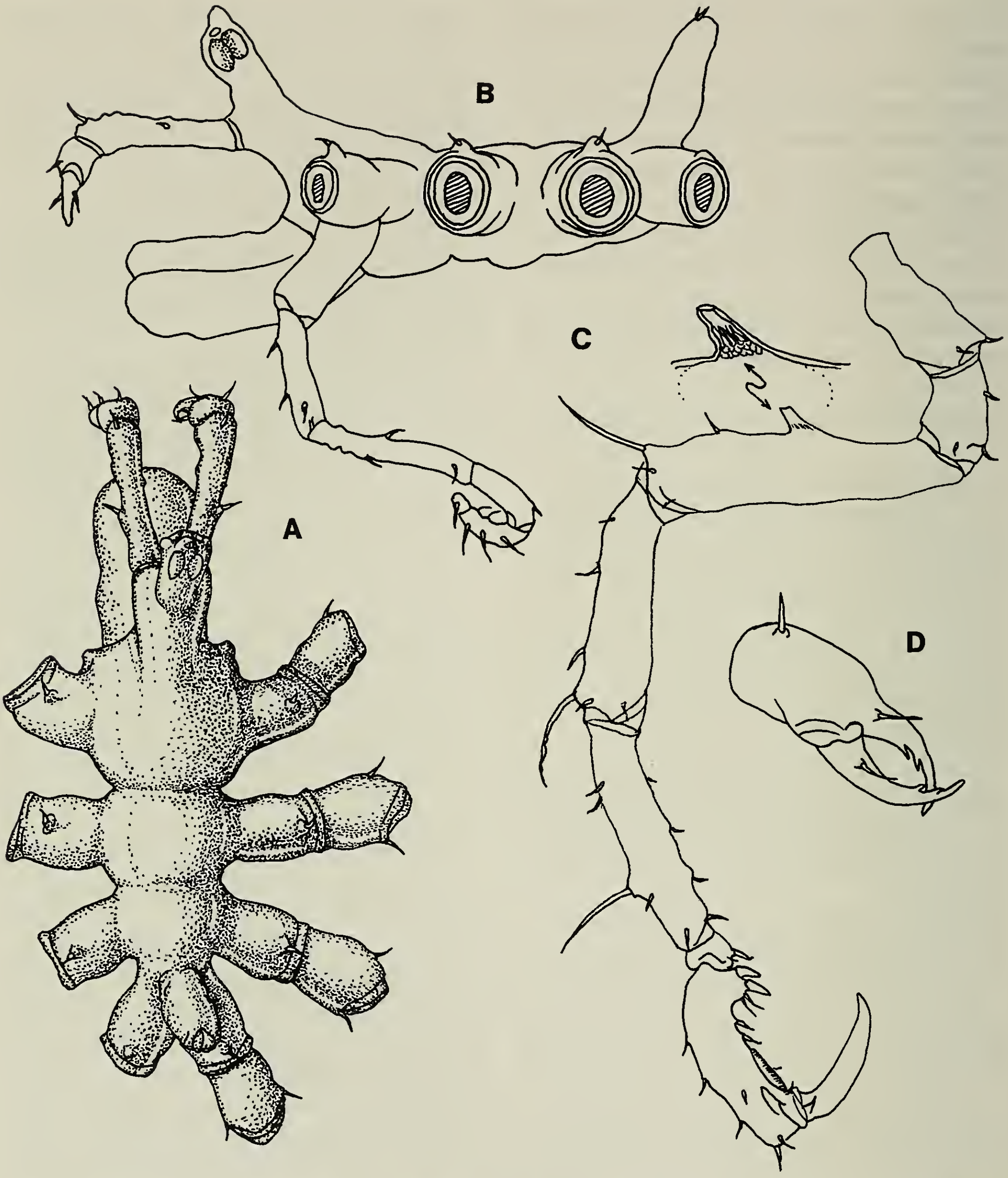

Fig. 3. *Anoplodactylus brochus,* new species. A, trunk, dorsal view; B, trunk, lateral view; C, third leg with enlargement of cement gland tube; D, chela, enlarged.

flated, armed with 2–3 short setae, 1 at base of immovable finger, 1 laterally on movable finger. Fingers only as long as palms, well curved with distal overlap, armed with 2 tiny slender teeth pointed distally.

Ovigers moderately short, first segment long, as long as second. Third the longest, but little longer than second. Second through fourth segments armed with few short lateral setae not in rows. Fifth segment with 3 longer lateral seta on each side. Sixth segment a tiny cone with 1–2 short setae. Fourth segment slightly longer than fifth and sixth combined.

Legs moderately short, armed with few setae and long dorsodistal spine on each major segment. Femur the longest segment, cement gland outlet placed at midlength dorsally. Outlet a moderately short tapering tube, less than half segment diameter, angled distally. Tibiae subequal, only about 0.75 length of femur. Tarsus very short, propodus with marked heel bearing 2 stout spines and 2 distal setae, sole with 2 curved spines before lamina half sole length. Lamina with tiny lateral setae. Claw robust, well curved, lateral auxiliary claws tiny.

Female characters unknown.

Measurements of holotype in mm.—Trunk length (chelifore insertion to tip 4th lateral processes), 0.56; trunk width (across first lateral processes), 0.34; proboscis length, 0.26; abdomen length, 0.15; third leg, coxa 1, 0.12; coxa 2, 0.18; coxa 3, 0.13; femur, 0.35; tibia 1, 0.27 (0.266); tibia 2, 0.27 (0.268); tarsus, 0.04; propodus, 0.21; claw, 0.15.

Etymology.—The specific name (Latin: *brochus,* meaning projecting) refers to the small lateral process tubercles of this species, an uncommon but not unique character in this genus.

Remarks.—This exceptionally tiny species has no outstanding character with which to separate it from many other plain species in this genus. Very few species are this tiny: *A. minusculus* Clark is comparable but has many basic characters which differ from the specimens in hand such as contiguous lateral processes and an extremely short oviger.

This species is perhaps closest to *A. minutissimus* Stock, 1954. The similarities occur mainly in their trunks which are not segmented. The palp bases are retained and conspicuous in dorsal aspect, an uncommon character in *Anoplodactylus.* The chelifores and ovigers are quite similar and their tiny sizes differ only in small percentages. The differences occur in this species having small setose lateral process tubercles not present in Stock's species, a shorter proboscis in relation to the trunk length, and a cylindrical abdomen rather than a tapering cone. The legs of each offer more character differences. Those of this species are shorter in each segment, the propodal lamina is shorter, the claw is much shorter and more curved, and the tibiae are subequal. The cement gland offers perhaps the greatest comparative difference. In this species, the truncate conical tube arises from a flat or slightly convex dorsal surface while the shorter truncates cone of *A. minutissimus* arises from a definite swelling of the femoral surface. The combination of its conspicuous palp buds, tiny lateral process tubercles, cement gland tube shape and placement, propodus characters, and tiny size render this new species different from all known species in this genus.

Anoplodactylus chamorrus Child, 1983

Anoplodactylus chamorrus Child, 1983: 705–707, fig. 3; 1988b:16; 1990:330–331; 1991:143.—Müller, 1992a:164.—Stock, 1994:55, fig. 22c.

Material examined.—PNG: Bootless Inlet, Manunouha (Lion) Island reef, rubble & algae in 1–2 m, coll. Child, 26 Jul 1980 (1 ♂).

Distribution.—This species was described from Guam and has subsequently been collected in shallow waters of the Philippines, Malaysia, Australia's Great Barrier Reef, and most recently from Papua New Guinea.

Remarks.—The proboscis, as Stock (1994) illustrated, has a definite taper from base to tip. The legs of this specimen are slightly more angular and the major segments a little more curved than those of the type. The specimen is otherwise much like it.

Anoplodactylus digitatus (Böhm, 1879)

Phoxichilidium (*Anoplodactylus*) *digitatum* Böhm, 1879a:184–185, pl. Ii, figs. 2–2b.
Anoplodactylus digitatus.—Stock, 1965: 28–29 [synonymy & literature].—Arnaud, 1973:958; 1988:45.—Müller,

1992a:164–166, figs. 18–26.—Stock, 1992:94; 1994:57.

Anoplodactylus cf. *digitatus*.—Arnaud, 1974:174.

Material examined.—Indonesia: north Sumatra, Lhokseumawe village, fuel dock pilings, 05°10′N, 097°08′E, 0–5 m, coll. D.E. Coleman (California Academy of Sciences), 24 Jan 1975 (3 ♂ with eggs, 1 ♂, 3 ♀, 2 Juv.).

Distribution.—This long-known species has been taken in sufficient localities to qualify it as a pantropical/temperate inhabitant. It is known from the Indo-West Pacific, West Indies, and the Mediterranean Sea in mostly shallow to sublittoral depths although one collection reports it from 600 m which is far deeper than its usual habitats.

Remarks.—Müller (1992a:164–166, figs. 18–26) gave an excellent description and set of illustrations for this species. There is apparently some variation in the size of the ventral proboscis "alar" processes in the female and in the length of the tubercles of the second coxae sexual pores in both sexes. This is otherwise a morphologically very stable species.

Anoplodactylus pectinus Hedgpeth, 1948

Anoplodactylus pectinus Hedgpeth, 1948: 234–236, fig. 34; 1954:427.—Stock, 1955:235, fig. 11; 1974:17.—Arnaud, 1973:955–957.—Child, 1974:500; 1979: 58; 1982a:372–373; 1988a:20.—Stock, 1979:15; 1994:64.—Nakamura & Child, 1988a:662–663.

Anoplodactylus pectinis [sic].—Stock, 1975:1050–1052, fig. 41a.

Material examined.—Indonesia: Java, Pulau Kelor, 06°02′S, 108°45′E, coll. Taylor, 26 Sep 1938 (1 spec.). Sumatra, Sunda Strait, Cape Tjina, 05°56′S, 104°45′E, coll. Taylor, 6 Oct 1938 (1 ♂, 1 ♀ juv). Java, SW end, Pulau Deli, algae and sponges, 07°00′S, 105°32′E, coll. Taylor, 5 Oct 1938 (1 ♂, 5 ♀). W Java, Sunda Strait, Tjikoneng, 06°04′S, 105°52′E, algae, coll. Taylor, 16 Oct 1938 (1 ♀). Sulawesi, off Ujang Pandang, Pulau Langkai, *Thalassia* bed with coral, 05°02.1′S, 119°05.1′E, 0.5 m, coll. Barnard, 6 Jul 1976 (1 ♂).

PNG: Madang, Hansa Bay, Laing Island, coral rubble, lagoon reef, coll. Child, 1–1.5 m, 31 Jul 1980 (1 ♂ with eggs, 1 Juv).

Fiji: Viti Levu, E of Suva, reef shallows across from Suva Point, soft corals, 1.5–2 m, coll. Child, 27 Jul 1978 (1 ♂ with eggs, 2 ♂, 2 ♀).

Caroline Islands: Yap Island, 10 m, 27 Oct. 1986 (1 ♂). Chuuk (Truk) Islands, lagoon, islet on outer reef, rubble in 1.0–1.5 m, 07°23.8′N, 151°58.6′E, coll. Child, 2 Jul 1986 (1 Juv.).

Distribution.—This species is probably pantropical and has been collected in many Indo-West Pacific localities along with many in Florida and the Caribbean Sea. It is known from the littoral to 33 m. It is new to several of the above localities undoubtedly because shallow marine collections are few and far between from islands of the western Pacific.

Remarks.—The serrate major heel spine of this species and its long slender habitus are excellent recognition characters in combination. There have been other (unrelated) species recently described which are long and slender and have serrate heel spines: most notably, *A. tenuicorpus* Child, 1991, and *A. exaggeratus* Stock, 1994. Both the latter species are much more slender and have much longer lateral processes than *A. pectinus,* although all three species have major heel spine teeth of varying numbers and have other major differences in appendage lengths and shapes. Another bizarrely attenuated new species from a different family, to be described from Okinawa, also has serrate heel spines, suggesting that these two characters are possibly linked genetically in more than one genus.

Anoplodactylus pycnosoma? (Helfer, 1938)

Peritrachia pycnosoma Helfer, 1938:176–177, fig. 7.

Anoplodactylus pycnosoma.—Stock, 1953a: 41, fig. 5; 1994:65, 67 [literature].

Material examined.—Indonesia: W Java, off Jakarta, Pulau Untongdjawa, 05°58′S, 106°42′E, coll. Taylor, 11 Oct 1938 (1 ♀).

Distribution.—This common intertidal Indo-Pacific species has been collected from localities circling Indonesia, but this appears to be the first capture from the many islands composing that country.

Remarks.—This single specimen, like many females in this difficult genus, has contradictory characters. It has angulate ventral proboscis corners like *A. pyconosoma,* but its legs and in particular the propodi are slightly longer and more slender than Helfer's species. The propodal lamina is difficult to see and appears shorter than those of *A. pycnosoma,* but the abdomen and ocular tubercle are both short as in this species. The leg segments are separated by dark brown bands as so often occurs in *A. pycnosoma,* and for the moment, I classify this female specimen as Helfer's often collected species.

Anoplodactylus tarsalis Stock, 1968

Anoplodactylus tarsalis Stock, 1968:52–54, fig. 19.—Arnaud, 1973:955.—Child, 1988a:20.—Müller, 1990a:78; 1992a: 171–173, figs. 37–42.—Stock, 1992:95.

Material examined.—Indonesia: Java, off Jakarta, Pulau Damar-Besar, 05°58′S, 106°50′E, coll. Taylor, 30 Sep 1938 (2 ♀). PNG: Madang, Kranket Island, inside reef, coral and algae rubble, 1.5–2.5 m, coll. Child, 28 Jul 1980 (1 ♂ with eggs). Madang, Paddock, 2nd reef past Gosem Island, rubble and sponges in 2 m, coll. Thomas & Clark, 9 Jan 1989 (1 ♂ with eggs, 2 ♂, 1 ♀, 1 Juv). Same area, in 3 m, coll. Thomas & Clark, 10 Jan 1989 (1 ♂). Same area, NW reef margin, rubble in 3 m, Thomas & Clark, 14 Jan 1989 (1 ♂, 1 ♀, 3 Lv). Madang, Yazi Reef, rubble from landward side in 1 m, Thomas & Clark, 15 Jan 1989 (3 ♂ with eggs, 2 ♂, 6 ♀, 12 Juv & Lv). Same area, in 3 m, coll. Thomas & Clark, 15 Jan 1989 (7 specimens).

Distribution.—This compact tiny species has been taken in the Philippines, Madagascar, Kenya, and Oman, from littoral depths to 13 m. These records mark the first time it has been collected in either Indonesia or Papua New Guinea, but all were taken from within its known shallow depth range.

Remarks.—Stock (1994) found specimens of *A. pseudotarsalis* Müller (1992a) in both Indonesia and Papua New Guinea. This species is obviously very closely related to *A. tarsalis.* Comparison of the above specimens with illustrations of both species by Müller and Stock confirms that these specimens are *A. tarsalis* and not its congener. These two species are therefore sympatric, a fact which will offer future systematists a fertile field for confusion.

Anoplodactylus tenuicorpus Child, 1988

Anoplodactylus attenuatus Child, 1988a: 12–14, fig. 5; 1988b:56 [preocc. *Phoxichilidium attenuatum* Hodge, 1864]

Anoplodactylus tenuicorpus n. comb. Child, 1991:142–143.—-Stock, 1994:67.

Material examined.—PNG: Madang, Riwa Bay, cemented rubble in 0.6 m, coll. Thomas & Clark, 17 Jan 1989 (1 ♀). Port Moresby Bootless Inlet, Manunouha (Lion) Island reef, 1–2.5 m, coll. Child, 26 Jul 1980 (1 ♀).

Distribution.—This extremely slender species has been found at Aldabra Atoll, Indian Ocean, Indonesia, Papua New Guinea, Guam, and was described from the Philippines in 1–6 m.

Remarks.—Stock (1994) described another *Anoplodactylus* species, *A. exaggeratus,* which is not quite as attenuated as this species. He outlined the differences between the two species very well and I can add nothing more of any consequence. The affinity (if any) between extreme trunk and appendage attenuation and the character of serrate propodal heel spines is discussed under *A. pectinus* in this report.

Anoplodactylus species indeterminate

Material examined.—Indonesia: W Java, Labuhan Village, on algae, 06°22′S, 105°50′E, intertidal, coll. Taylor, 17 Oct 1938 (1 juv). W Java, Pulau Damar-Besar, off Jakarta, algae, 05°58′S, 106°50′E, intertidal coll. Taylor, 30 Sep 1938 (1 larva).

PNG: near Port Moresby, Bootless Inlet, Manunouha (Lion) Island reef, rubble & algae in 1–2 m, coll. Child, 26 Jul 1980 (2 juv). Madang, Paddock Reef, rubble from NW margin in 3 m, coll. Thomas & Clark, 14 Jan 1989 (2 juv., 1 larva).

Remarks.—All specimens are too immature for determination.

Family Endeididae Norman, 1908

Genus *Endeis* Philippi, 1843

Endeis biserata Stock, 1968

Endeis biserata Stock, 1968:57–60, fig. 21: 1970:1; 1974:17; 1979:28–30, fig. 9.—Child, 1988a:20; 1990:332–333.—Stock, 1992:134.

Material examined.—PNG: Madang, Paddock Reef, 40 m off Gosem Island, rubble in 3 m, coll. Thomas & Clark, 7 Jan 1989 (1 ♀, 1 juv.)

Distribution.—An Indo-West Pacific species distributed from the Red Sea and Madagascar to Australia, Indonesia, and the Philippines. There is a record from Hawaii and one from Brazil, the latter suggesting that this species is possibly pantropical in distribution. It has been collected from the shore to 37 m.

Remarks.—These specimens have the long spines and dorsodistal tubercle of the femora as in the type description and lack the lateral intestinal caeca of other species. The propodi appear slightly longer in these specimens but they are otherwise close to the type.

Endeis holthuisi Stock, 1961

Endeis holthuisi Stock, 1961:28–29, figs. 1–6; 1968:69 [key]; 1994:68.

Material examined.—PNG: Madang, Kranket Island, rubble from seaward reef crest in 4 m, coll. Thomas & Clark, 11 Jan 1989 (1 ♀). Madang, patch reef between Gosem Island and Jais Aben Resort, coral rubble in 1 m, coll. Thomas & Clark, 13 Jan 1989 (1 ♀). Madang, Yazi Reef, landward side, rubble in 1 m, coll. Thomas & Clark, 15 Jan 1989 (1 ♂, 1 Juv.).

Distribution.—Stock's distinctive species has been known only in a very restricted range: two places in NW New Guinea Island (Irian Jaya, Indonesia), in 1–7 m. This collection places it at the opposite (eastern) end of the same Island in Papua New Guinea and within its known depth range.

Remarks.—This species is much more compact than *E. biserata.* The legs of most other species are longer and much more slender. Both are characters which set this species apart from all Indo-Pacific members of the genus.

Family Callipallenidae Hilton, 1942

Genus *Callipallene* Flynn, 1929

Callipallene novaezealandiae (Thomson, 1884)

Pallene novae-zealandiae Thomson, 1884: 246–247, pl. 14, figs. 1–4.

Callipallene novaezealandiae.—Child, 1982b:277 [literature]; 1983:708; 1988a: 20.—Nakamura & Child, 1988a:664; 1991:38.—Müller, 1990b:106.—Stock, 1994:48.

Callipallene novae-zealandiae.—Nakamura, 1990:pl. 4, figs. 6–10.

Material examined.—Caroline Islands: Chuuk (Truk) Islands, eastern lagoon, islet on outer reef, rubble in 1.0–1.5 m, 07°23.8′N, 151″58.6′E, coll. Child, 2 Jul 1986 (1 ♂).

PNG: Madang, Paddock Reef, off Gosem Is., rubble in 3 m, coll. Thomas & Clark, 7 Jan 1989 (1♂, 2 Lv.). Madang, Paddock

Reef, near Gosem Is., sponges & rubble in 3 m, coll. Thomas & Clark, 8 Jan 1989 (1 ♂ juv., 1 ♀). Madang, Paddock Reef, rubble from NW margin in 3 m, coll. Thomas & Clark, 14 Jan 1989 (1 ♀, 2 Juv.). Madang, Yazi Reef, landward side, rubble in 1 m, coll. Thomas & Clark, 15 Jan 1989 (1 Juv.). Madang, Yazi Reef, coral rubble in 3 m, coll. Thomas & Clark, 15 Jan 1989 (1 ♀, 1 Juv.).

Distribution.—A widely distributed Indo-Pacific species taken from East Africa to Japan in 2–274 m.

Callipallene species indeterminate

Material examined.—PNG: Madang, Hansa Bay, Laing Island, rubble from reef in 1.0–1.5 m, coll. Child, 31 Jul 1980 (1 ♀ juv.).

Remarks.—The juvenile female is longer in most measurements than the previous species but lacks distinguishing characters with which to identify it.

Genus *Pallenopsis* Wilson, 1881
Subgenus (*Pallenopsis*) Stock, 1975
Pallenopsis (*Pallenopsis*) *hoeki* (Miers, 1884)

Phoxichilidium hoeki Miers, 1884:324–326, pl. 35, fig. b.

Pallenopsis hoeki.—Child, 1975:19 [literature].

Material examined.—Indonesia: Arafura Sea, Aru Archipelago, W of Wasir Island, 05°30′S, 134°12′E, 33–40 m, coll. Western Australian Museum, 15 May 1970 (2 ♂, 2 ♀, 1 Juv.).

Distribution.—The corridor of pycnogonid species from Australia, north through the western Pacific islands to Japan, includes this long known but seldom collected species. It has a relatively shallow depth range of 7–134 m.

Pallenopsis (*Pallenopsis*) *virgata* Loman, 1908

Pallenopsis (*Rigona*) *virgatus* Loman, 1908:69–70, pl. IX, figs. 135–136.

Pallenopsis (*Pallenopsis*) *virgata.*—Nakamura & Child, 1991:41 [literature].—Stock, 1991:197.

Material examined.—PNG: Madang, Paddock Reef near Gosem Island, from sponges and rubble in 3 m, coll. Thomas & Clark, 8 Jan 1989 (1 ♀ juv.).

Distribution.—This is another relatively shallow-water (20–112 m) species with a north-south distribution from Japan to the Philippines, Indonesia, and New Caledonia Islands. This specimen marks the shallowest known depth for the species.

Family Nymphonidae Wilson, 1878
Genus *Nymphon* Fabricius, 1794
Nymphon diabolum Child, 1988

Nymphon diabolus Child, 1988a:23–25, fig. 10; 1988b:75.—Nakamura & Child, 1988a:668.

Material examined.—Caroline Islands: Chuuk (Truk) Islands, eastern lagoon, islet on outer reef, rubble in 1.0–1.5 m, 07°23.8′N, 151°58.6′E, coll. Child, 2 Jul 1986 (1 subadult).

Distribution.—This recently described species was collected in the southern Philippines, and subsequently from the Ryukyu Islands and at Aldabra Atoll in the Indian Ocean, in 1–3 m. This young specimen extends its distribution eastward into the Caroline Islands.

Remarks.—This specimen has the same small-sized anterior appendages as the type and has the paired ocular tubercle "horns," slender legs with few setae, chelae with moderately long teeth, long auxiliary claws in relation to the short main claw, and a terminal palp segment longer than the fourth segment. It has the usual reduced juvenile oviger with only 1 or 2 denticulate spines per strigilis segment. No other Indo-Pacific species shares this group of characters. The reduced size of its anterior in comparison to the rest of the species is its best recognition character. This specimen has a wrinkle artifact encircling its neck which does not, under high magnification, have a segmentation line. Its anterior appendages were forced back slightly or twisted on the neck.

Nymphon draconum Child

Nymphon draconis Child, 1990:324–327, fig. 5.—Müller, 1992a:163.

Material examined.—Indonesia: Sulawesi, Pulau Langkai, off Ujung Pandang, in *Thalassia* and coral in 0.5 m, coll. Barnard, 6 Jul 1976 (1 juv., 1 lv.).

Distribution.—Australia's Great Barrier Reef (Lizard Is.) is the type locality for this species. It has also been collected at Malaysia in the Gulf of Siam. The present specimens come from an intermediate locality between the two earlier captures, but within its known depth range of 0–3 m.

Remarks.—The juvenile is very like the male adult except it lacks the inflated chelae, a character which is probably related to age and undoubtedly related to sex. The species belongs to the *N. aequidigitatum* group of species (Child, 1988b) which share inflated male chelae, a reduced main propodal claw with larger auxiliaries, bifurcate chelae teeth, a longer than usual terminal palp segment, and an oviger claw which usually lacks teeth.

Acknowledgments

I wish to thank the many collectors for contributing these specimens and the late David Montgomery, Secretary of the Western Society of Naturalists (WSN), for making such thorough travel arrangements and logistical support for several enjoyable field trips to very remote places. Collections were made in these places which otherwise would have been impossible to assemble.

Thanks go to those curators of the Western Australia Museum and the California Academy of Sciences who loaned several lots of specimens for inclusion in this report. The loaned specimens have been returned to the appropriate institutions and the remaining specimens are deposited in the collections of the National Museum of Natural History, Smithsonian Institution.

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Bathysabellaria spinifera (Polychaeta: Sabellariidae), a new species from deep water off New Caledonia, southwest Pacific Ocean

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Abstract.—A new species of the genus *Bathysabellaria* Lechapt & Gruet, 1993, is described from New Caledonia (southwest Pacific Ocean). *Bathysabellaria spinifera,* new species, is known from depths between 570 and 700 m. The only other described species in this genus is the type species, *Bathysabellaria neocaledoniensis* Lechapt & Gruet, 1993, which also occurs off New Caledonia at more shallow depths; between 440 to 450 m. *Bathysabellaria spinifera* differs from the type species in having two forms of opercular paleae in the inner row instead of a single kind. The presence of a ventral median organ near the anterior end of the prostomium is described. This feature has not been previously noted in species of Sabellariidae. A table of the primary diagnostic characters that distinguish *Bathysabellaria* from other known genera in the subfamily Lygdaminae Kirtley, 1994, is included.

The genus *Bathysabellaria* Lechapt & Gruet, 1993, was erected to include distinctive and previously unrecognized forms of Sabellariidae from localities off new Caledonia. Although species of other genera in the family have been described by various authors from the general region of the southwest Pacific Ocean area (see *Remarks,* below), Lechapt & Gruet's account was the first report of Sabellariidae from the immediate vicinity of New Caledonia.

Examples of the new species described in this paper were received from the Centre National de Tri d'Océanographie Biologique, Brest, France. They were collected during a bathyl and abyssal benthos survey designated "Biologie de Nouvelle Calédonie" (BIOCAL) during a cruise of the N/O *Jean Charcot* in August, 1985. The cruise was part of a cooperative effort, "Programme Interdisciplinaire de Recherche Océanographique," sponsored jointly by the Centre National de Recherche Scientifique (CNRS) and the Muséum National d'Histoire Naturelle, Paris (MNHNP) under the direction by C. Levi. A total of 446 samples of this species were recovered from four stations with Waren type rock dredge. At the time of collection the animals were fixed in formalin and sea water solution and later stored in 60% ethanol.

The external morphology of the worms and of diagnostic hard parts, excised and mounted on glass slides, were examined using binocular light microscopes. An individual specimen was mounted on a brass Scanning Electron Microscope (SEM) stub, dehydrated in acetone; dried using critical-point drying procedures, sputter-coated with a thin layer of gold-palladium, and examined and photographed in a SEM. Some excised chaetae were also mounted on SEM stubs and prepared for study using the same procedure.

The holotype (MNHNP UC341) and some paratypes (MNHNP UC 342) have been deposited in the Museum National d'Histoire Naturelle, Paris. Other specimens have been deposited in the Allan Hancock Foundation Polychaete Collection of the Los Angeles County Museum of Natural History (LACM-AHF POLY 1689), the Smithsonian Institution, National Museum of Natural History, Washington, D. C. (USNM 172587-172588); and the Harbor Branch Oceanographic Institution Museum (HBOM 050-2584). The remaining specimens are retained in the authors' personal collections. The uncatalogued SEM stubs are available on loan from (JPL) from the MNHN, Laboratoire Maritime, Dinard, France.

Family Sabellariidae

Subfamily Lygdaminae Kirtley, 1994

Genus *Bathysabellaria* Lechapt & Gruet, 1993

Bathysabellaria spinifera, new species

Figs. 1–8

Material examined.—Southwest Pacific Ocean, BIOCAL stations off New Caledonia; N/O *Jean Charcot*; Waren rock dredge; Coll. C. Levi; Holotype (MNHNP UC 341): Station DW 46; 22°53′S, 167°17′E; depth 570–610 m; 30 Aug 1985, (type locality). Paratypes: 144 specimens (MNHNP UC 342). Station DW 51, 23°05′S; 167°45′E, 680–780 m, 30 Aug 1985. (287 specimens). Station DW 36 23°08′S; 167°11′E, 659–680 m, 29 Aug 1985, (11 specimens). Station DW 33, 23°10′S; 167°10′E, 675–680 m, 29 Aug 1985, (3 specimens).

Description.—Body length of holotype 12 mm excluding the cauda, distal portion of which is missing; width of opercular crown 1.8 mm. Prostomium cryptocephalic (Figs. 1a, 2a; 6B; and see *Remarks,* below). With ventral unpaired median organ near anterior midline of prostomium (Figs. 1a, 2a, b). Anterior ends of opercular lobes and crown completely fused along anterior midline; without midventral declivity (Figs. 1a, b; 2a, b; 6B). With numerous small eye spots in longitudinal series on both sides of posterior end of midline of prostomium (Fig. 2a). Eye spots partially obscured by tiny blotches of dark dermal pigment (Fig. 2a). Anterior margin of opercular lobe completely encircled with 18–20 small conical papillae (= "opercular papillae" of Orrhage, 1978: 345, and fig. 1c; "cirri" of several authors; "fleshy papulae" of Smith, 1981:24, fig. 2A; "subulate palpi" of Lechapt & Gruet (1993: 244); "pericoronal palpi" of Kirtley (1994: 185. fig. 11.1.1 c, d)) (Figs. 1a, b; 2a, b; 6B). The two papillae adjacent to the ventral midline appear to be different from the others in the series (see *Remarks,* below). Opercular paleae in two concentric rows. Outer paleae 20 on each side, forming two complete half-rings on periphery of crown; with bright yellow, wide, thick, translucent blades. Inner surface of blades slightly concave; with transverse thecal bands (sensu Kirtley, 1994: 5); bands more closely spaced toward distal ends (Fig. 3a) than through proximal portion of blade (Figs. 3a; 4B; 5C), thecae with irregularly pectinate (frayed) distal margins (Fig. 5C); trace of thecae roughly horizontal through middle part and base of blade (Fig. 3a). Blades with smoothly tapering, mucronate, distal ends; some tips frayed and abraded (Figs. 4B, C). Outer paleae are all of similar size and shape with lateral margins of blades overlapping edges of adjacent blades (Figs. 3a; 6B). The basal (proximal) parts of the blades are slightly widened and rotated at small angles to the vertical axis of the shafts (Figs. 3a; 4B, C), producing a left- and right-hand (mirror image) symmetry according to which of the two sides of the crown that they occur. Paleal shafts almost cylindrical, slightly thicker at distal end than at proximal end. Inner paleae consist of 15 long and 20 short forms. Long forms with erect spiniform blades; distal ends of blades curving inward toward center of operculum, terminating in smooth points (Figs. 1a, b; 2 b; 3b; 4A, 5A, B). Short forms with stout transversely constricted blades; distal ends with obliquely truncated inner surfaces with medial, slightly convex, longitudinal ridge; distal ends terminating abruptly as blunt tips (Figs. 3a; 5b); shafts of inner paleae more slender than those in long forms; both forms

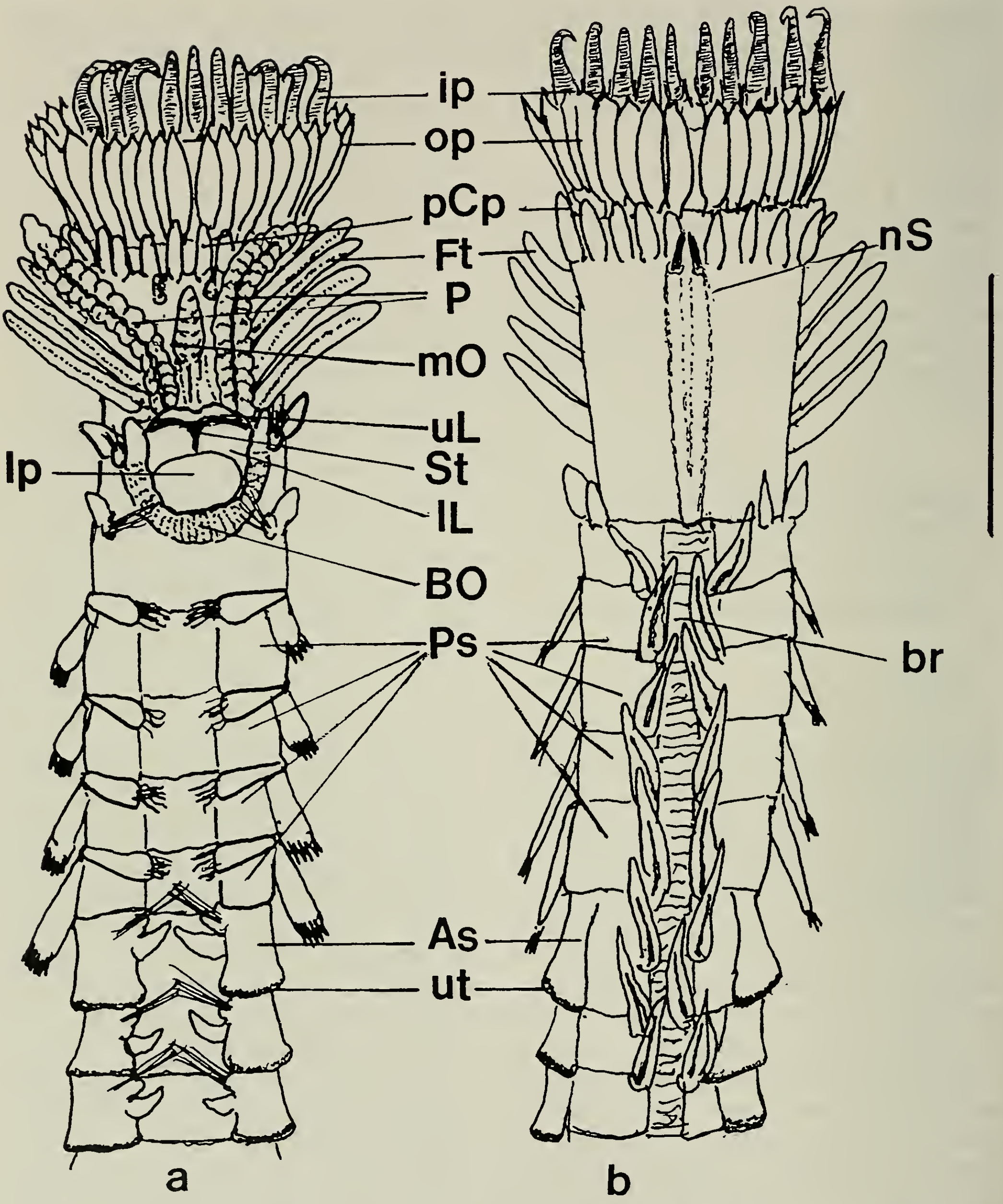

Fig. 1. *Bathysabellaria spinifera,* new species, paratype. (a) anterior end, ventral view. (b) anterior end, dorsal view. ip, inner paleae; op, outer paleae; pCp, pericoronal papulae; Ft, feeding tentacles; P, palpi; mo, median organ; ul, upper lip; St, stoma; lL, lower lip; lp, labial pouch; BO, building organ; ps, parathoracic segments; As, abdominal segments; ut, uncinigerous tori; nS, nuchal spine; br, branchia. Scale bar = 1.5 mm.

with transverse thecal bands with frayed distal fringes (Figs. 2b, c; 5B); thecae in middle portion of blades more widely spaced than those near proximal and distal ends. The irregular crowding of the middle paleae apparent in Fig. 5A is thought to result from post-mortem shriveling of soft tissue. Paired, yellow-gold, fusiform, distally attenuate and

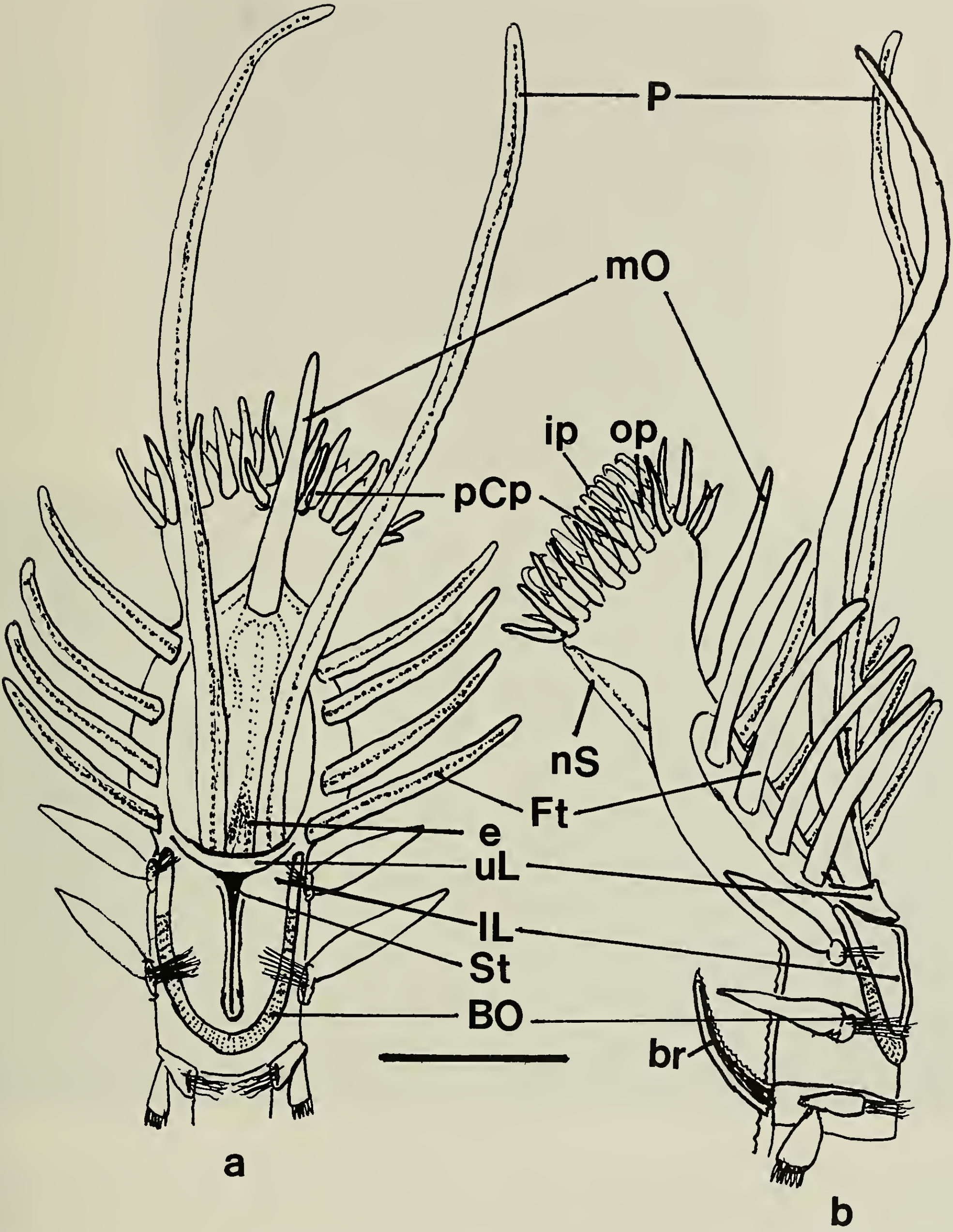

Fig. 2. Conceptual drawing of *Bathysabellaria spinifera* in feeding position with anterior appendages extended. (a) Ventral view. (b) Right-lateral view. Symbols as in Fig. 1. Scale bar = 1.5 mm.

weakly bent nuchal spines on dorsal side of opercular stalk (Figs. 1b; 2b; 6A).

Four (in some specimens three) filiform, ciliated, feeding tentacles ("oral tentacles" of Dales, 1952:436; "oral filaments" of Orrhage, 1973, fig. 1c) in ventral longitudinal series on both sides of prostomium. The series of feeding tentacles arises from the line of fusion of the paleal stalks and the prostomium (Figs. 1a, b; 2a, b; 6B); beginning

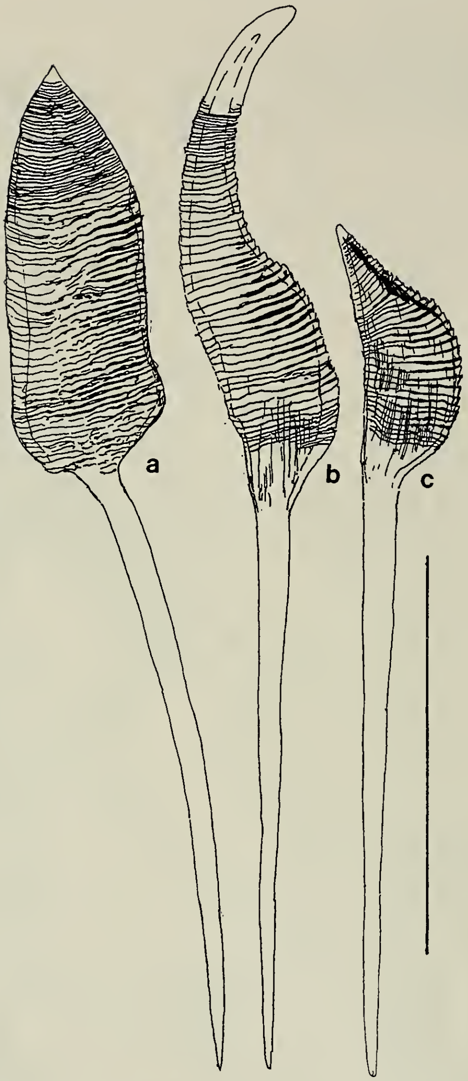

Fig. 3. *Bathysabellaria spinifera,* paratype. (a) View of inner surface of outer palea; (b) inner palea; long form; (c) inner palea; short form. Scale bar = 750 μm.

anterior to the antero-lateral ends of the upper lip (but not *from* it, as stated by Orrhage 1978:343) and continue to the base of the crown (Figs. 1a; 5B). Tentacles with narrow, longitudinal, ventral, grooves lined with small cilia and transverse bands of cilial tufts (described as "membranelles" from SEM images by Thoms 1988:24) with larger cilia. Large, paired, palpi ("prostomial tentacles" of Dales 1952:450; "preoral prehensile tentacles" of Kirtley 1994:5); with conspicuous ciliated longitudinal grooves; arising from both sides of the midline of the posterior margin of prostomium, anterior to the border of the upper lip (see *Remarks,* below).

First thoracic segment includes stoma with transverse upper lip and lower lip (in fixed specimens) with medial longitudinal fissure and bulbous, transverse, basal fold or labial pouch (Figs. 1a: 6B). Glandular, horseshoe-shaped building organ surround-

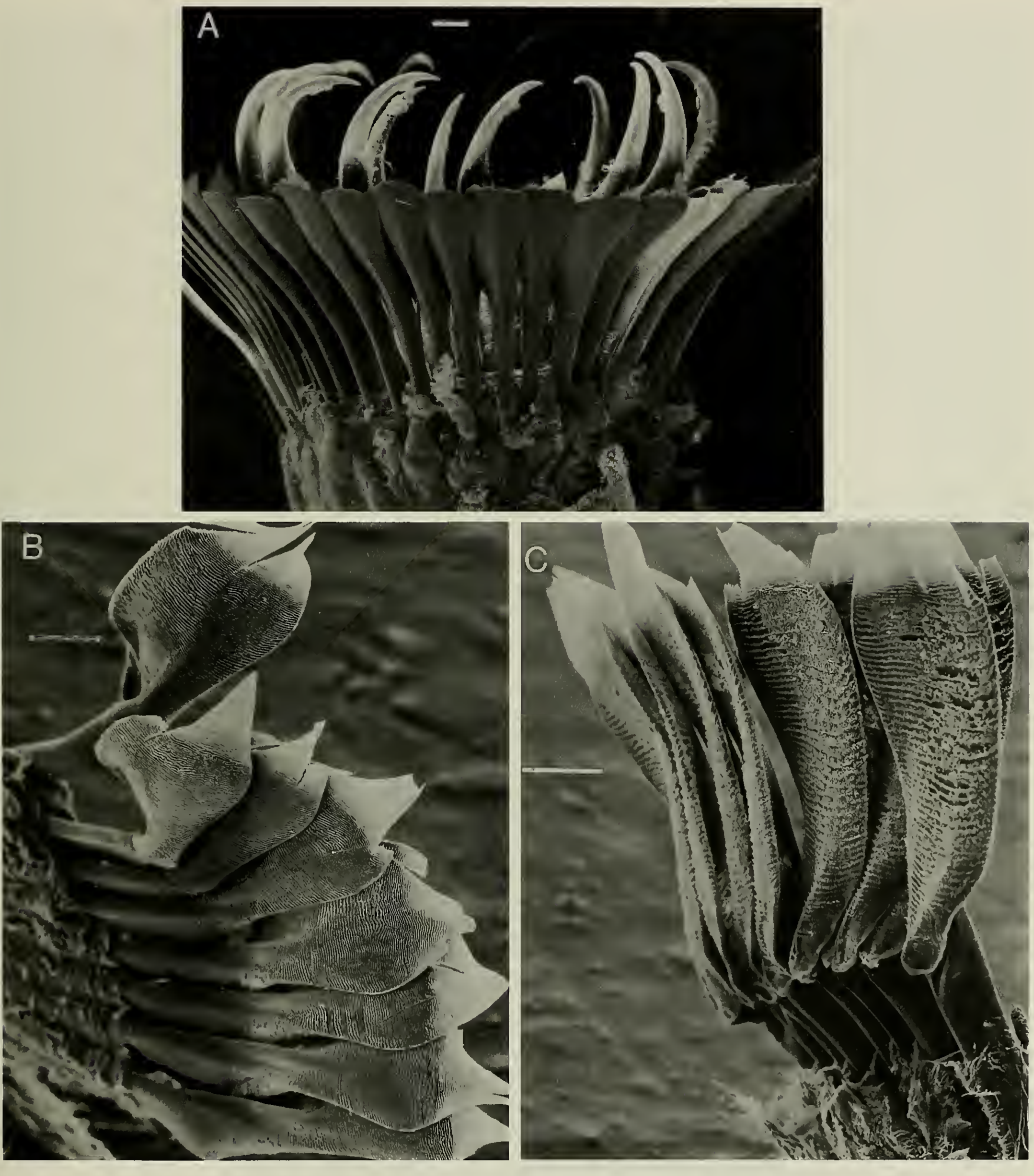

Fig. 4. *Bathysabellaria spinifera,* paratype. (A) SEM photo of crown. (B) Inner surfaces of outer paleae. Scale bars = (A) = 10 μm; (B) = 100 μm.

ing posterior and lateral margins of stoma. Anterior ends of building organ terminate as extensible conical lobes with fascicles of fine capillary neurosetae arising from base of small, fleshy, triangular, lobate cirri (Figs. 6B, C: C_1).

Second thoracic segment with bundles of large and small capillary neurosetae with pectinate thecae (Figs. 6A, C: C_2), arising from base of inferior conical cirri; with small superior asetigerous cirri; without paired dorsal branchiae.

Parathoracic segments four. Notopodial fascicles ("sheaves" of Dales 1952:357) muscular; with transverse series of from four to six pairs of capillary and lanceolate

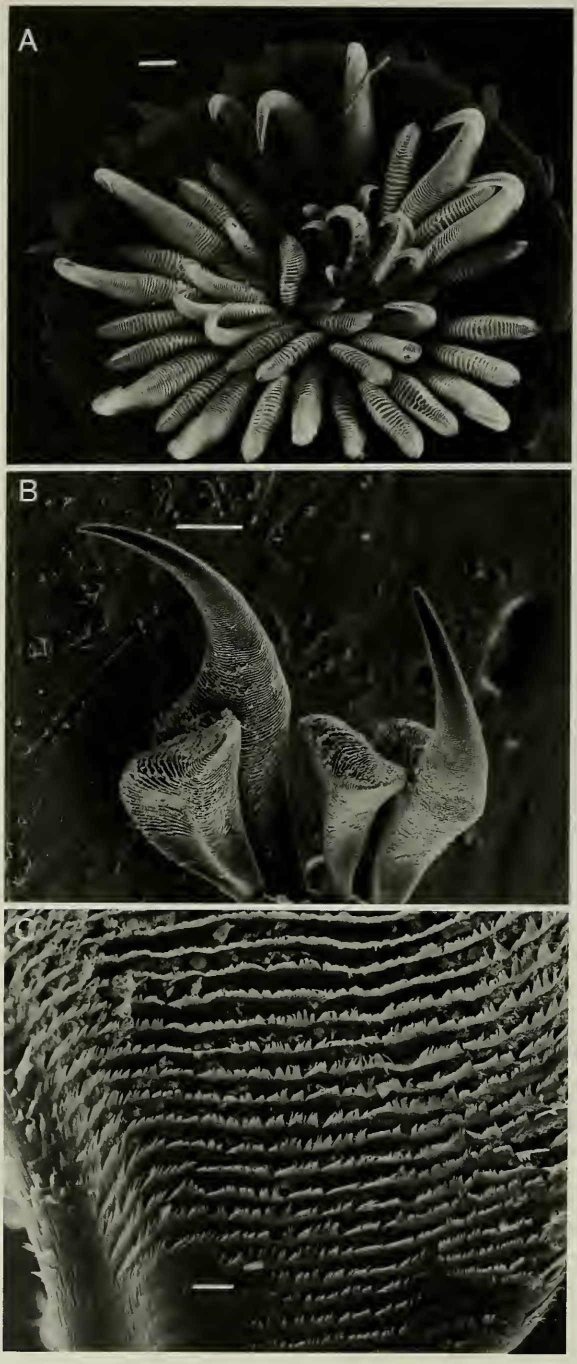

Fig. 5. *Bathysabellaria spinifera,* paratype. (A) Anterior surface of crown. (B) Long and short forms of inner paleae. (C) High magnification SEM photo of inner surface of outer palea showing fringes on thecal bands. Scale bars = 100 μm.

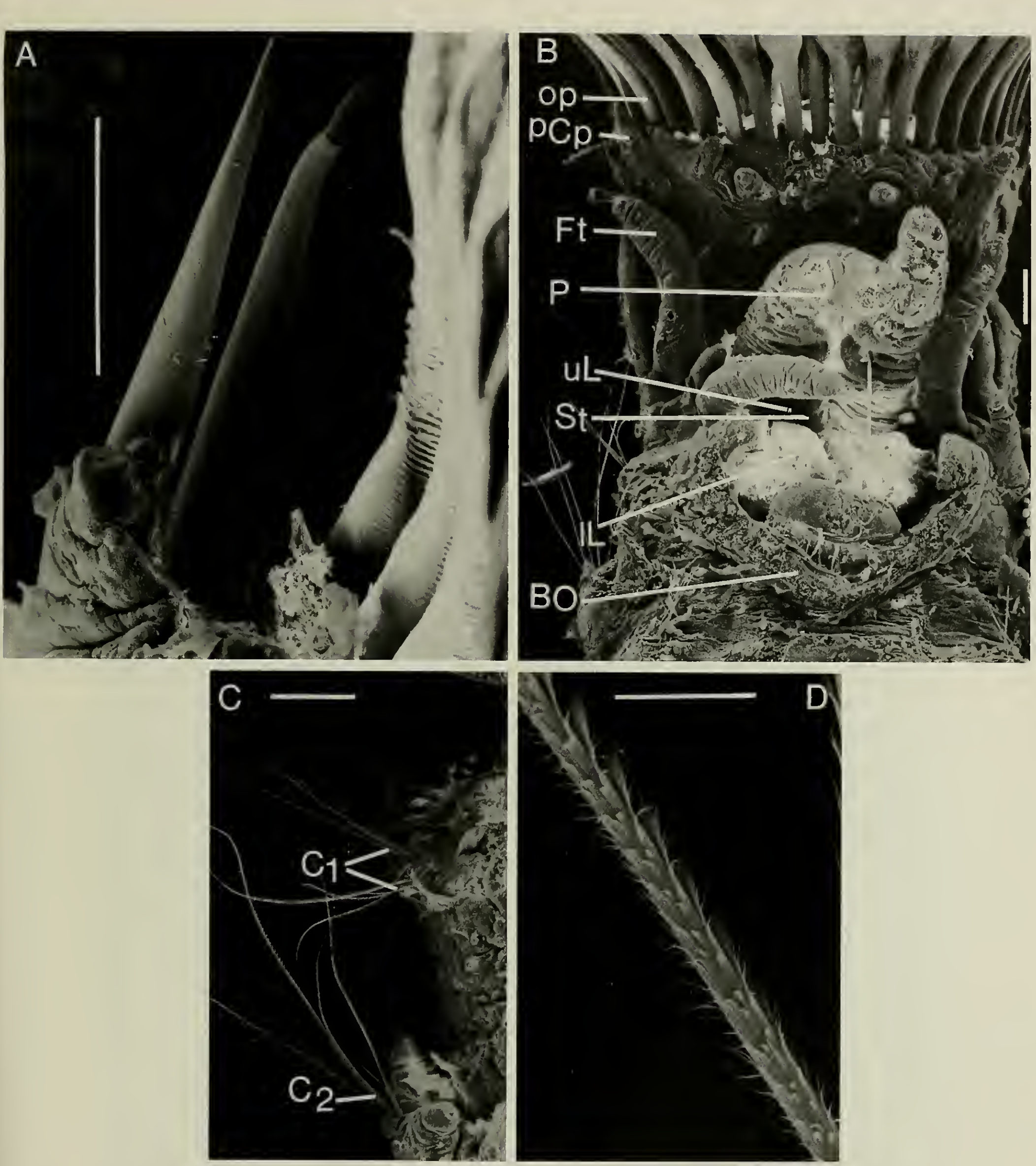

Fig. 6. *Bathysabellaria spinifera,* paratype. (A) tips of nuchal spines. (B) Ventral view of anterior end. op, outer paleae; pCp, pericoronal papulae; Ft, feeding tentacle; P, palpi; uL, upper lip; S, stoma; lL, lower lip; BO, building organ. (C_1), setae of first thoracic segment; (C_2), setae of second thoracic segment. (D) large and small forms of capillary setae from second thoracic segment, (C_2), adjacent photo. Scale bars (A, B, C) = 100 μm; (D) = 10 μm.

setae (Figs. 1a, b; 7A, B). Capillary setae thin, with finely hirsute distal fringes; lanceolate setae with coarsely frayed distal ends (Fig. 7C). Neurosetae capilliform, of two kinds: small form with hirsute distal fringes, large form with asymmetrically whorled thecae with delicately pectinate distal fringes; thecae of smaller form with smooth margins (not shown); parathoracic notopodia successively larger and longer toward posterior (Figs. 1a, b; 2a, b; 7A). Paired dorsal branchiae on each parathora-

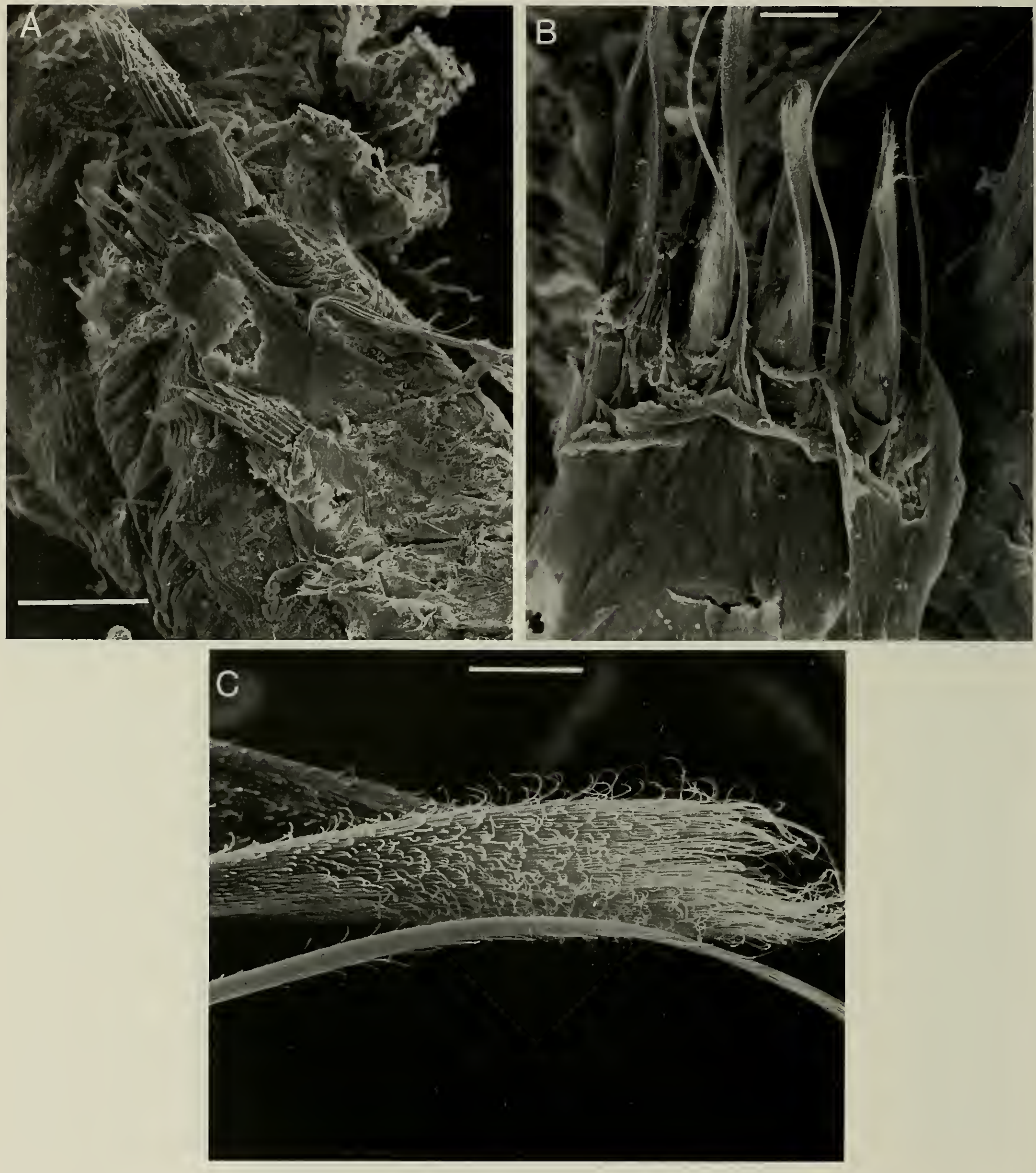

Fig. 7. *Bathysabellaria spinifera,* paratype. (A) left-lateral view of parathoracic notopodia. (B) magnified view of notopodia of third parathoracic segment. (C) tips of lanceolate and capillary forms of neurosetae from third parathoracic segment. Scale bars (A, B) = 100 μm; C = 10 μm.

cic segment. Branchiae also present on first few abdominal segments; reduced in size or absent on posterior segments. Abdominal region consists of 16 setigers. Neuropodial bundles with two kinds of setae: thin form with finely hirsute distal thecal margins; thick form with spiral whorls of thecae with serrate distal margins (Fig. 8A). Abdominal notopodia with broad uncinigerous tori; posterior margin of tori with transverse series of many small uncini; each unicinus with paired marginal rows of eight or nine strongly bent teeth; points directed anteriorly (Fig. 8B). Cauda smooth, reflected on

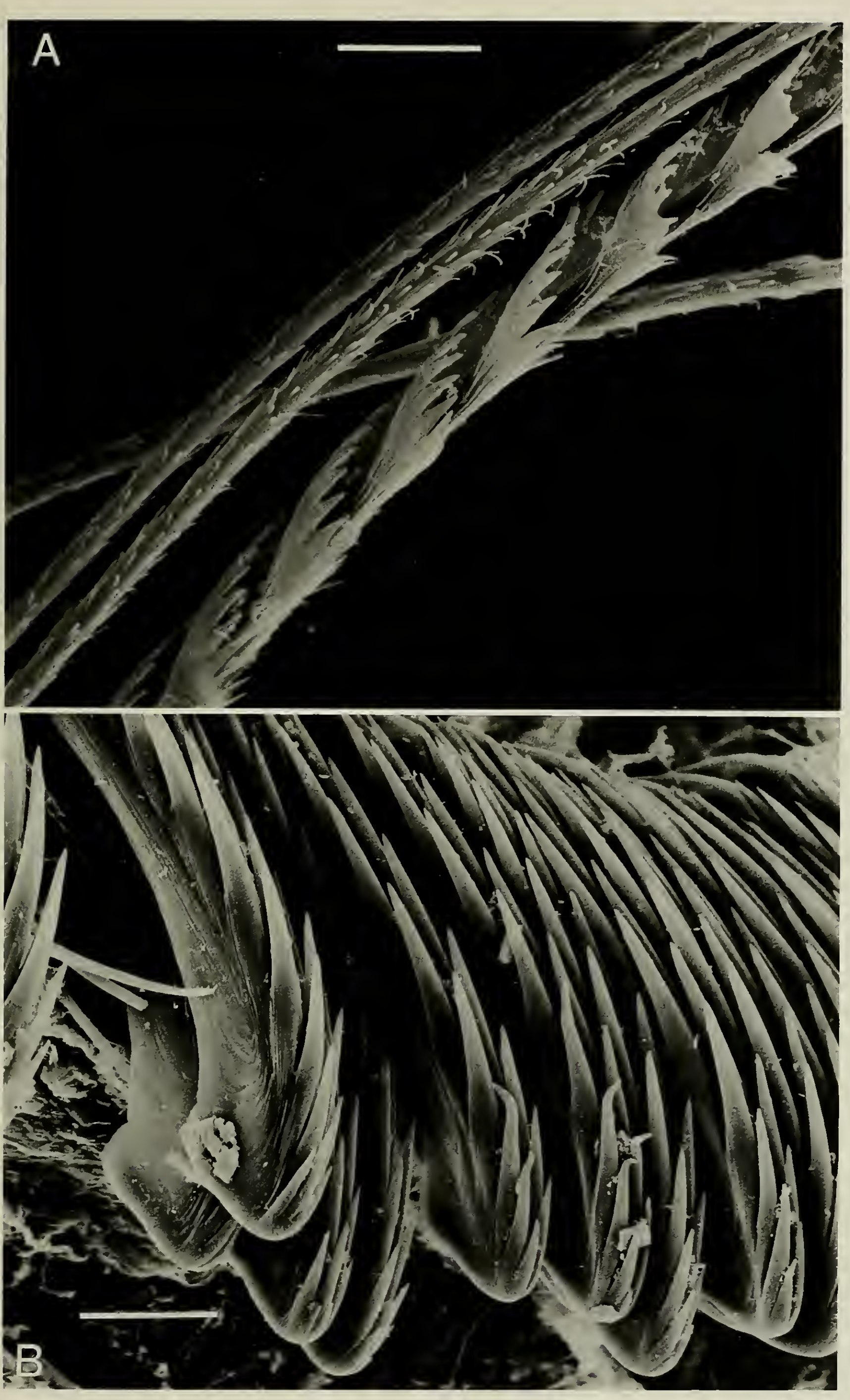

Fig. 8. *Bathysabellaria spinifera,* paratype. (A) Large and small forms of neurosetae from first abdominal segment. (B) notopodial uncini from first abdominal segment. Scale bars = 10 μm.

Table 1.—Primary differentiating characters of the genera in the subfamily Lygdaminae Kirtley, 1994. (1 = present; 0 = absent).

Genus	Feeding tentacles compound (branched)	Feeding tentacles simple (un-branched)	Opercular stalk bilobate	Opercular crown entire	Crown with mid-ventral declivity	Nuchal chaetae with hooks	Nuchal chaetae without hooks	Median organ dorsal	Median organ ventral	Median organ indis-tinct
Bathysabellaria	0	1	0	1	0	0	1	0	1	0
Gesaia	0	1	1	0	0	1	0	1	0	0
Lygdamis	1	0	1	0	0	1	0	1	0	0
Mariansabellaria	0	1	1	0	0	0	1	0	0	1
Phalacrostemma	0	1	1	0	0	1	0	1	0	0
Tetreres	0	1	0	0	1	1	0	1	0	0

ventrum. Only proximal part of the cauda present; distal portion macerated and missing.

Specimens all removed and separated from tubes at sorting center. Fragments of tube walls found adhering to bodies of some individuals consist mostly of foraminifera and small bioclasts, cemented to each other with mucous cement produced by the worms.

Etymology.—spinifera = Latin (spina/fero) = thorn-bearing; referring to the shape of the long form of inner opercular paleae that distinguishes this species from the type-species.

Remarks:—Relatively few species of Sabellariidae have been reported from the southwestern Pacific Ocean area. Caullery (1913:200; 1994:54–66) examined the Sabellariidae collected during the *Siboga* Expedition to the vicinity of what is now called Indonesia. He listed two species of *Idanthyrsus* Kinberg, 1867; a new species of *Phalacrostemma* Marenzeller, 1895; two species of *Lygdamis* Kinberg, 1867; and a new species of *Tetreres* Caullery, 1913; (see synonymy in Kirtley 1994:188). Hoagland (1920:627) described a species of *Lygdamis,* as *Tetreres treadwelli* from a depth of 18.3 m from the *Albatross* station D5109; between Cebu and Leyte Islands in the Philippines. Gibbs (1971:192) collected *Lygdamis gibbsi* Kirtley, 1994:127, from the near shore benthos in the Solomon Islands. Species of *Neosabellaria* Kirtley, 1994, and a species of *Paraidanthyrsus* Kirtley, 1994, are known from near shore waters of New Zealand. Bailey-Brock (1985:202, fig. 5a–e) described an intertidal sabellariid (as *Sabellaria* sp.) from Suva Harbor, Fiji Islands.

The presence of a completely fused opercular lobes and crown, the morphology of the paleae, and the presence of a ventral median organ are the principal diagnostic features that distinguish *Bathysabellaria* from all other genera of Sabellariidae with four parathoracic segments (subfamily Lygdaminae, Kirtley 1994:14). Differentiating morphologic features within the subfamily are summarized in Table 1.

The arrangement of the outer paleae in some species of *Tetreres* Caullery, 1913, and *Bathysabellaria* are similar in that the outer paleae have flattened blades and form nearly complete circles around the anterior periphery of the crown. In *Bathysabellaria* the paleal lobes and crown are completely fused but in *Tetreres,* the opercular lobes are completely fused except for a cleft (invagination) at the ventral midline. The inner paleae and nuchal chaetae in the two genera are remarkably different (Kirtley 1994:15, pl. 1). In species of *Bathysabellaria* the nuchal spines are elongate and fusiform and, except for their exposed distal tips, are embedded in the muscular tissue of the dorsum of the stalk. In *Tetreres* the nuchal chaetae are large and prominently visible as elongate, wide bosses conforming to the shape of the thick shafts beneath the epidermis and muscular tissue of both sides for most of the length of the dorsum of the stalk (Kirtley 1994, pl. 1, and fig. 12.10.1a–e). The hooks have large, rounded shafts and geniculate, outward-bent distal ends with stout, inward curving hooked tips. In species of *Mariansabellaria* Kirtley, 1994, the paleae are arranged in incomplete semicircles on the surface of bilobate crowns and the nuchal spines are flattened (ensiform) blades (Kirtley 1994:136, and fig. 8.2.1d).

Similarly fused opercular lobes, flattened, discoidal crowns, and completely encircling paleae are seen in some sabellariid genera having three parathoracic segments (subfamily Sabellariinae Kirtley, 1994), *Neosabellaria* Kirtley, 1994, *Phragmatopoma* Mörch, 1863, and *Gunnarea* Johansson, 1927. In the genus *Gunnarea,* when the animals are withdrawn into their tubes, the row of outer paleae appear as a complete circle. When the animals extend their anterior ends from their tubes and assume the feeding position the crown is discoidal except for a shallow, wide, depression that interrupts the continuity of the circle of paleae at the antero-ventral midline (Day 1967:668; 673; and fig. 33.1i; Kirtley 1994: 15, plate 1 and fig. 3.1.2d, e). A conspicuous median organ is not present in any species of the above listed three genera. A median organ is present in species of the genera *Sabellaria, Paridanthyrsus,* and *Idanthyrsus.* Most species in Lygdaminae have a conspicuous median organ, except those in the genus *Mariansabellaria.* In *Tetreres* there is a small, conical median organ at the dorsal midline of the opercular stalk (Kirtley 1994, fig. 12.10.1c).

Figures 1a, b, are diagrams of the ventral and dorsal sides of the anterior end of a paratype of *B. spinifera*; as it appears in a fixed and preserved condition. These figures approximate the shape of the animal in the position assumed when withdrawn into its tube; while still living. Figures 2a, b, are conceptual diagrams depicting a possible posture that the animals might assume in life; while feeding and collecting particles for tube construction. The diagrams portray the relationship of the prostomium, with its eyespots and median organ, to the feeding tentacles, palpi, paleal stalks and crown. Although the species described in this paper has not been actually observed while still alive, it is nevertheless instructive to visualize the possible posture and function of the anterior appendages in assessing and comparing the anatomy and homology of these organs in other sabellariid taxa. The dorsad arching of the anterior end and the orientation and extension of the appendages is characteristic of the posture seen in observations and photographs of other sabellariids with homologous appendages while living (e.g., Wilson 1969:323: *Sabellaria alveolata*; Fitzhugh, 1991:47, *Idanthyrsus* sp.; and personal observation by (DWK): *Phragmatopoma* spp. and *Sabellaria* spp.). The lengths and diameters of the extended appendages portrayed in the drawing are arbitrary, but are consistent with configuration of similar appendages observed in living forms. It is noted that, while in the feeding position, the prostomium (as defined below), stoma, and tentacles are directed anteriorly (upward), and the crown is held backward at up to 90° (or greater) angle to the longitudinal axis of the worm. As seen in this diagram the "operculum" also functions as a type of protective dorsal "shield" and the sensory cilia on the pericoronal papillae can control the flow of water around the periphery of the crown and provide sensory information from the dorsal and lateral regions of the anterior end.

The pair of pericoronal papillae on both sides of the ventral midline (Fig. 6B) appear to be anatomically and functionally different from the rest of the series. This possibility is suggested by their particularly shrunken and wrinkled appearance, as compared to the shape and size of other papillae (Figs. 1a; 6B).

The lateral and dorsal portion of the prostomium ("cephalon" of Binard & Jeener 1928:208); is obscured by overgrowth of the opercular stalks and crown which develop from the protoparapodia of first setigerous segment. The ontogenic development of the stalks and crown has been fairly well documented in several species of Sabellariidae (below). The following abbreviated interpretation of this process differs in certain details from previous explanations presented by Johansson (1927:25–39) and Hartman (1944:324–325) and is more consistent with the anatomical descriptions of von Drasche (1885:5) and Meyer (1887, 1888).

The protoparapodia (the "great chaeta sacs" of Wilson 1929:229) of sabellariid larvae first develop as a doublet of chaetoblastic organs (von Drasche 1885: pl. 2; figs. 3–5), which develop high in the episphere and protrude at the surface on both lateral sides of the hyposphere, at short time (as soon as 10 hours) after the trochophore stage is reached (Quatrefages 1848:190, pl. 4, figs. 7–9; Wilson 1929: 225, pl. 1, figs. 3–7; Cazaux 1964, pl. 1, 4–6; Eckelbarger 1976:123, fig. 1B–D). The doublets produce 2 kinds of primary chaetae: one form from the inner lobe of the sac and a different form from the outer lobe of the sac. In early growth stages the chaetae are quite similar but vary distinctively as the paleae are subsequently produced in several, successive, intermediate forms before the adult stage is reached (Wilson 1929:240, pl. 9, A1–10; B11–18; Eckelbarger 1976:124, fig. 9c–j: Eckelbarger & Chia 1976:2084, figs. 12–15). Near the time of settlement the innermost series of paleae begins to show the general form of the outer paleae of the adults; and the outermost series of paleae begins to resemble the inner paleae in adults. When the chaeta sacs are rotated anteriorly (and occipitally) during settlement metamorphosis the paleae that were in the innermost sac then become the outer paleae and the outermost series of chaetae become the inner series on the crown. The chaeta sacs grow larger and develop into muscular "stalks" which overgrow the lateral and dorsal margins of the peristomial region of the episphere and either become fused together along the anterior midline in *Bathysabellaria* and some other genera; or remain as separate lobes. In both cases a kind of cephalic cage (sensu Fauchald 1977:156) is formed.

Fauchald (1977:118) states that the "Prostomium [is] a narrow ridge fused laterally to the first setiger" in the Sabellariidae. This definition is appropriate in genera with bilobed opercular stalks but where the lobes are completely fused, as in the case of *Bathysabellaria, Neosabellaria, Phragmatopoma,* and *Gunnarea,* or almost completely fused, as in *Tetreres,* the lateral boundaries of the surface expression of the prostomium on the ventrum are less restricted and a relatively wide area on both sides of the ventral midline is included. The external expression of the prostomium in genera with completely fused stalks, including *Tetreres,* is a roughly triangular area on the anterior ventrum between fused paleal stalks, anterior to the upper (transverse) lip of stoma and bounded on both sides by the longitudinal series of feeding tentacles. The anterior limit of the external portion of the prostomium appears to be the posterior midline of the fused paleal lobes and pericoronal papillae (as noted above). In *Bathysabellaria* spp. the prostomium includes the ventral median organ (Figs. 1a; 2a, b). In Fig. 6B the median organ is not visible because it is behind the two palpi. The area has been designated the "buccal cavity" by some previous authors. It is properly the surface expression of the prostomium, and not an anterior extension of the peristomium (as inferred by the statements of Orrhage, 1978.)

Species in genera in the subfamily Sabellariinae Kirtley, 1994, with completely fused anterior ends, the presence of an organ homologous with the median organ has not previously been recognized.

Acknowledgments

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Two new species of *Dysponetus* (Polychaeta: Chrysopetalidae) from Italy and Papua New Guinea

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Abstract.—*Dysponetus bipapillatus,* new species, and *D. macroculatus,* new species, are described from shallow sediments in the Bay of Naples, Italy, and from the Madang area, Papua New Guinea, respectively. Comparisons are made with other *Dysponetus* species. *Dysponetus bipapillatus* appears closely related to *D. caecus* (Langerhans, 1880) and *D. macroculatus* to *D. bidentatus* Day, 1954. *Dysponetus bipapillatus* is unique in having a pair of papillae on segment 8 on some of the examined specimens, and *D. macroculatus,* in the combination of large distinct eyes and presence of ventral tentacular cirri on segment 2.

The family Chrysopetalidae Ehlers, 1864 currently includes 43 species, referred to 11 genera (Dahlgren & Pleijel 1995). Most chrysopetalids are easily distinguished from other polychaetes in that they possess chambered, flattened notosetae (paleae) more or less covering the dorsum, giving the characteristic golden color. They are commonly found in shallow waters, in temperate or tropical areas, often in association with corals. One group of small (1–5 mm) forms found in sediments, however, have circular rather than flattened notosetae. Three such genera have been described: *Dysponetus* Levinsen, 1879; *Acanthopale* San Martín, 1986; and *Victoriella* Kisseleva, 1992. *Acanthopale* is distinguished from *Dysponetus* by the presence of a mouth cover and a caruncle, both of which are similar to those found in chrysopetalids with flattened paleae. *Victoriella* is characterized by the absence of median antennae, and the presence of biramous first segment, platelate jaws and paired pygidial cirri.

Dysponetus currently includes six species described from the Atlantic, and one from the Indian Ocean (see appended checklist). *Dysponetus* species are small, fragile and easily overlooked in normal handling of samples. They are characterized by circular notosetae, mouth appendage, single pygidial projection, and accessory simple neurosetae.

In this paper two new *Dysponetus* species from Ischia, near Naples in Italy, and Madang, Papua New Guinea are described. The generic assignment is based on results from a cladistic analysis on *D. caecus* (Langerhans, 1880) and type species of ten chrysopetalid genera (Dahlgren & Pleijel 1995). *Dysponetus bipapillatus,* new species, and *D. macroculatus,* new species, share two of the three character state-changes that separate the clade *D. pygmaeus-D. caecus* from the next closest chrysopetalid taxon, i.e., absence of paired pygidial cirri and presence of single pygidial projection. Additional potential synapomorphies for *Dysponetus* are discussed. Further phylogenetic considerations have to await results from ongoing studies treating the relationship within Chrysopetalidae and related families. Type material is deposited at the Swedish Museum of Natural History, Stockholm.

Materials and Methods

Sediment samples were collected in fine mesh net bags during SCUBA dives. Specimens were carefully extracted using a suspension-decantation method, collected on 100 or 250-μm mesh screen, relaxed with magnesium chloride (7% in distilled water), studied alive, fixed for a few days in 10% formalin in filtered sea water, rinsed in tap water and stored in 80% alcohol. SEM specimens were similarly relaxed, fixed for a few hours in osmium tetraoxide (1% in artificial sea water), rinsed in distilled water, and transferred to 100% alcohol in a graded series, critical-point dried with CO_2, mounted on aluminium stubs, sputter-coated with gold, and examined in a Zeiss DSM 950. Drawings were made from SEM micrographs (Fig. 1A), or with a camera lucida (Figs. 1B–D; 3A, B; 6A–E).

All measurements were carried out, either on live, relaxed specimens, or on specimens relaxed prior to preservation.

Institutions, museums and other collections are indicated by following abbreviations: CMNA (Canadian Museum of Nature); LACM-AHF (Los Angeles County Museum of Natural History, Allan Hancock Foundation); SMNH (Swedish Museum of Natural History, Stockholm, Sweden); TD (author's collection); USNM (United States National Museum, Smithsonian Institution, Washington D.C.); ZISP (Zoological Institute, Academy of Sciences of Russia, St Petersburg); ZMH (Universität Hamburg, Zoologisches Institut und Museum); ZMUC (Zoological Museum, University of Copenhagen, Denmark).

Dysponetus bipapillatus, new species
Figs. 1–5

Material examined.—Italy: Ischia, off Ischia harbor, 40°45.3′N, 13°55.8′E, 9 m, SCUBA, "*Amphioxus* sand", holotype (SMNH 4789), 9 Jul 1994; 11 paratypes (SMNH 4790), 9 Jul 1994; 4 specimens used for SEM, 9 Jul 1994; 1 paratype (SMNH 4791), 15 Jul 1994; 1 specimen mounted on slide (TD), 15 Jul 1994.

Description.—Body, excluding parapodia, cylindrical; venter flattened. Posterior segments successively smaller, resulting body shape of fairly constant width, slightly posteriorly tapered.

Prostomium rectangular, longer than wide. Four minute eyes visible in live specimens, posterior pair larger and more widely separated. Anterior pair not visible in fixed specimens. Median antenna half length of lateral antennae, digitiform, anterodorsally inserted on prostomium. Lateral antennae fusiform, inserted immediately dorsal to palps (Fig. 1A). Antennae without distinct ceratophores. Palps stout, oval, twice as long as wide, not extending ventrally (Fig. 1A). Nuchal organs present as pair of ciliated lateral patches inserted posteriorly on prostomium.

Pronounced single mouth appendage on lower lip, extending anteriorly, slightly conical, with blunt tip (Fig. 1A). Single pair of stylet-shaped jaws (length 60 μm), visible through body wall in live specimens. Pharynx visible through body wall, extending to segment 6. Everted proboscis not observed.

First two segments with four pairs tentacular cirri, longer than but with same shape as, dorsal cirri of third and following segments, anteriorly directed (Fig. 1A). First segment achaetous, visible lateral to prostomium, slightly ventrally dislocated; second segment with notosetae only (Fig. 1A). Third segment biramous; dorsal cirri present, ventral cirri absent (Figs. 1A; 3B). Biramous segments from segment 4, all with dorsal and ventral cirri (Fig. 1B). Single noto- and neuroacicula present from segment 2 (Fig. 1B); aciculae in segment 1 not detectable.

Notopodial lobes reduced. Dorsal cirri fusiform, as long as setae (length 130 μm in median segments), cirrophores present, styles slightly proximally inflated, distally tapering, tips blunt. Notoaciculae difficult to detect in dense notosetal fascicle, length 70 μm (Fig. 1B). Notosetae internally chambered, D-shaped in cross-section, 10–15 denticles on each side, dorsally (Fig. 2A). Notosetal count, mid-body segments

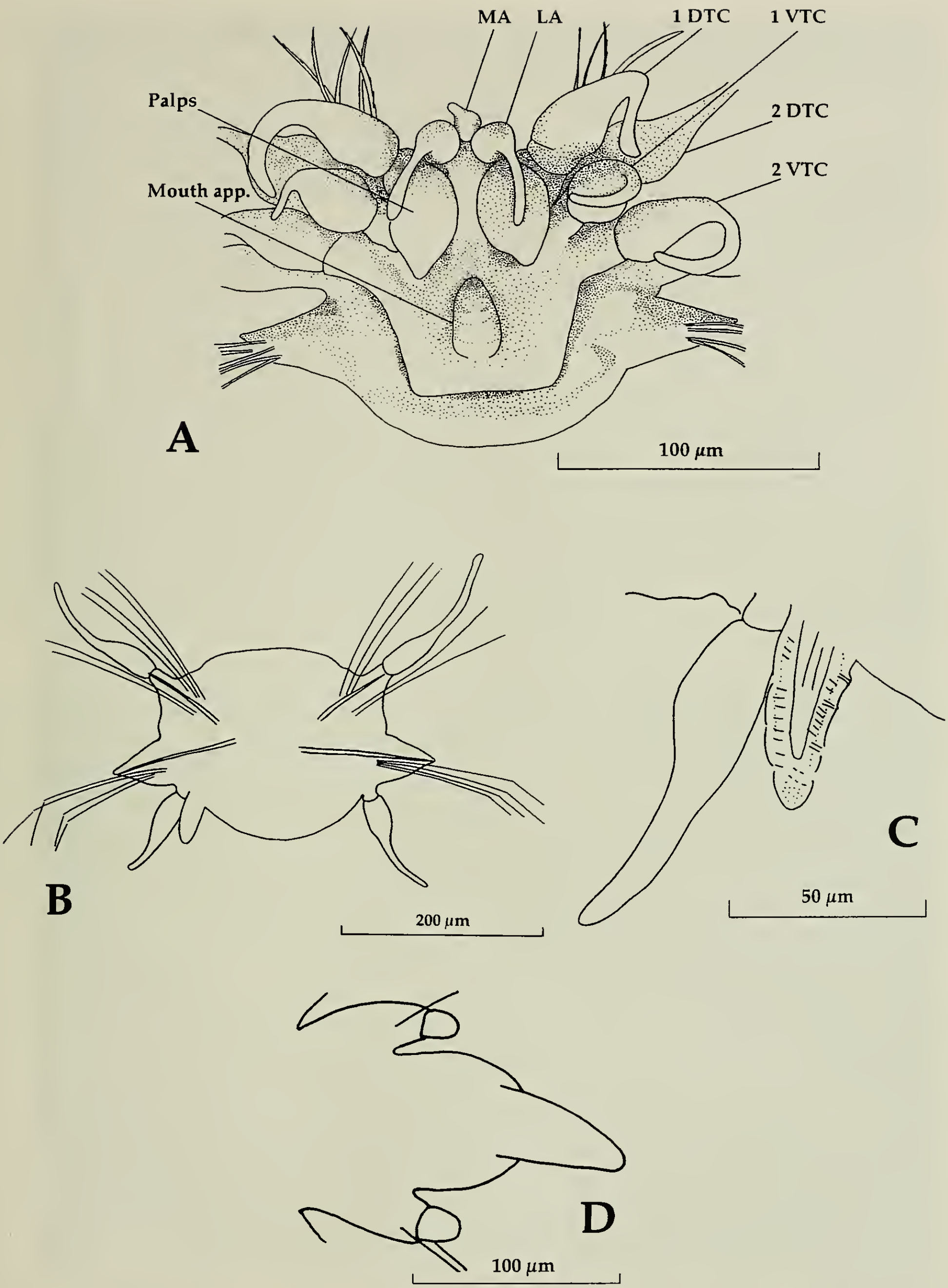

Fig. 1. *Dysponetus bipapillatus,* new species. A, anterior end, anteroventral view; B, segment 8, anterior view, ca. half the number of setae shown. Right papilla lost; C, papilla, left side of segment 8, anterior view; D, pygidium, ventral view. Abbreviations.—MA, median antenna; LA, lateral antenna; DTC, dorsal tentacular cirri; VTC, ventral tentacular cirri.

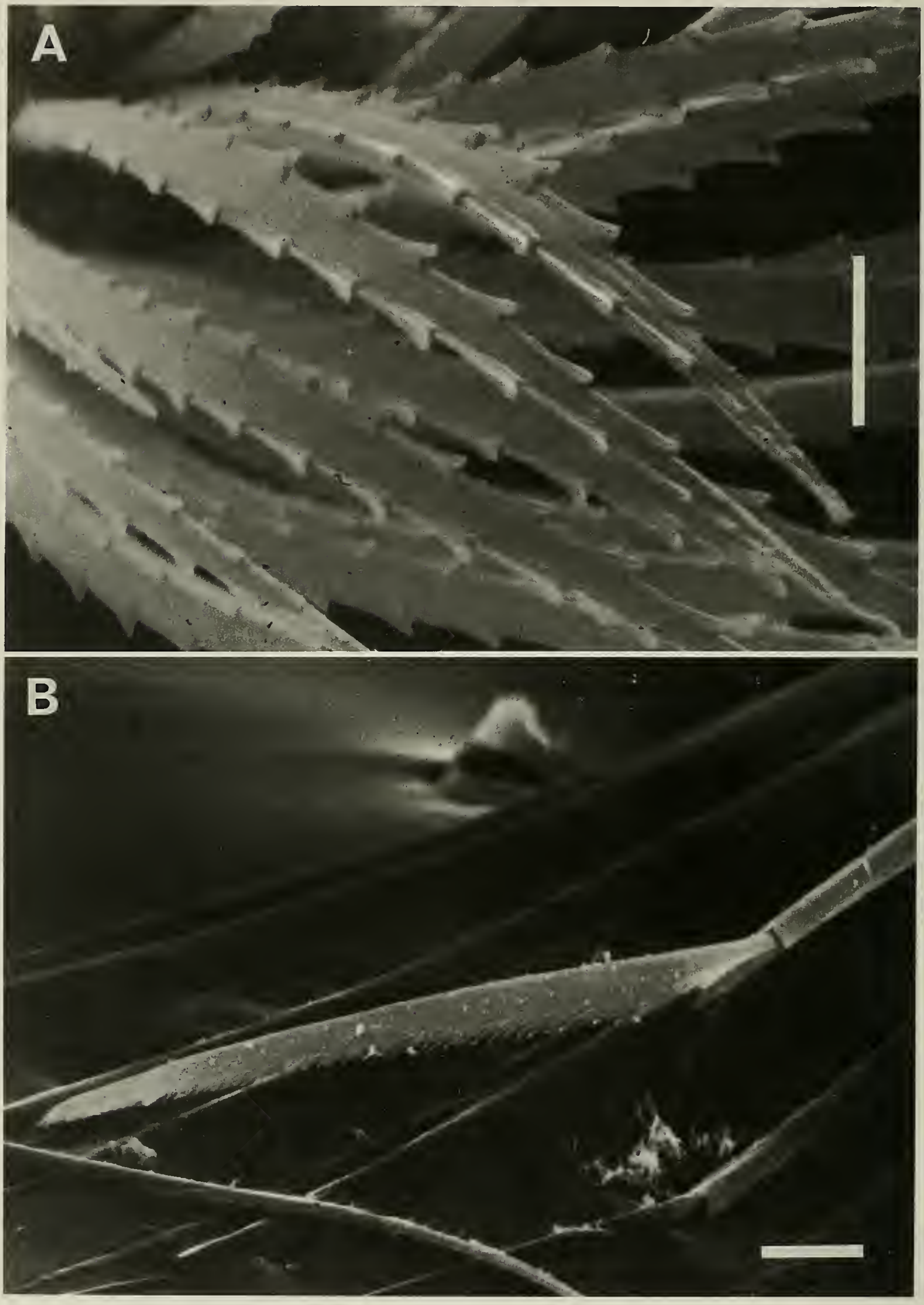

Fig. 2. *Dysponetus bipapillatus,* new species. A, notosetae, midbody segment, dorsal view; B, neuroseta, midbody segment, posterior view. Scale bars equal 10 μm (A), and 5 μm (B).

Table 1.—Summary of some morphological characters for described *Dysponetus* species.

Species	Tentacular segments formula	Eyes	Median antenna	Shape of palps	Mouth appendage	Accessory neurosetae
Dysponetus bidentatus Day, 1954	$\frac{0-1}{0-1}+\frac{S-1}{0-0}+\frac{S-N}{S-0}$	4	Dorsal	Elongated	Single	?
D. bipapillatus, new species	$\frac{0-1}{0-1}+\frac{S-1}{0-1}+\frac{S-N}{S-0}$	4	Anterior	Elongated	Single	Present
D. bulbosus Hartmann-Schröder, 1982	$\frac{S-1}{0-0}+\frac{S-1}{S-?}+\frac{S-N}{S-N}$	4	Anterior	Elongated	?	?
D. caecus (Langerhans, 1880)	$\frac{0-1}{0-1}+\frac{S-1}{0-1}+\frac{S-N}{S-N}$	0	Anterior	Elongated	Single	Present
D. gracile Hartman, 1965	$\frac{0-1}{0-0}+\frac{S-1}{S-1}+\frac{S-N}{S-N}$	0	Dorsal	Sphaerical	?	?
D. hebes (Webster & Benedict, 1887)	$\frac{0-1}{0-0}+\frac{S-1}{S-?}+\frac{S-N}{S-?}$	2	Anterior	Sphaerical	Double	?
D. macroculatus, new species	$\frac{0-1}{0-1}+\frac{S-1}{0-1}+\frac{S-N}{S-0}$	4	Anterior	Elongated	Single	Present
D. Paleophorus Hartmann-Schröder, 1974a	$\frac{0-1}{0-0}+\frac{S-1}{S-0}+\frac{S-N}{S-N}$	0	Dorsal	Sphaerical	Absent	Present
D. pygmaeus Levinsen, 1879	$\frac{0-1}{0-0}+\frac{S-1}{S-0}+\frac{S-N}{S-N}$	0	Dorsal	Sphaerical	Double	Present

23–28. Notosetal fascicles separated, leaving middle part of dorsum exposed.

Neuropodia well-developed. Compound neurosetae, with heterogomph shafts, and fine bidentate falcigerous blades (Fig. 2B). Neurosetal count, mid-body segments 9–13. One or two accessory simple setae, similar to but smaller than notosetae, present from segment 7, inserted distally and anteriorly on neuropodial lobe. Ventral cirri fusiform, shorter than dorsal cirri (length 100 μm in segments 7 & 8, 40–70 μm in others), inserted posteroventrally on neuropodial lobe, visible on live specimens in dorsal view. Some specimens of 10 or more segments possess single pair of digitiform appendages inserted proximal to ventral cirri in segment 8 (length 50 μm), internally possibly with ducts and duct openings (Fig. 1B, C; see Remarks).

Pygidium conical with single projection (length 50 μm), cylindrical, slightly distally tapering, inserted posteroventrally (Fig. 1D).

Color.—Live specimens colorless, transparent with red eyes. Preserved specimens white, eyes brown.

Reproduction.—No eggs or sperm visible in any specimens. Possible external genital organs on segments 8 in 3 out of 10 specimens with 10 or more segments.

Measurements.—Largest specimen 1.1 mm for 13 segments (Fig. 4). Length of holotype, 0.73 mm for 11 segments.

Habitat.—Found in relatively "clean" "*Amphioxus* sand" with wave ripples near large colonies of *Polysiphonia* sp.

Distribution.—Known only from Ischia, Bay of Naples, Italy.

Remarks.—Anterior (tentacular) segments and characters associated with cephalization exhibit variations within the chrysopetalids (Table 1). Perkins (1985:862) stated that when ventral cirri are lost in the ontogeny during cephalization, they are lost from segment 2 or segments 2 and 3. Adults (11–15 segments) of *D. bipapillatus* have ventral cirri on achaetous segment 1 and uniramous segment 2, but ventral cirri are absent on biramous segments 3 (Fig. 1A). Juvenile specimens of 9-segments have a biramous segment 2 with numerous noto- and neurosetae, but lacking ventral cirri (Figs. 3A; 5A). In 10-segment juveniles,

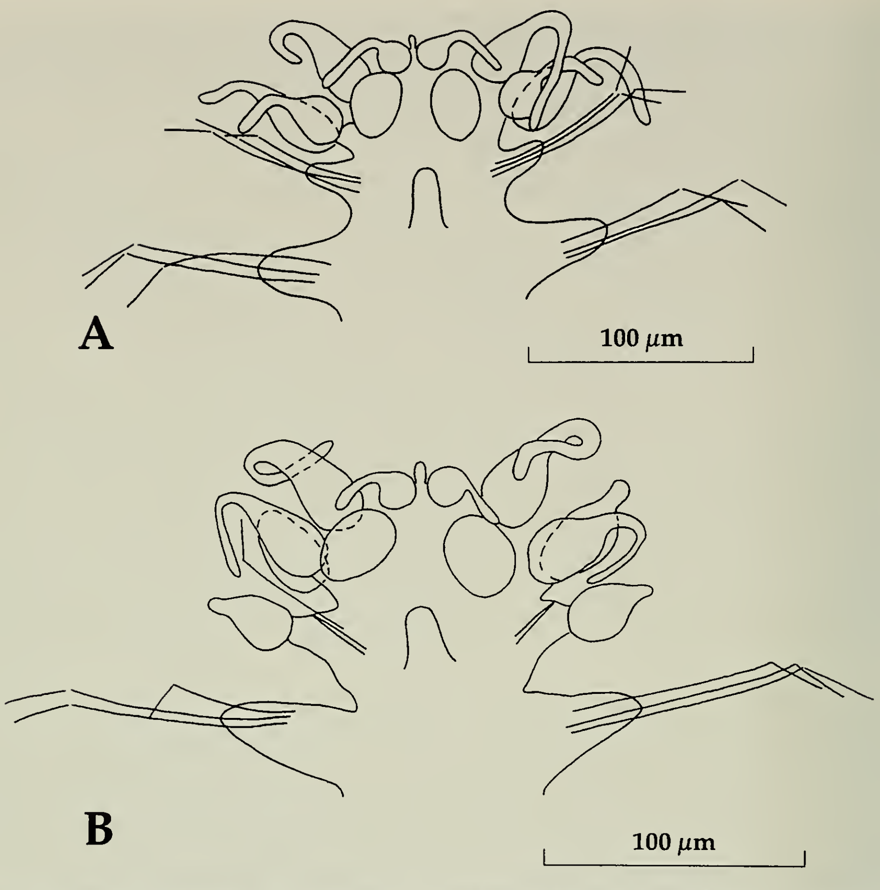

Fig. 3. *Dysponetus bipapillatus,* new species. A, 9 segment specimen, anterior end, ventral view; B, 10 segment specimen, anterior end, ventral view.

most neurosetae of segment 2 are absent, and ventral cirri present (Figs. 3B; 5B). A similar development was described for the chrysopetalid *Paleanotus bellis* (Johnson, 1897) by Blake (1975). This indicates that setae are lost from segments 1 and 2, ventral cirri of segment 2 develop in a late stage, and that ventral cirri of segment 3 are never present during ontogeny (Fig. 5). Late development of ventral cirri of segments 2 and 3, as well as development of tentacular segments from anterior setigers, is also reported for some hesionids (Haaland & Schram 1982, 1983; Schram & Haaland 1984).

The digitiform appendages found ventrally on segment 8 in some of the specimens (3 out of 10 specimens with 10 or more segments) are presently a unique feature within the Chrysopetalidae (Fig. 1B, C). Similar appendages were recently described for an interstitial hesionid which function as genital organs, as indicated by ultrastructural evidence (Westheide et al. 1994). Ultrastructural information, however, from *Dysponetus bipapillatus* is lacking, and the matter needs further investigation.

Dysponetus bipapillatus is similar to other *Dysponetus* species by the presence of serrated but not flattened notosetae, and a single pygidial projection. The accessory setae, present also in *D. pygmaeus, D. paleophorus* Hartmann-Schröder, 1974a, *D. caecus* (Dahlgren & Pleijel 1995) and *D. macroculatus,* new species (see below), are difficult to detect in normal parapodial

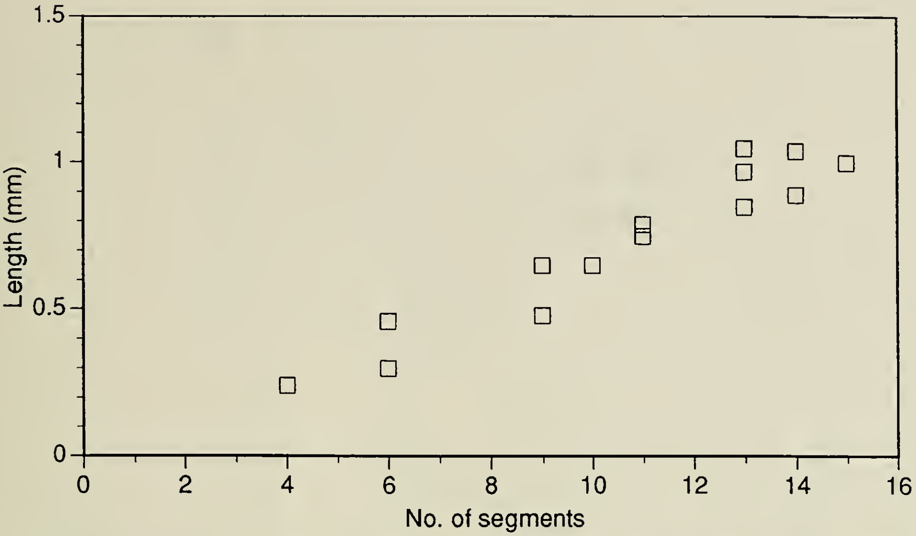

Fig. 4. *Dysponetus bipapillatus*, new species. Relationship between number of segments and length (mm).

preparations and require SEM for proper determination, which may explain why they have not been reported for other *Dysponetus* species. Further, *D. bipapillatus* is similar to *D. bidentatus, D. caecus* and *D. macroculatus* by the presence of two pairs of tentacular cirri on the first segment, uniramous second segment, and a single mouth appendage on the posterior mouth margin (Table 1).

Although no visible sexual products were present in any of the specimens, the ontogenetic development of anterior segments described above, and the presence of papillae on segment 8 in some of the specimens, here interpreted as genital organs, strongly suggest that the present description is based on adults.

$$\frac{0-1}{0-1}+\frac{S-1}{S-0}+\frac{S-1}{S-0} \quad \mathbf{A}$$

$$\frac{0-1}{0-1}+\frac{S-1}{S-1}+\frac{S-1}{S-0} \quad \mathbf{B}$$

$$\frac{0-1}{0-1}+\frac{S-1}{0-1}+\frac{S-1}{S-0} \quad \mathbf{C}$$

Fig. 5. Formulae showing setal (S) and tentacular (1) distribution on first three segments of *Dysponetus bipapillatus*, new species. A, 9 segment stage; B, 10 segment stage; C, adult stage.

Etymology.—The species name is derived from the Latin words *bi* meaning two, and *papillatus* which refers to the presence of papillae on segment 8 in some of the specimens.

Dysponetus macroculatus, new species
Figs. 6–7

Material examined.—Papua New Guinea: N. Madang, 05°10.3′S, 145°50.6′E, 10 m, SCUBA, clean sand with *Halimeda* remains, 3 paratypes (SMNH 4793), 26 Dec 1994; 1 specimen mounted on slide, 26 Dec 1994; holotype (SMNH 4792), 3 Jan 1995; 3 paratypes (SMNH 4794), 3 Jan 1995; 1 specimen used for SEM, 3 Jan 1995; 1 specimen mounted on slide, 3 Jan 1995.

Description.—Body, excluding parapodia, cylindrical; venter flattened. Posterior segments successively smaller, resulting body shape of fairly constant width, slightly tapered posteriorly.

Prostomium rectangular, longer than

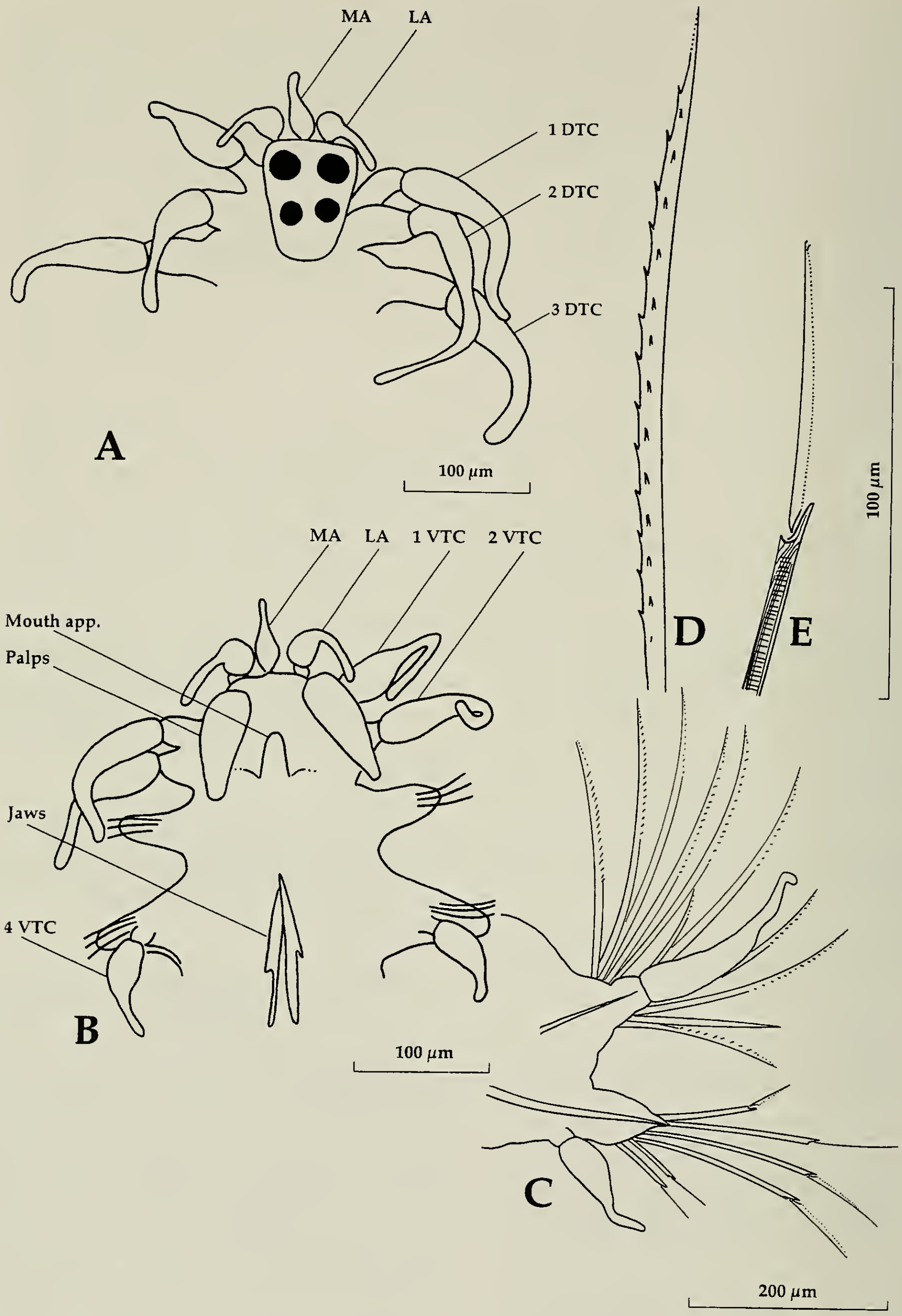

Fig. 6. *Dysponetus macroculatus,* new species. A, anterior end, dorsal view; B, anterior end, ventral view; C, midbody parapodium, anterior view (for clarity only half of number of setae drawn); D, notoseta (internal structures not illustrated); E, neuroseta. Abbreviations.—See Fig. 1.

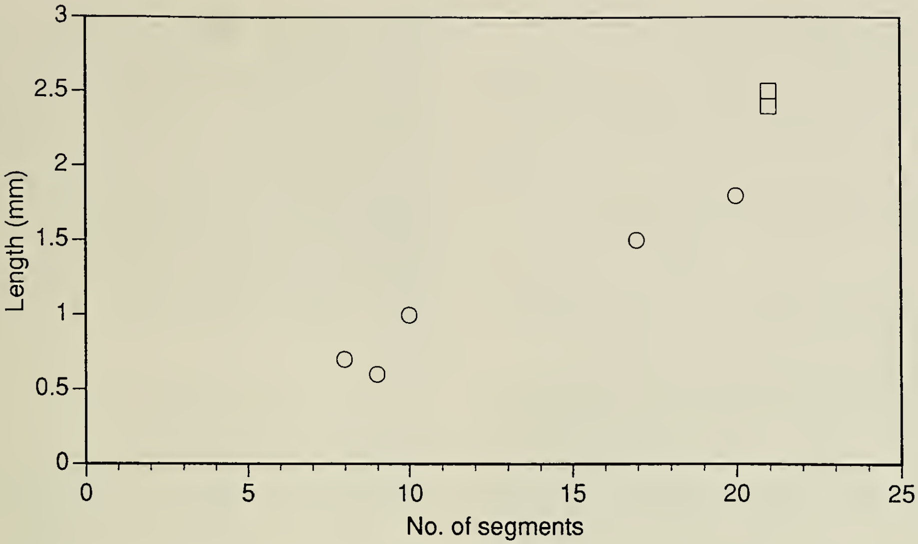

Fig. 7. *Dysponetus macroculatus,* new species. Relationship between number of segments and length (mm). Circles indicate entire specimens; squares incomplete specimens.

wide. Two pairs of large, rounded eyes, posterior pair smaller and closer together (Fig. 6A). Median antenna fusiform, inserted anterior to anterior pair of eyes (Fig. 6A). Lateral antennae fusiform, twice length of median antenna, inserted immediately dorsal to palps (Fig. 6B). Antennae without distinct ceratophores. Palps short, stout, inserted anteroventrally on prostomium, folded backwards ventrally, reaching about segment 2 (Fig. 6B); palpophores short. Nuchal organs not observed.

Single mouth appendage inserted on lower lip, anteriorly extended, subconical, with blunt tip (Fig. 6B). Single pair of stylet-shaped jaws (length 110 μm), visible through body wall in live specimens (Fig. 6B). Pharynx visible through body wall, extending to segment 6. Everted proboscis not observed.

First two segments with four anteriorly directed pairs tentacular cirri, longer but with same shape as, dorsal cirri of third and following segments (Fig. 6A, B). Segment 1 achaetous; segment 2 with notosetae only. Segment 3 biramous with dorsal cirri; ventral cirri absent (Fig. 6B). Biramous segments from segment 4 on with dorsal and ventral cirri (Fig. 6C). Single noto- and neuroacicula present from segment 2 (Fig. 6C); aciculae not detectable in segment 1.

Notopodial lobe well-developed. Dorsal cirri as long as setae, with cirrophores, proximally slightly inflated, distally tapering with blunt tips (Fig. 6C). Notopodial acicula faintly visible in dense notosetal fascicle. Notosetae internally chambered (not illustrated), with 15–17 pairs of fine denticles (Fig. 6D). Notosetal count, midbody segments 23–28. Notosetal fascicles covering most of dorsum.

Neuropodium well-developed. Compound neurosetae with heterogomph shaft and bidentate falcigerous blades (Fig. 6E). Neurosetal count, mid-body segments 19–22. Single accessory simple setae, similar to but smaller than notosetae, present in midbody segments, inserted distally and anteriorly on neuropodial lobe. Ventral cirri short, fusiform (Fig. 6C).

Pygidium shape rounded, similar to *D. bipapillatus.* Single median pygidial projection, inserted on posteroventral edge of pygidium.

Color.—Live specimens without pigmentation, eyes red, eggs white. Preserved specimens white.

Reproduction.—Specimens with mature eggs (ϕ = 100 μm) and sperm found in Papua New Guinea in December.

Measurements.—Largest specimen 2.5 mm for 21 segments (Fig. 7). Length of holotype, 2.4 mm for 21 segments.

Habitat.—Shallow water near coral reefs in clean sand wtih *Halimeda* remains.

Distribution.—Known only from the Madang area, Papua New Guinea.

Remarks.—*Dysponetus macroculatus* is similar to other *Dysponetus* species in the presence of serrated but not flattened notosetae and a single pygidial cirrus and the presence of simple accessory setae in the neuropodial lobe (see remarks for *D. bipapillatus*). *D. macroculatus* is similar to *D. bidentatus* Day in the presence of two pairs of large, red eyes, the absence of ventral cirri on segment 3, and the presence of bidentate neurosetal falcigers, but differs in the presence of ventral tentacular cirri on segment 2, and absence of ventral cirri on segment 3 (Table 1).

Specimens carrying eggs and sperm indicate that the description is based on adult characters.

Etymology.—The species name is derived from the combination of Latin terms *macro* and *oculatus,* meaning provided with large eyes.

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Appendix

Checklist of species of *Dysponetus,* with notes on material examined and major references.

Dysponetus Levinsen, 1879. Type species *Dysponetus pygmaeus* Levinsen, 1879, by monotypy.—Annenkova 1935.

D. bidentatus Day, 1954. Tristan da Cunha. Type material? Syntype 1955.3.20.7 at BMNH lost (A. Muir, in litt). No type material examined.—Hartmann-Schröder 1974b.

D. bipapillatus, new species. Ischia, Italy. Holotype (SMNH), paratypes (SMNH) and non-types (TD) examined.

D. bulbosus Hartman-Schröder, 1982. Cape Naturaliste, Australia. Holotype (ZMH) and non-types (ZMH) examined.—Hartmann-Schröder 1986, 1993.

D. caecus (Langerhans, 1880). As *Chrysopetalum caecum.* Madeira. Neotypes (SMNH) and non-types (TD) examined.—Laubier 1964, 1968; Dahlgren & Pleijel 1995.

D. gracilis Hartman, 1965. Off New England. Holotype (LACM-AHF) and non-types (LACM-AHF) examined.

D. hebes (Webster & Benedict, 1887). As *Taphus hebes.* Maine. Holotype (USNM) examined.—Annenkova 1935.

D. macroculatus, new species. Papua New Guinea. Holotype (SMNH), paratypes (SMNH) and non-types (TD) examined.

D. paleophorus Hartman-Schröder, 1974a. Norwegian Trench. Holotype (ZMH) and non-types (TD) examined.

D. pygmaeus Levinsen, 1879. Egedesminde, Grønland. Holotype (ZMUC) and non-types (ZISP, CMNA, TD) examined.—Annenkova 1935; Imajima & Hartman 1964.

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109(3):586–590. 1996.

Leptonerilla diplocirrata, a new genus and species of interstitial polychaetes from the island of Hainan, south China (Nerillidae)

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Abstract.—A new nerillid polychaete, *Leptonerilla diplocirrata,* new genus and species, is described from subtidal sandy sediments of Hainan Island, China. The species possesses the maximal number of prostomial appendages observed in the taxon: three antennae and one pair of palps. The body is composed of 9 segments, all of which bear cirri and compound chaetae. With the exception of one species it differs from hitherto known nerillids by the presence of two cirri on the parapodia of segments 2 to 9. This most disparate character is considered to be primitive for the family Nerillidae: it is the decisive diagnostic character of the new genus, which now also includes *Leptonerilla prospera* (Sterrer & Iliffe 1982).

The Nerillidae are all very small polychaetes with a constant number of segments in each species: they are distributed worldwide, predominantly in the interstices of coarse sediments in intertidal and subtidal areas. The only species of this family previously reported for the Chinese coastline is *Nerilla sinica* Wu and Chen, 1980 (Wu & He 1994). However, it is most likely that the number of species here is no less than in other coastal regions of the earth, and that the reason more of them have not been discovered is the paucity of research directed specifically to the meiofauna. Other meiofaunal genera, though previously documented only occasionally or not at all in this region, have been found in abundance when a concentrated search is made (see, e.g., Zhao & Wu 1991, Wu & Zhao 1992, Ding & Westheide 1994, Westheide et al. 1994). These records derive from several expeditions carried out since 1987 as part of a joint project between the First Institute of Oceanography in Qingdao and the Biology Department of the University of Osnabrück. In the course of these collecting trips the nerillid species introduced here was found off the island Hainan in the south of China. It is especially interesting because it exceeds all previously described genera in the profusion of its external structures and hence appears especially primitive.

Methods

Extraction was carried out with a $MgCl_2$ solution isotonic to seawater (for details see Westheide & Purschke 1988). First microscopic investigation and tracing with a camera lucida took place when the animals were still alive. For a more detailed observation one fixed specimen (with SPAFG) was whole mounted in Zeiss W15 medium.

Leptonerilla, new genus

Diagnosis.—Three thread-like antennae. Two palps. Nine chaetigerous segments. Parapodia with two cirri except in the first segment with only one. Chaetae jointed. Two long anal cirri.

Etymology.—"Lepto" is a greek prefix for "thin, small, minute" to which "-nerilla" is attached referring to a nerillid.

Leptonerilla diplocirrata, new species
Fig. 1

Material examined.—Living specimens came from a subtidal patch of sand between coral reefs, 2–3 m deep, Hainan Island, South China Sea: near Island Xizhou off Sanya (18°14′N, 109°30′E), 19 Oct 1991.

Type material.—Holotype is a whole mount of the single mature specimen, deposited in the Senckenberg Museum, Frankfurt (No. SMF 5300).

Description.—Almost colorless. Length ca. 690 μm. Width between segments 1 and 2: 56 μm, between segments 4 and 5: 90 μm (parapodial cirri not included). Separation of the relatively short prostomium from the trunk not distinctly visible (Fig. 1A). With three thread-like, more or less smooth, non-jointed antennae; the median one somewhat longer (ca. 250 μm) than the lateral antennae (ca. 215 μm); antennae positioned in a semicircle directly above the anterior margin of the prostomium. Two ventrolaterally positioned spoon-shaped palps (length ca. 56 μm); partly ciliated. Two eyes, probably with lenses. Two lateral ciliary tufts behind the palps indicate the nuchal organs.

Trunk with 9 chaetigerous segments, the posteriormost ones shortest. Parapodial cirri thread-like, resembling the antennae. Conspicuous constriction of the trunk between first and second segment. First chaetigerous segment (buccal segment or peristomium) different, in possessing only one relatively short (length ca. 50 μm) posteriorly bent parapodial cirrus on each side and in having the two chaetal bundles each conspicuously directed backwards. Parapodia in the following segments with two cirri each, positioned one above the other between the dorsal and the ventral bundle of chaetae. Dorsal and ventral cirri differing in length, the ventral one longer than the dorsal cirrus, especially obvious in chaetiger 2 (185 μm to 85 μm), and chaetiger 9 (215 μm to 130 μm). Chaetae all jointed (compound) (Fig. 1C) of identical shape and mostly equal in size, except for single simple capillary chaetae (Fig. 1B), which were found in the dorsal bundle of segments 1 and 4. Number of jointed chaetae per bundle differing between segments; highest number (more than 10) in the first segment and in segments 6 to 8; lowest numbers (1 or 2) in segments 3 and 4.

Pygidium rather narrow (width ca. 25 μm), ventrally with very short appendage, dorsally with two long (ca. 270 μm) thread-like anal cirri. Pharyngeal bulb possessing two (?) buccal pieces, not clearly visible. One vitellogenic oocyte (length: ca. 80 μm) positioned in segments 6 and 7; no other details of reproductive organs discernible.

Etymology.—The species name refers to the presence of two cirri in the parapodial structures.

Discussion

As in the case of the small Dinophilidae (Westheide 1985, Eibye-Jacobsen & Kristensen 1994), a progenetic origin can also be inferred for the Nerillidae. However, there is strong evidence that the Dinophilidae are closely related to the Dorvilleidae, which makes it likely that these two groups are paedomorphic Eunicida; in contrast, the Nerillidae do not resemble any juvenile stages of extant polychaetes in any obvious respects. The most that can be said is that the body configuration of juvenile Onuphidae (Hsieh & Simon 1987) is at least superficially consistent with that of the nerillids. Apart from these considerations, for every group of morphologically distinct paedomorphic species there remains the practically insoluble question whether they originated from a single progenetically evolved stem species or evolved independently several times by progenesis from different though closely related macrofaunal species (Westheide 1987). Only in the first case is it possible to describe a phylogenetic sequence and to construct a cladogram that illustrates the phylogenetic relationships. With this qualification, we shall briefly discuss the

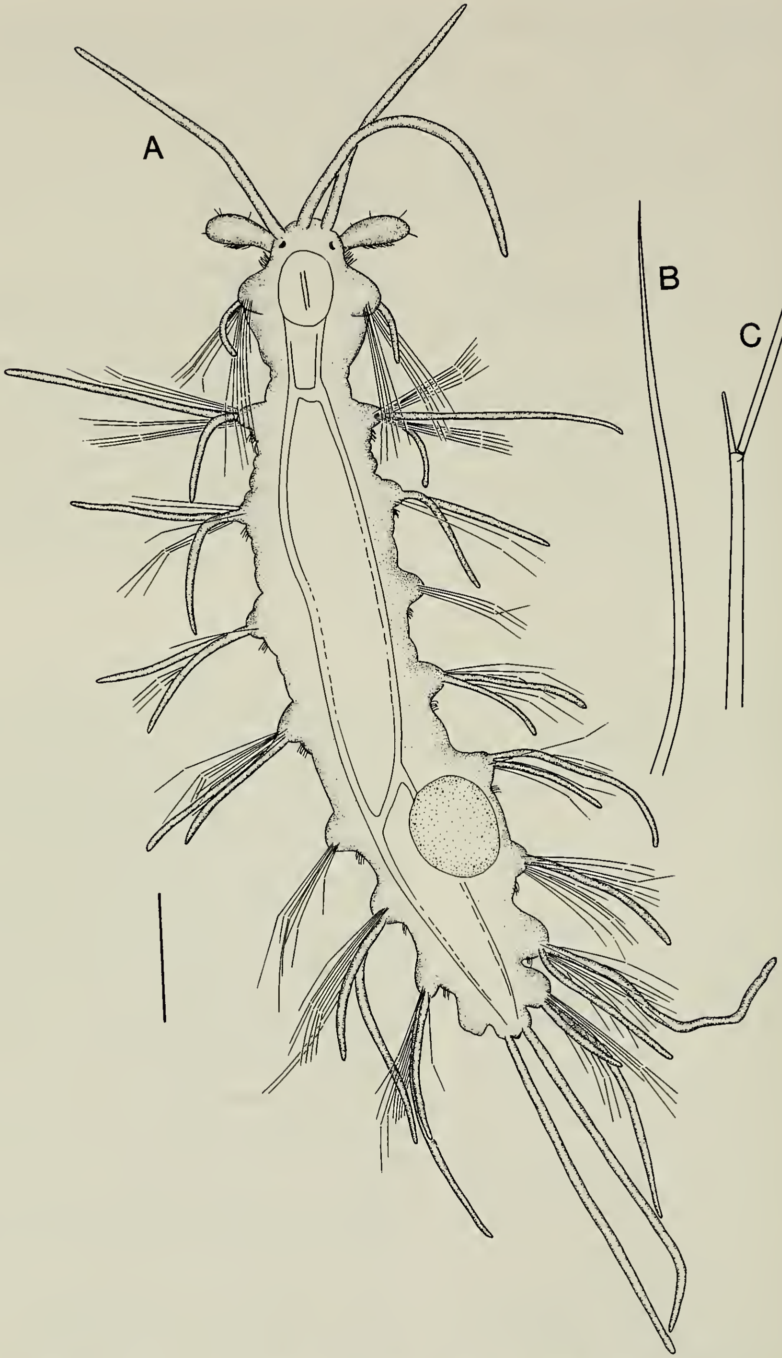

Fig. 1. *Leptonerilla diplocirrata,* new genus and species. A, dorsal view of living specimen, scale = 100 μm; B, simple chaeta; C, compound chaeta.

phylogenetic position of the new taxon. Assuming further that the postulated progenetic stem species was the least paedomorphic in general structure (admittedly an a priori assumption unsupported by any fundamental arguments), a nerillid species particularly close to the stem species ought to have a relatively complex configuration, with larger numbers of segments and of appendages, more complex and numerous chaetae, etc.

By these criteria, the new species presented here is the most primitive nerillid yet known, one that would be especially close to the stem species, as follows. The prostomium has the greatest number of antennae (3) and palps (2) known for the Nerillidae (Westheide 1990); the body is composed of the maximal number of segments (9), all of which bear cirri and chaetae; anal cirri are present; the chaetae are jointed; and there are also a few simple chaetae. The appendages are the same as are present in the various *Mesonerilla* species (e.g., *M. intermedia* Wilke, 1953) (Westheide 1990). A disparate character, which could be considered especially primitive, is the presence of two cirri on the parapodia of each of the segments 2 to 9; like the two bundles of chaetae, these can be interpreted as indicating a biramous structure of the parapodia in the macrofaunal species from which the Nerillidae are derived. The attempt to homologize these cirri with specific structures of typical biramous parapodia, such as the neuropodial or notopodial cirri or lobes, would be premature. Two cirri have been reported for some of the individuals in a population of *Micronerilla minuta* (Swedmark, 1959) (Jouin 1970); they occurred in segments 2 to 6 (Westheide 1990), an indication that this otherwise distinctly different and more highly evolved form originated from a species with double cirri like the new species presented. Another form with two cirri on just the same segments, 2 to 9, is *Mesonerilla prospera* Sterrer & Iliffe, 1982 from inland marine caves of Bermuda. These animals are relatively close to the new species in also possessing 9 chaetigerous segments, 3 threadlike antennae, and compound chaetae, but they differ distinctly in their morphometric data: their length ranges from 1500–2050 μm, their maximum width is 250–420 μm, the median antenna is up to 650 μm long, the palps have a length of 230 μm and that of the parapodial cirri is 550 μm. The single cirri of the parapodia of the first segment, however, are much shorter (30 μm), as are the anal cirri, with a length of only 120 μm. Hence, this Bermudan species is one of the largest nerillids, and the females were observed to carry up to 8 mature eggs with a diameter of up to 200 μm (Sterrer & Iliffe 1982). Because this species is consistent with the new genus *Leptonerilla* with respect to the decisive diagnostic character, the possession of two cirri in the chaetigerous segments 2 to 9, we likewise assign it to this genus: *Leptonerilla prospera* (Sterrer & Iliffe, 1982).

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A quantitative comparison of hectocotylus morphology between Mediterranean and western Atlantic populations of the squid *Illex coindetii* (Mollusca: Cephalopoda: Oegopsida: Ommastrephidae)

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Abstract.—Geographic variation in morphology of the commercially important squid species *Illex coindetii* has led to speculation about possible taxonomic differences among populations. We compared hectocotylus morphology between western Atlantic specimens, from the Gulf of Mexico and Caribbean, and Mediterranean specimens, from the Tyrrhenian Sea. Although a few differences were found in morphometrics and meristics, we conclude that the two populations are conspecific.

Although *Illex coindetii* is important to fisheries, systematic questions about relationships among populations referred to this species remain unresolved. Several authors disagree on the number of species-level taxa of the genus *Illex.* This is due primarily to the presence of several different "morphs" that are difficult to assign to a recognized species (Zuev 1966, Aldrich & Lu 1968). Indeed, various morphological clines exist among the different species of *Illex,* especially in the area off the southeastern United States where distributions of three species overlap (Roper et al. 1996).

Until Roper et al. (1969) recognized *Illex coindetii* in the western North Atlantic, all *Illex* in that region had been referred to *I. illecebrosus.* Other cephalopod researchers, such as G. L. Voss, were reluctant during the 1970s and 80s to accept multiple species of *Illex* in the western North Atlantic (K. Mangold, pers comm). Nesis (1987) listed *argentinus, illecebrosus* and *coindetii* as subspecies of *I. illecebrosus.* Whereas Nesis (1987) recognized only *I. illecebrosus* and *I. oxygonius* as full species, Chingus Nigmatullin considers *I. illecebrosus, I. coindetii* and *I. argentinus* to be valid species, but oxygonius to be a reproductive morph found in all *Illex* species (pers. comm. Also see e.g., fig. 1 in Laptikhovsky & Nigmatullin 1993).

Illex coindetii inhabits the continental shelf and upper slope. Its distribution as currently defined is very broad, ranging from the eastern to the western Atlantic. The species can be found along the European coast of the Atlantic Ocean, from Oslo Fjord and the North Sea (ca. 59°N), to the Bristol Channel southward; the Mediterranean, Adriatic and Aegean seas; and the Atlantic coast of Africa as far south as Namibia (19–20°S). The species is absent from the upper Adriatic Sea and the Black Sea. In the western Atlantic *I. coindetii* lives from 37°N through the Florida Straits, Gulf of Mexico, Caribbean Sea, to northeastern South America, including Venezuela, Surinam and French Guiana (ca. 3°N). According to Roper et al. (1996), multiple morphs of *Illex coindetii* occur in both the eastern and western Atlantic, but all appear to be conspecific. Although Roper et al. (1996) compared specimens of *I. coindetii* from both sides of the Atlantic, they did not include detailed quantitative anaylses.

An alternative explanation for the disjunct distribution of *I. coindetii* is that eastern and western Atlantic populations now considered to be *I. coindetii* are separate species, with gene flow interrupted by the spreading of the Atlantic since the end of the Cretaceous. Because this species has never been reported from mid-ocean samples, gene flow between eastern and western Atlantic populations now may be limited or non-existent. Therefore, allopatric processes may have allowed genetic divergence to occur between these populations.

Hectocotylus morphology includes several characters that are among the most important for definition of the species of *Illex,* and they were used by Roper and Mangold (1997) to redefine *I. coindetii.* As part of a larger study of development of the hectocotylus in *I. coindetii,* we examined meristics and morphometrics of hectocotylus characters in specimens from the Gulf of Mexico/Caribbean Sea area of the western North Atlantic and from the Tyrrhenian Sea in the Mediterranean to determine whether any differences are equivalent to those used to distinguish among other species of *Illex.*

Materials and Methods

Twenty-seven adult male specimens were examined both from the North Tyrrhenian Sea and from the region of the Gulf of Mexico and Caribbean Sea.

Tyrrhenian specimens were obtained from two samples taken from commercial catches landed at Porto S. Stefano, Grosseto, Italy. The first sample was caught in November 1992, the second sample in May 1993. Specimens were fixed in formalin/seawater as recommended by Roper & Sweeney (1983). Then they were drained, rolled in cheesecloth (lightly soaked in a 7% solution of formalin), and shipped to the National Museum of Natural History (NMNH) in Washington, D.C. Upon arrival, the specimens were transferred into 45% isopropyl alcohol.

Specimens from the Gulf of Mexico and Caribbean Sea came from the NMNH collections and from the Marine Invertebrate Museum of the University of Miami's Rosenstiel School of Marine and Atmospheric Science (RSMAS) in Miami, Florida. All had been fixed in formalin. Specimens from NMNH had been preserved in 45% isopropyl alchohol whereas those from RSMAS were in 70% ethanol for varying lengths of time. Specimens from these collections were selected to equal the number of mature males from the Tyrrhenian Sea, based on sex, maturity, collecting location, and physical condition.

For the present work, only mature males were selected. The maturity scale used was modified from that of Lipinski (1979); a fully mature male has the Needham's sac swollen with spermatophores and the testis at its maximum development.

Measurements.—We examined the following characteristics: mantle length; the basal section of the hectocotylized arm, which has no suckers; the proximal section of the hectocotylized arm, which has normal suckers; the medial section of the hectocotylized arm, which has reduced suckers and fringed trabecular flaps; the distal section of the hectocotylized arm and its major modifications, lamellae and papillae; and the dentition of the suckers.

Most measurements were made with a flexible ruler. The diameter of the suckers and number of tiny suckers on the tip of the hectocotylus were assessed using a dissecting microscope with an ocular micrometer.

Statistical comparisons used the Tukey-Kramer method (Sokal & Rohlf 1981) to compare averages of measurements, indices, and counts of the two populations. Linear regressions were compared to evaluate differences between relationships of the measured characters with ML. The following abbreviations were used: ML: Dorsal mantle length; HALt: total length of hectocotylized arm from proximal V-notch to distal tip (see Fig. 1); OALt: total length of opposite arm from proximal V-notch to distal tip; HAb: length of hectocotylized arm from V-notch to the first (most proximal) sucker—This is the basal, suckerless part of the arm; HA1: length of proximal region of hectocotylized arm, bearing normal suckers; HA2: length of medial region of hectocotylized arm, bearing reduced suckers and fringed trabecular flaps; HA3: length of distal hectocotylized arm tip, bearing lamellae and papillae; HASn: greatest diameter of exposed part of horny ring of normal suckers on HA1; HASr: greatest diameter of exposed part of horny ring of reduced suckers on HA2; HA1SC: number of suckers on HA1; HA2SC: number of suckers on HA2; LC: number of lamellae on HA3; (this includes, unless otherwise specified, the number of knobs present on the lamellae row); PC: number of papillae (and knobs) on HA3; HALti: index of HALt as percentage of ML; OALti: index of OALt as percentage of ML (note that this index and HALti are the only ones standardized to ML); XXXi: index of the measure XXX (e.g., HAb) as percentage of HALt: R: correlation coefficient of the linear regression.

Results

Basic modifications of the hectocotylized arm are similar in both populations. Either the right or left ventral arm is hectocotylized. It is longer (about 4–5%) and more robust than the opposite arm. The hectocotylus tip (HA3) is about 26% (± ca. 3%) of the length of the hectocotylized arm. Distal to the proximal 7th normal pair, the suckers diminish in size and the trabeculae are modified into 10–14 lobate flaps that are fringed and papillose (HA2). The second or third pair of modified trabeculae are the largest; distally, they are reduced in size. Suckers and protective membranes are not found on the modified tip (HA3). In the dorsal row of HA3, 1–2 conical knobs are followed by a series of transversely broad, thin, nearly truncate flaps or lamellae that gradually reduce in size distally. Minute papillae occur on the distal tip. In the ventral row of HA3, there is a series of conical papillae that gradually diminish in size toward the tip of the arm. A low, weak zigzag ridge is sometimes visible between papillae and lamellae. The aboral keel is broadly expanded along the distal portion of the hectocotylus (HA3).

Quantitative observations.—Statistical comparisons of measurements, counts, and indices are summarized in Tables 1–3. Average measurements show that the specimens from the western Atlantic are larger than those from the Mediterranean. The larger western Atlantic squids have longer arms, both hectocotylized and opposite, and larger suckers than those from the Mediterranean, although relative to ML the arms of western Atlantic squids were shorter. Regression analysis (Fig. 2), showed that all of these characters overlapped greatly when considered as a function of overall size of the specimens (ML).

Sucker counts do not differ significantly between populations, although western Atlantic squids tend to have one sucker more in the medial section (HA2) and one fewer in the proximal section (HA1) than in the Mediterranean squids. There are significantly fewer papillae in the Tyrrhenian specimens and the reduction in number of lamellae in the Tyrrhenian specimens is highly significant.

The differences in indices between populations are not statistically significant except for the length of the opposite arm. In Tyrrhenian specimens the non-hectocotylized ventral arm is longer relative to the mantle length than in western Atlantic specimens. Although not statistically significant, a similar trend is seen in the relative lengths of the hectocotylized arms. It is important to remember, though, that finding a significant difference in one of several analyses can result from random effects, resulting in incorrect rejection of a true null hypothesis (no difference). Thus, a conservative inter-

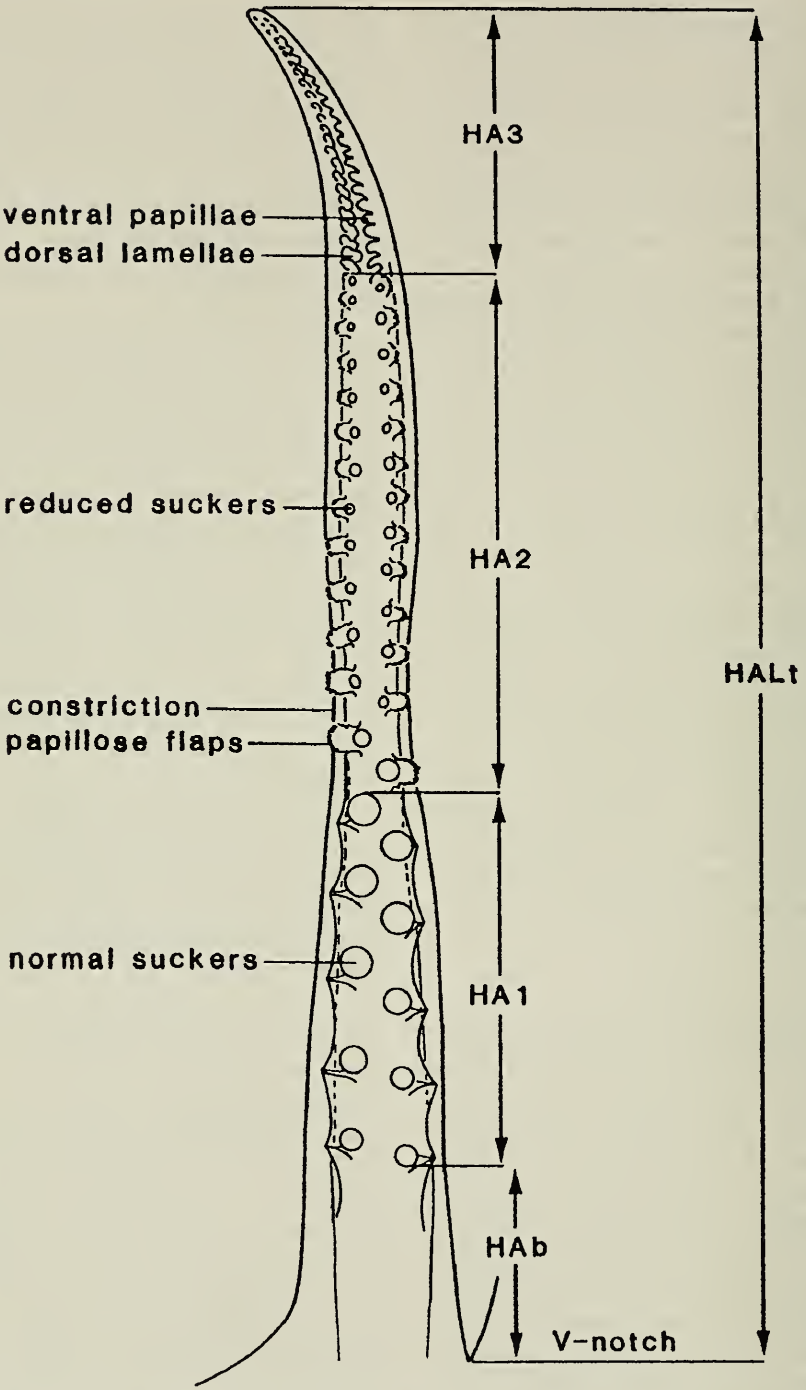

Fig. 1. The hectocotylus of *Illex coindetii* and its parts; knobs are not represented. Slightly modified from Roper & Mangold (1997).

Table 1.—Comparison of measurements (in mm) between *Illex coindetii* from the Tyrrhenian Sea (TYR) and from the Gulf of Mexico/Caribbean Sea (MEX). Mean values are presented along with standard deviation and the probability that there is no difference between the populations.

Measurement	TYR	MEX	Probability
ML	131.23 ± 19.88	148.33 ± 16.75	$P = 0.001$
OALt	87.89 ± 13.03	95.11 ± 9.94	$P = 0.025$
HALt	92.16 ± 12.01	98.63 ± 10.49	$P = 0.038$
HAb	9.63 ± 2.22	10.37 ± 2.02	$P = 0.199$
HA1	26.21 ± 5.61	28.33 ± 4.67	$P = 0.135$
HA2	31.95 ± 4.94	34.37 ± 4.74	$P = 0.069$
HA3	24.41 ± 4.77	25.93 ± 3.33	$P = 0.179$
HASn	1.845 ± 0.313	2.016 ± 0.297	$P = 0.043$
HASr	0.556 ± 0.163	0.625 ± 0.138	$P = 0.304$

pretation of the analyses of indices is that the two populations are not different.

As a rule, in the comparison of linear regressions for relationships between measures and mantle length (Table 4), the western Atlantic specimens show more variance in the vertical-axis coefficient than do the Mediterranean ones. In general, the slopes of the regressions are steeper for Tyrrhenian specimens, than for western Atlantic ones. This means that for the same increase in length of the mantle, the arms or their parts generally grow more in Mediterranean specimens. The only exception is HAb, the suckerless basal region of the hectocotylus. This shows a higher slope (faster growth) in specimens from the Gulf of Mexico/Caribbean Sea.

Qualitative differences.—Specimens from the Gulf of Mexico/Caribbean have modifications on the hectocotylized arm that show a greater degree of development and usually are relatively larger than in the Tyrrhenian specimens. For example, the development of fringed flaps is greater in western Atlantic specimens. However, the flaps diminish in size gradually toward the tip of the arm in specimens from both areas. Papillae in the ventral row are longer and set along the ventral side of a zigzag ridge always present on the hectocotylus in animals from the Gulf of Mexico/Caribbean. The dorsal row of lamellae usually has one or two knobs, although sometimes there are no knobs and rarely there are 3 or 4 knobs. No specimens from the Mediterranean had four knobs. The suckers have the same kind of dentition in both geographic areas.

Table 2.—Comparison of counts of meristic characters of hectocotylized arms between specimens of *Illex coindetii* from the Tyrrhenian Sea (TYR) and from the Gulf of Mexico/Caribbean Sea (MEX). Mean values are presented along with standard deviation and the probability that there is no difference between the populations.

Meristic	TYR	MEX	Probability
HA1SC	11.96 ± 1.45	11.42 ± 1.30	$P = 0.156$
HA2SC	23.29 ± 3.62	24.15 ± 3.04	$P = 0.346$
PC	20.36 ± 8.51	25.15 ± 5.18	$P = 0.016$
LC	19.71 ± 5.22	24.19 ± 5.68	$P = 0.004$

Squids from the Gulf of Mexico/Caribbean have papillae and lamellae that are more similar in numbers, because of the presence of the zigzag ridge connecting the lamellae dorsally and papillae ventrally. The zigzag ridge is very rare in Tyrrhenian specimens, and when present its shape usually is not so well defined. This seems to be related to the higher variability in numbers of papillae in the Mediterranean squids.

Discussion

All species of the genus *Illex* possess hectocotyli with the same basic structure, i.e., the primary modification is the tip of the hectocotylized arm (HA3). Only this

Table 3.—Comparison of morphometric indices of *Illex coindetii* from the Tyrrhenian Sea (TYR) and from the Gulf of Mexico/Caribbean Sea (MEX). Mean values are presented along with standard deviation and the probability that there is no difference between the populations.

Index	TYR	MEX	Probability
OALti	67.67 ± 5.95	64.55 ± 5.25	$P = 0.044$
HALti	71.26 ± 7.15	66.76 ± 5.47	$P = 0.177$
HAbi	10.47 ± 2.35	10.44 ± 1.68	$P = 0.096$
HA1i	28.46 ± 4.48	28.69 ± 3.27	$P = 0.823$
HA2i	34.66 ± 3.10	34.84 ± 3.01	$P = 0.829$
HA3i	26.29 ± 3.19	26.32 ± 2.51	$P = 0.970$
HASni	2.008 ± 0.280	2.020 ± 0.281	$P = 0.874$
HASri	0.606 ± 0.169	0.634 ± 0.128	$P = 0.493$

part, with major modifications of sucker stalks into lamellae, knobs, and papillae, should be considered the true hectocotylus. The opposite arm shows no signs of hectocotylization. The opposite arm is shorter than the hectocotylized arm in all *Illex* species except *Illex illecebrosus,* in which the opposite arm is longer than the hectocotylized one. The mean, range, and standard deviation of ratio of length of the hectocotylus tip to the total length of the hectocotylized arm is (according to Roper et al. 1996): 13.0–22.1–30.3% ± 4.6% in *Illex illecebrosus,* 17.1–25.1–30.0% ± 2.7% in *I. coindetii,* 23.8–28.8–32.0% ± 2.7% in *I. oxygonius,* 19.8–50.3–70.3% ± 11.0% in *I. argentinus.*

Illex coindetii is the only species of this genus in which the medial part of the hectocotylized arm (HA2) forms a distinctive section. The medial section in *I. argentinus* is indistinguishable from the tip, resulting in the high ratio of tip length to arm length listed above. The medial section is unmodified in both *I. illecebrosus* and *I. oxygonius.* In *I. coindetii,* distal to the 7th pair of suckers the trabeculae (i.e., the fingerlike appendages from the sucker bases) are transformed into papillose fringed flaps. This feature, along with the reduction of sucker size, and the dentition of the horny rings of the suckers, is distinctive of the medial part of the hectocotylized arm (Lu 1973).

According to Lu (1973), the modified trabeculae and flaps are larger and more papillose in *Illex coindetii* specimens from African waters (primarily the Gulf of Guinea) than in specimens from the Gulf of Mexico, the Caribbean Sea or the Mediterranean Sea. The length of the hectocotylized arm is different in these diverse areas; the Mediterranean Sea has animals with the longest hectocotylized arms, 71.1% of the mantle length, compared with 68.8% from the Caribbean Sea, 59.7% from the Gulf of Mexico, and 58.6% in those from West Africa.

Besides the presence of the more developed zigzag ridge on the tip of the hectocotylus in the western Atlantic specimens, no major differences have been detected between samples from the two study areas. We confirm that animals from the Gulf of Mexico/Caribbean Sea have relatively shorter hectocotylized and opposite arms, but this seems to be a general feature of all arms in this species in these areas. The number of suckers on the arm is approximately equal on animals from both areas, usually 10–14 suckers on HA1, 22–26 suckers on HA2. Considering that relative length of the tip of the modified arm is one of the key characters distinguishing the species of *Illex,* the two populations should be considered as belonging to the same species because the HA3i is not significantly different between areas.

Morphological variability across the broad geographic range of *I. coindetii* and

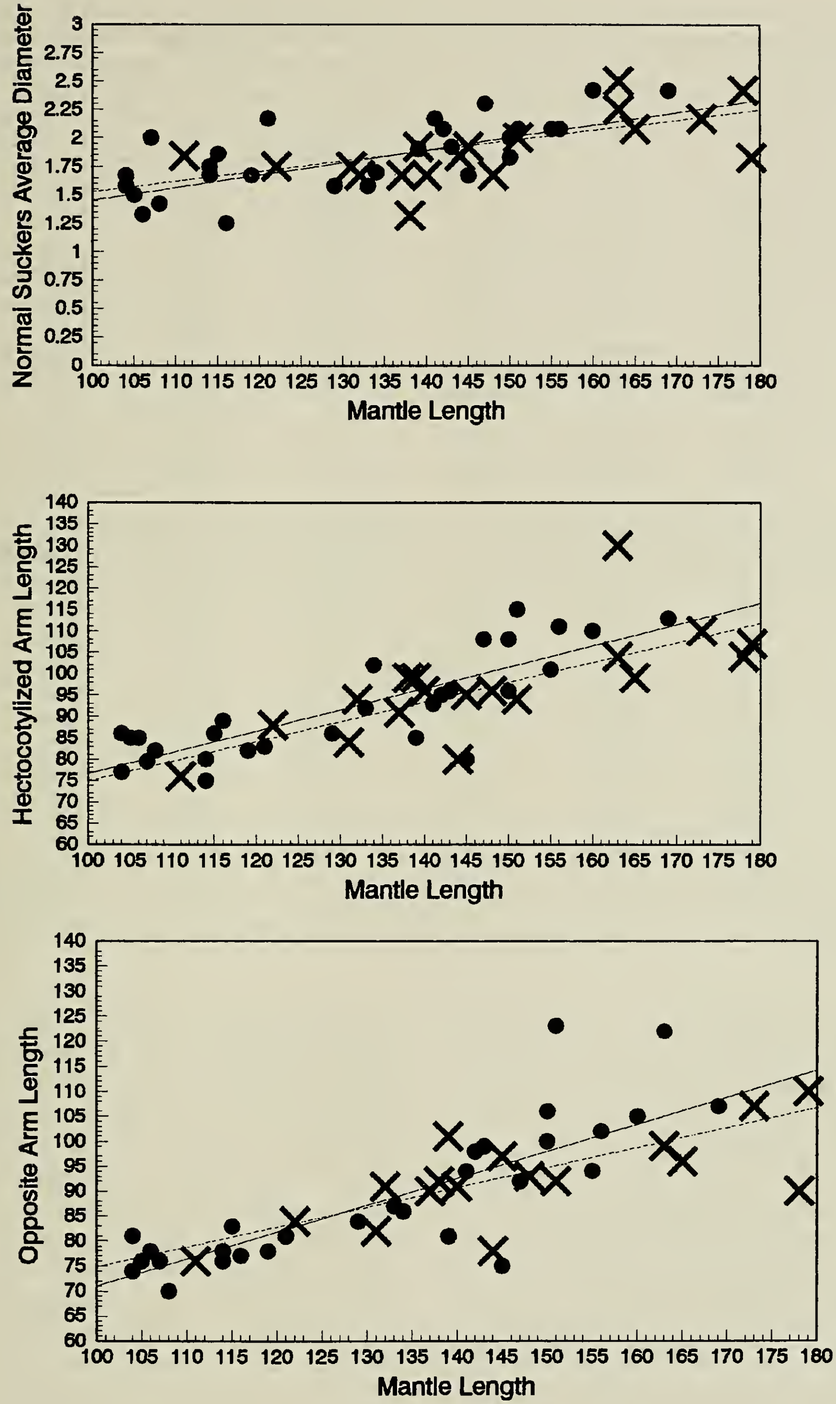

Fig. 2. Regressions of various measurements against mantle length. The graphs here are for the three measurements for which statistically significant differences were shown in Table 1. × = Gulf of Mexico/Caribbean specimens; ● = Tyrrhenian Sea specimens.

Table 4.—Linear regression indices with standard errors (SE) for morphometric and meristic characters regressed against mantle length. TYR, Specimens from the Tyrrhenian Sea in the Mediterranean; MEX, Specimens from the Gulf of Mexico and Caribbean; m, slope; q, vertical-axis intercept; *R*, correlation coefficient.

	TYR						
Character	m	SEm	q	SEq	R^2	R	$P_R > 0.95$
OALt	0.539	0.073	17.150	9.718	0.675	0.822	Y
HALt	0.498	0.067	26.777	8.903	0.680	0.825	Y
HAb	0.029	0.021	5.867	2.813	0.066	0.257	N
HA1	0.103	0.052	12.668	6.838	0.133	0.365	N
HA2	0.205	0.027	5.030	3.648	0.682	0.826	Y
HA3	0.160	0.035	0.035	3.355	0.669	0.818	Y
HA1Sn	0.011	0.002	0.351	0.282	0.524	0.724	Y
HA2Sr	0.002	0.002	0.243	0.204	0.085	0.292	N
HA1SC	−0.036	0.012	16.699	1.658	0.243	0.493	Y
HA2SC	0.062	0.034	15.156	4.458	0.116	0.341	N
PC	0.205	0.074	−6.606	9.777	0.230	0.480	Y
LC	0.126	0.055	2.501	7.366	0.166	0.407	Y
	MEX						
	m	SEm	q	SEq	R^2	R	$P_R > 0.95$
OALt	0.399	0.109	34.944	16.274	0.455	0.675	Y
HALt	0.460	0.109	29.006	16.300	0.525	0.725	Y
HAb	0.071	0.023	0.052	3.438	0.372	0.610	Y
HA1	0.202	0.053	−1.379	7.914	0.474	0.688	Y
HA2	0.069	0.055	22.851	8.176	0.091	0.302	N
HA3	0.110	0.039	9.276	5.840	0.330	0.574	Y
HA1Sn	0.009	0.003	0.629	0.376	0.434	0.659	Y
HA2Sr	0.003	0.001	0.218	0.217	0.157	0.396	N
HA1SC	0.012	0.016	10.021	2.324	0.035	0.187	N
HA2SC	0.021	0.035	21.009	5.335	0.022	0.148	N
PC	0.083	0.059	11.197	8.826	0.110	0.332	N
LC	−0.007	0.035	22.313	5.275	0.008	0.089	N

Linear function is: $Y = (m \pm SEm) X + (q \pm SEq)$ where Y is the anatomical character, and X is the Mantle Length (ML).

the apparent isolation of the eastern and western populations have given rise to speculation about relationships among the populations (Zuev 1966, M R. Lipinski and Ch. M. Nigmatullin, pers. comm.). The present study does not support the concept of distinct taxa represented by the Gulf of Mexico/Caribbean and Tyrrhenian Sea populations. Although some differences were found in hectocotylus characters, most were not consistent enough to be statistically significant. We interpret these results to mean that the two populations studied are indeed conspecific.

Acknowledgments

Paola Belcari at the Dipartimento di Scienze dell'Ambiente e del Territorio, Universita' degli Studi di Pisa provided valuable advice as well as assistance in obtaining specimens. Nancy Voss of the Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida, kindly sent additional specimens from the Gulf of Mexico/Caribbean Sea area. Michael Sweeney of the Department of Invertebrate Zoology (Mollusks), National Museum of Natural History helped in many ways. He also reviewed a draft of the manuscript, as did Bruce Collette and Austin Williams of the NMFS National Systematics Laboratory.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
109(3):600–601. 1996.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Applications published in the *Bulletin of Zoological Nomenclature*

The following Applications were published on 28 June 1996 in Vol. 53, Part 21 of the *Bulletin of Zoological Nomenclature.* Comment or advice on any of these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary (I.C.Z.N.), % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Case No.

2932 *Hapalotrema* Looss, 1899 (Digenea): proposed designation of *H. loossi* Price, 1934 as the type species.
2961 *Alcyonidium mytili* Dalyell, 1848 (Bryozoa): proposed designation of a replacement neotype.
2964 S.D. Kaicher (1973–1992), *Card Catalogue of World-Wide Shells*: proposed suppression for nomenclatural purposes.
2925 *Crenitis* Bedel, 1881, *Georissus* Latreille, 1809 and *Oosternum* Sharp, 1882 (Insecta, Coleoptera): proposed conservation.
2974 *Stilpon* Loew, 1859 (Insecta, Diptera): proposed conservation.
2905 *Labrus* Linnaeus, 1758, *Cichlasoma* Swainson, 1839 and *Polycentrus* Müller & Troschel, 1848 (Osteichthyes, Perciformes): proposed conservation of usage by the designation of neotypes for *Labrus bimaculatus* Linnaeus, 1758 and *L. punctatus* Linnaeus, 1758.
2976 *Holotropis herminieri* Duméril & Bibron, 1837 (currently *Leiocephalus herminieri*) and *Proctotretus bibronii* T. Bell, 1842 (currently *Liolaemus bibronii*) (Reptilia, Squamata): proposed conservation of the specific names.
2970 *Tyrannula minima* Baird & Baird, 1843 (currently *Empidonax minimus*) and *Contopus pertinax* Cabanis & Heine, 1859 (Aves, Passeriformes): proposed conservation of the specific names.

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 28 June 1996 in Vol. 53, Part 2 of the *Bulletin of Zoological Nomenclature.* Copies of these Opinions can be obtained free of charge from the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Opinion No.

1834. *Fursenkoina* Loeblich & Tappan, 1961 (Foraminiferida): conserved.
1835. *Vejdovskyella* Michaelsen, 1903 (Annelida, Oligochaeta): given precedence over *Macrochaetina* Bretscher, 1899.
1836. *Scottia* Brady & Norman, 1889 (Crustacea, Ostracoda): *Scottia pseudobrowniana* Kempf, 1971 designated as the type species.
1837. *Oniscus asellus asellus* Linnaeus, 1758 (Crustacea, Isopoda): neotype designated.
1838. *Temnorhynchus* Hope, 1837 (Insecta, Coleoptera): conserved.
1839. *Coproica* Rondani, 1861 and *Ischiolepta* Lioy, 1864 (Insecta, Diptera): conserved by the designation of *Limosina acutangula* Zetterstedt, 1847 as the type species of *Coproica.*
1840. *Bagrus hoevenii* Bleeker, 1846 (currently *Hemibagrus hoevenii*; Osteichthyes, Siluriformes): neotype designated.
1841. *Scomber dentex* Bloch & Schneider, 1801 (currently *Caranx* or *Pseudocaranx dentex*) and *Caranx lugubris* Poey, [1860] (Osteichthyes, Perciformes): specific names conserved.
1842. *Coelurus bauri* Cope, 1887 (currently *Coelophysis bauri*; Reptilia, Saurischia): lectotype replaced by a neotype.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
109(3):602–603. 1996.

BIOLOGICAL SOCIETY OF WASHINGTON

123rd Annual Meeting, 7 May 1996

President Janet Reid called the meeting to order at 12:02 p.m. in the Waldo Schmitt Room, National Museum of Natural History. Following approval of the minutes from the 1995 annual meeting, Janet announced results of the 1996 elections of officers and Council members: President Elect—Richard Vari (NMNH); Secretary—Carole Baldwin (NMNH); Treasurer—Chad Walter (NMNH); Council—John Fornshell (Thomas Jefferson High School), Al Gardner (NMNH), Susan Jewett (NMNH), Rafael Lemaitre (NMNH), Diana Lipscomb (George Washington University), and Jim Norris (NMNH). Nominating Committee members Dave Pawson (Chairman) and Brian Kensley were recognized for their efforts in assembling a ballot for the elections.

Janet reported that the Council had voted to increase dues the Society pays to the American Association of Zoological Nomenclature from $150 to $200, and to allow the Association of Systematics Collections to use the Society's mailing list in an attempt to reach potential candidates for their Taxonomic Resources and Expertise Directory (TRED).

Proceedings Editor Brian Robbins reported that four issues of Volume 108 were published comprising 72 papers and 752 pages. There were 87 submissions in 1995, and as of 1 May 1996, there were 34 submissions, two fewer than at the same time in 1995 but the same as in 1994. Brian announced a decision by the Council to modify the statements on subsidized page charges that appear in each issue on the inside back cover. Beginning with this issue, the Society's policy on subsidizing page charges will be described as follows: "The Society, on request, will subsidize a limited number of contributions per volume."

Treasurer Chad Walter reported that income for the Society between 1 January 1995 and 31 December 1995 was $70,413.44 ($41,776.00 from publication charges, $23,220.00 from dues and subscriptions, $4,588.44 from interest on the Society's accounts, $829.00 from sales of back issues), and expenditures were $70,317.99 ($59,868.85 for publication costs, $10,070.47 for management costs, $378.67 for bank charges). The net gain of $95.45 for this period (Table 1) does not reflect all income and expenditures associated with the publication of issue 108-4. Chad noted that no remuneration was received by the Society for 72.7% of the pages published in issue 108-1, a record high for this accounting category. The average number of printed pages paid for by authors was 54% for the year.

Austin Williams was recognized for his service as Publications Manager from 1989–1995, particularly for effecting a major reorganization of the Society's stored paperwork. He was assisted in this effort by President Janet Reid. Austin has been replaced as Publications Manager by Storrs Olson, and will join Richard Banks and Chad Walter on the Financial Committee.

The Society notes with sorrow the deaths of three past presidents. Thomas E. Bowman, who held the office of President in 1974–1975, passed away on 10 August 1995. Tom also served as Vice-President (1973–1974), Council member (1968–1970), and Associate Editor for invertebrates (1974–1987). Ernest Lachner, 1967–1968 President, passed away 7 January 1996. Ernie served as 1st Vice-President of the Society (1966–1967), on the Council (1962–1963), and as a consulting specialist

Table 1. Summary Financial Statement for 1995.

	General Fund	*Endowment Fund	Total Assets
ASSETS: JANUARY 1, 1995	34,016.35	71,966.83	105,983.18
TOTAL RECEIPTS FOR 1995	65,829.50	4,583.94	70,413.44
TOTAL DISBURSEMENTS FOR 1995	70,317.99	00.00	70.317.99
ASSETS: DECEMBER 31, 1995	29,527.86	76,550.77	106,078.63
NET CHANGES IN FUNDS	−4,488.49	4,583.94	95.45

* The proceeds from sales were not directly deposited into the Endowment Fund (Calvert Account), but were deposited into the General Fund. However, sales are reported herein as being part of the Endowment Fund.

for ichthyology on the Editorial Board (1961–1963). Meredith Jones, 1970–1971 President, passed away 5 March 1996. Meredith's other Societal contributions included Vice-President (1967–1968, 1969–1970), 1st Vice President (1968–1969), Council (1988–1989), and Editor of "The Panamic biota: some observations prior to a sea-level canal," published in 1972 as Bulletin 2.

The meeting was turned over to incoming President Steve Cairns, who thanked Janet for her contributions to the Society over the past three years. The meeting was adjourned at 12:22 p.m.

INFORMATION FOR CONTRIBUTORS

Content.—The *Proceedings of the Biological Society of Washington* contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers are published in English (except for Latin diagnoses/descriptions of plant taxa), with an Abstract in an alternate language when appropriate.

Submission of manuscripts.—**Submit three copies of each manuscript in the style of the Proceedings to the Editor, complete with tables, figure captions, and figures** (plus originals of the illustrations). Mail directly to: Editor, Proceedings of the Biological Society of Washington, National Museum of Natural History NHB-108, Smithsonian Institution, Washington, D.C. 20560. (Do not submit manuscripts to an associate editor).

Presentation.—Clarity of presentation, and requirements of taxonomic and nomenclatural procedures necessitate reasonable consistency in the organization of papers. Telegraphic style is recommended for descriptions and diagnoses. The style for the Proceedings is described in "GUIDELINES FOR MANUSCRIPTS for Publications of the BIOLOGICAL SOCIETY OF WASHINGTON" a supplement to Volume 103, number 1, March 1990. Authors are encouraged to consult this article before manuscript preparation. Copies of the article are available from the editor or any associate editor.

The establishment of new taxa must conform with the requirements of appropriate international codes of nomenclature. Decisions of the editor about style also are guided by the General Recommendations (Appendix E) of the International Code of Zoological Nomenclature. When appropriate, accounts of new taxa must cite a type specimen deposited in an institutional collection.

Review.—One of the Society's aims is to give its members an opportunity for prompt publication of their shorter contributions. Manuscripts are reviewed by a board of Associate Editors and appropriate referees.

Proofs.—Authors will receive first proofs and original manuscript for correction and approval. Both must be returned within 48 hours to the Editor. Reprint orders are taken with returned proofs.

Publication charges.—Authors are required to pay full costs of figures, tables, **changes in proofs ($3.00 per change or revision),** and reprints. Authors are also asked to assume costs of page-charges. The Society, on request, will subsidize a limited number of contributions per volume. Payment of full costs will facilitate speedy publication.

Costs.—Printed pages @ $60.00, figures @ $10.00, tabular material @ $3.00 per printed inch per column. One ms. page = approximately 0.4 printed page.

CONTENTS

PROCEEDINGS
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PROCEEDINGS

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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The gorgonacean genus *Arthrogorgia* (Octocorallia: Primnoidae)

Frederick M. Bayer

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Abstract.—Operations by National Marine Fisheries vessels in Alaskan waters have collected specimens of two species of the gorgonacean genus *Arthrogorgia* Kükenthal, 1908, one of them undescribed. *A. utinomii,* new species, is described and compared with *A. ijimai* (Kinoshita 1907), the type species, as well as with *A. otsukai* Bayer, 1952, and *A. kinoshitai* Bayer, 1952. All species are illustrated by scanning electron micrographs (SEM).

Family Primnoidae
Arthrogorgia Kükenthal, 1908

Arthrogorgia Kükenthal in Kükenthal & Gorzawsky, 1908:625 (type species, *Calyptrophora ijimai* Kinoshita, 1907).—Kükenthal, 1919:476; 1924:319.—Bayer, 1952:63; 1981:937 (in key).—Bayer & Stefani, 1989:455 (in key).

Remarks.—This genus is similar to *Paracalyptrophora* but has several "infrabasal" scales rather than only one pair. The flexible, pinnate colonies of *A. ijimai* Kinoshita, always with a thin, membranous coenenchymal expansion between main axis and branches harboring a polychaete commensal, are conspicuously different from the more robust dichotomous or bipectinate colonies of *Paracalyptrophora.* Two previously described species of *Arthrogorgia* (Bayer 1952) approach *Paracalyptrophora* in this respect, as does a third species described below.

It could be argued that only *A. ijimai* is generically distinct, and that the three stout, dichotomously branched species should be ranked with *Paracalyptrophora.* However, the increased number of infrabasal scales seems to be a consistent character. The new species described below is even more peculiar in the extensive development of accessory scales between the operculars and the buccals.

Key to Species of *Arthrogorgia*

1(2). Colonies openly pinnately branched, with membranous coenenchymal expansions between the side branches and the main stem; polyps with strongly developed marginal spines on both basal and buccal pairs of body scales .... *ijimai* (Kinoshita)
2(1). Colonies dichotomously branched.
3(4). Basal scale pair of polyps without projecting spines .... *otsukai* Bayer
4(3). Basal scale pair of all or most polyps having marginal spines.
5(6). Free margin of buccal scales wide and developing projecting spines in some polyps but not all; when present, accessory scales below the operculars partly or completely concealed by the margin of the buccal scales. Outer surface of scales ornamented with blunt granules .... *kinoshitai* Bayer
6(2). Margin of buccal scales projecting little, not concealing the accessory scales below the operculars, bluntly rounded or with a blunt projecting angle not a prominent spine. Outer surface of scales ornamented with radial lines of sharp prickles .... *utinomii,* n. sp.

Arthrogorgia ijimai (Kinoshita, 1907)
Figs. 1, 2

Calyptrophora ijimai Kinoshita, 1907: 234.—Nutting, 1912:57, pl. 16, figs. 2, 3.
Arthogorgia membranacea Kükenthal & Gorzawski, 1908a:626; 1908b:29, pl. 2, figs. 10, 11; 1919:477; 1924:320, fig. 174.
Calyptrophora (Arthrogorgia) ijimai.—Kinoshita, 1908:59, pl. 4, fig. 28; pl. 6, fig. 54.
Not *Calyptrophora ijimai.*—Broch, 1935: 26, figs. 15, 16.

Material.—Japan. Sagami Bay: 35°09′40″N, 139°19′05″E, 1123 m, U.S.F.C. str. *Albatross* sta. 5087, 23 Oct. 1906. 5 colonies, USNM 30028 (SEM 2541). West of Izu Islands: 34°10′30″N, 138°40′E, 924 m, U.S.F.C. str. *Albatross* sta. 5080, 19 Oct. 1906. 2 colonies, USNM 30074 (SEM 94). South of Omae Zaki, Shizuoka, Honshu: 34°15′N, 138°E, 869–924 m, U.S.F.C. str. *Albatross* sta. 5079, 19 Oct. 1906. Shiono Misaki, Wakayama, Honshu: 33°23′40″N, 135°33′E, 1074 m, U.S.F.C. str. *Albatross* sta. 4969, 29 Aug. 1906. 4 colonies, USNM 49617. Shiono Misaki, Wakayama, Honshu: 33°23′40″N, 135°34′E, 1127 m, U.S.F.C. str. *Albatross* sta. 4971, 30 Aug. 1906. 6 colonies, USNM 49689.

Diagnosis.—Slender, pinnately branched *Arthrogorgia* usually with membranous coenenchymal expansion between proximal part of lateral twigs. Margin of buccal scales of polyps each with two, rarely three long, slender, fragile spines; both basal scales with a strong marginal spine (Figs. 1, 2); no infraopercular scales. Outer surface of body scales sculptured by fine, simple granules.

Description.—See Kinoshita 1908, Kükenthal & Gorzawski 1908b, Nutting 1912.

Remarks.—The species has been described adequately. The characteristic colonial form was well illustrated by Kinoshita (1908: pl. 4, fig. 28), Kükenthal & Gorzawski (1908b: pl. 2, figs. 10, 11) and Nutting (1912: pl. 16, figs. 2, 3). An isolated polyp is now illustrated by SEM (Fig. 2) for comparison with *A. otsukai* (Fig. 4), *A. utinomii* new species (Fig. 16, top) and, especially, *A. kinoshitai* (Fig. 8).

Gross evidence shown by young polyps suggests that the developmental origin of the infrabasal scales may differ among the species of *Arthrogorgia.* Young polyps of *A. ijima* about 1 mm long do not yet have infrabasals (Fig. 1, bottom), but such scales are present in young polyps of *A. otsukai* at a similar size (Fig. 4, bottom).

There can be no doubt that the "3 grosse Bruchstücke" from the Okhotsk Sea identified as *Calyptrophora ijimai* by Broch (1935) are, in fact, *A. kinoshitai* Bayer (see below).

Arthrogorgia otsukai Bayer, 1952
Figs. 3, 4

Arthrogorgia otsukai Bayer, 1952:65, pl. 2, figs. 9–12; pl. 3, figs. 13–27.

Material.—Bering Sea, between Bowers Bank and codfish banks off mouth of Aangan River, Kamchatka. U.S.F.C. str. *Albatross,* exact station data obliterated. Numerous syntypic fragments, USNM 49979.

Diagnosis.—Stout, dichotomously branched *Arthrogorgia.* Margin of buccal scales of polyps not widely extending around operculars and without projecting spines; one or more small infraopercular scales below each opercular scale, visible beyond margin of buccal scales; margin of basal scales without a projecting spine. Outer surface of scales ornamented with widely scattered low, simple granules.

Description.—(See Bayer 1952.) As the species has not been taken since the original damaged lot, nothing can be added to the information originally provided. Incomplete whorls (Fig. 3) and individual adult and young polyps (Fig. 4) from the type are now illustrated by SEM for comparison with *A. utinomii* new species (Figs. 15–18), *A. ijimai* (Figs. 1, 2) and *A. kinoshitai* (Figs. 7–9, 12).

Arthrogorgia kinoshitai Bayer, 1952
Figs. 5–12

Calyptrophora ijimai.—Broch, 1935:26, figs. 15, 16; 1940:12, 20.

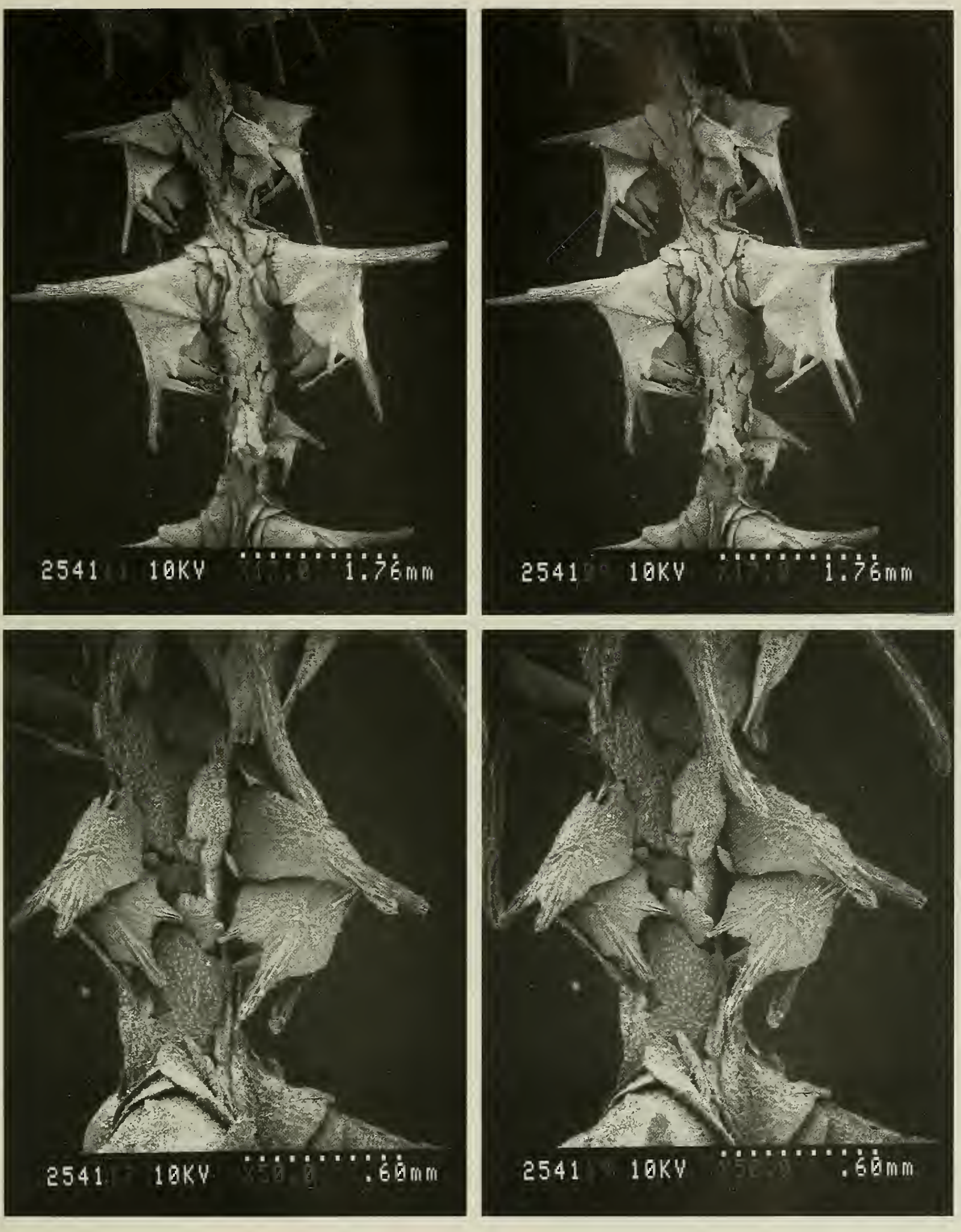


Fig. 1. *Arthrogorgia ijimai,* USNM 30028. Top, Part of lateral branchlet with whorl of fully developed polyps and two whorls of younger individuals; Bottom, Whorl of immature polyps still without infrabasal scales. SEM 2541. Stereo pairs.

Fig. 2. *Arthrogorgia ijimai,* USNM 30028. Abaxial and lateral views of fully developed polyp. SEM 2541. Stereo pairs.

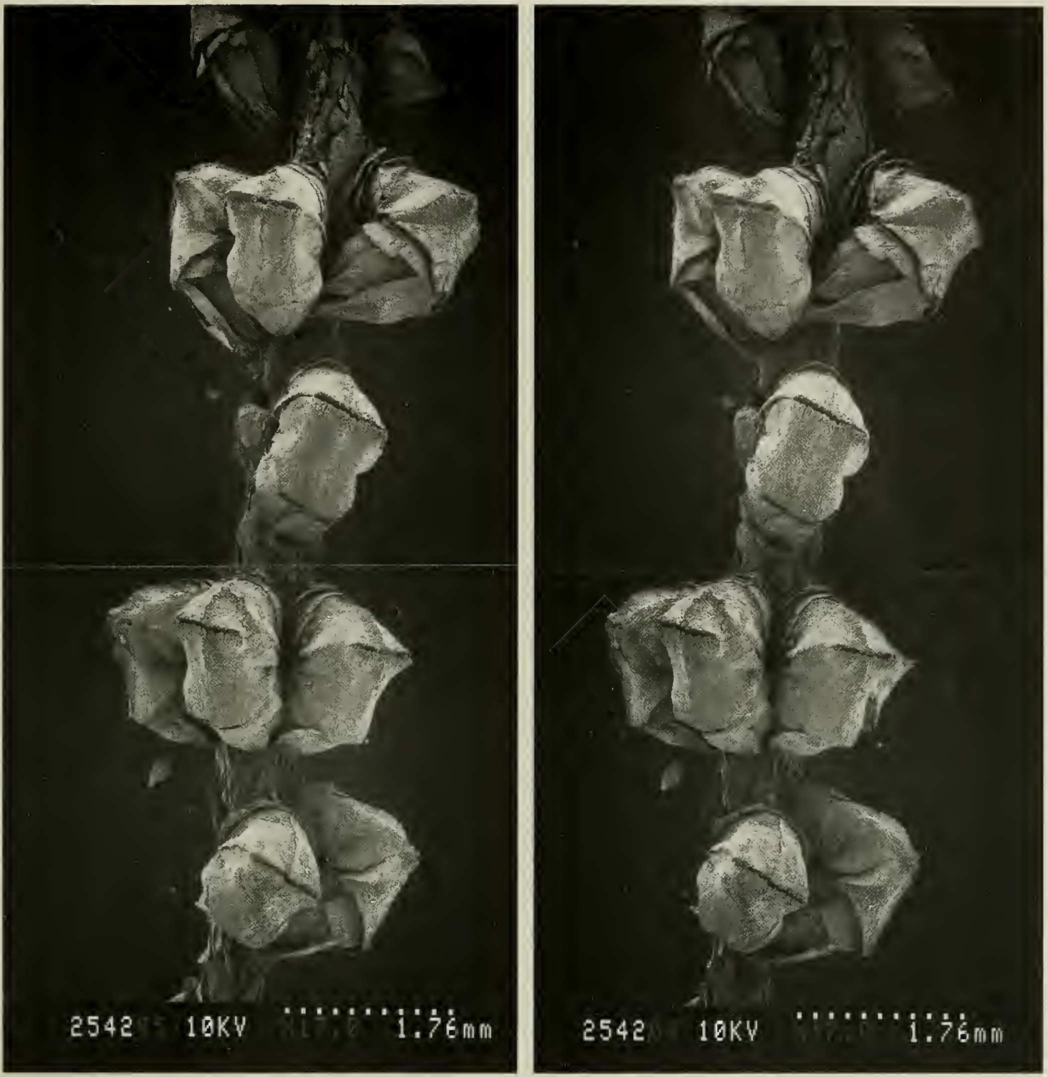


Fig. 3. *Arthrogorgia otsukai,*, USNM 49979. Part of terminal branch with four damaged whorls from syntypic fragment. SEM 2542. Stereo pair.

Not *Calyptrophora ijimai* Kinoshita, 1907: 234.
Arthrogorgia kinoshitai Bayer, 1952:64: pl. 2, figs. 1–8; pl. 3, figs. 1–12.

Material.—Alaska. Aleutian Islands SE of Agattu: 52°14′30″N, 174°13′E, 882 m, fine grey sand and pebbles, bottom temp. 38.6°F, USFC str. *Albatross* sta. 4781, 7 June 1906. One damaged colony, holotype, USNM 49978 (SEM 2499–2501, 2548). Aleutian Islands, off Near Islands: 53°05.79′N, 171°42′E, 455 m, bottom temp. 3.8°C, F/V *Pacific Knight* cruise 94-1, haul 204, 31 Jul 1994. Two colonies in good condition: colony 1, USNM uncatalogued (SEM 2510); colony 2, USNM uncatalogued (SEM 2543–2547).

Diagnosis.—Stout, dichotomously branched *Arthrogorgia* (Fig. 5) with distal margin of buccal scales widely extended as a broad, blunt lobe (Fig. 7) that in some polyps

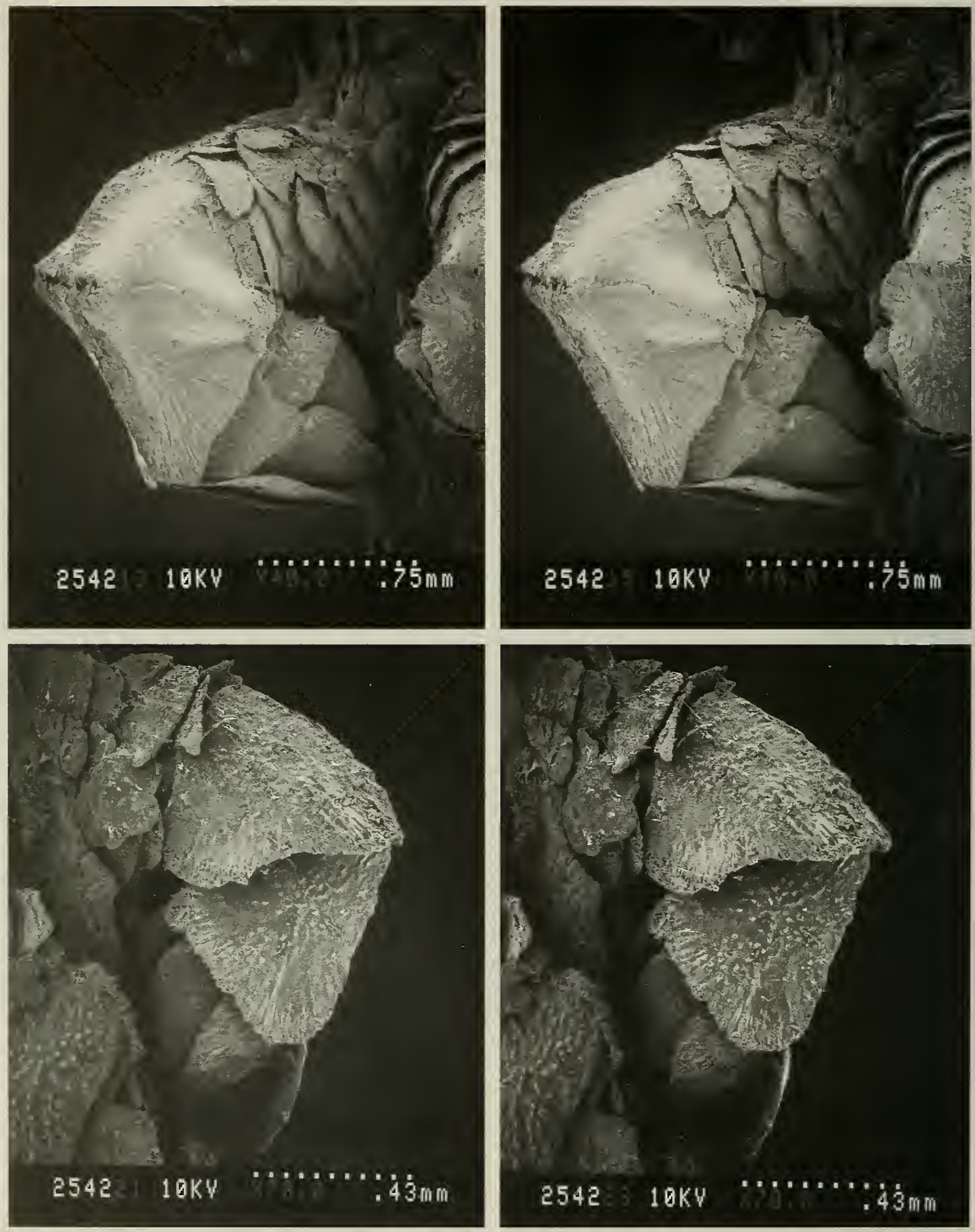


Fig. 4. *Arthrogorgia otsukai,* USNM 49979. Top, Lateral view of fully developed polyp showing multiple infrabasal scales; Bottom, Lateral view of young polyp showing multiple infrabasal scales. SEM 2542. Stereo pairs.

Fig. 5. *Arthrogorgia kinoshitai* from Near Islands, Aleutian Islands. Colony.

is divided into a few projecting spines (Figs. 8, 12); margin of basal scales usually with a strong marginal spine. Outer surface of scales ornamented with low, simple granules.

Description.—See Bayer 1952:64.

Remarks.—The two specimens taken by F/V *Pacific Knight* are almost intact save for the holdfast and are in very good condition. They agree with the type in all significant respects.

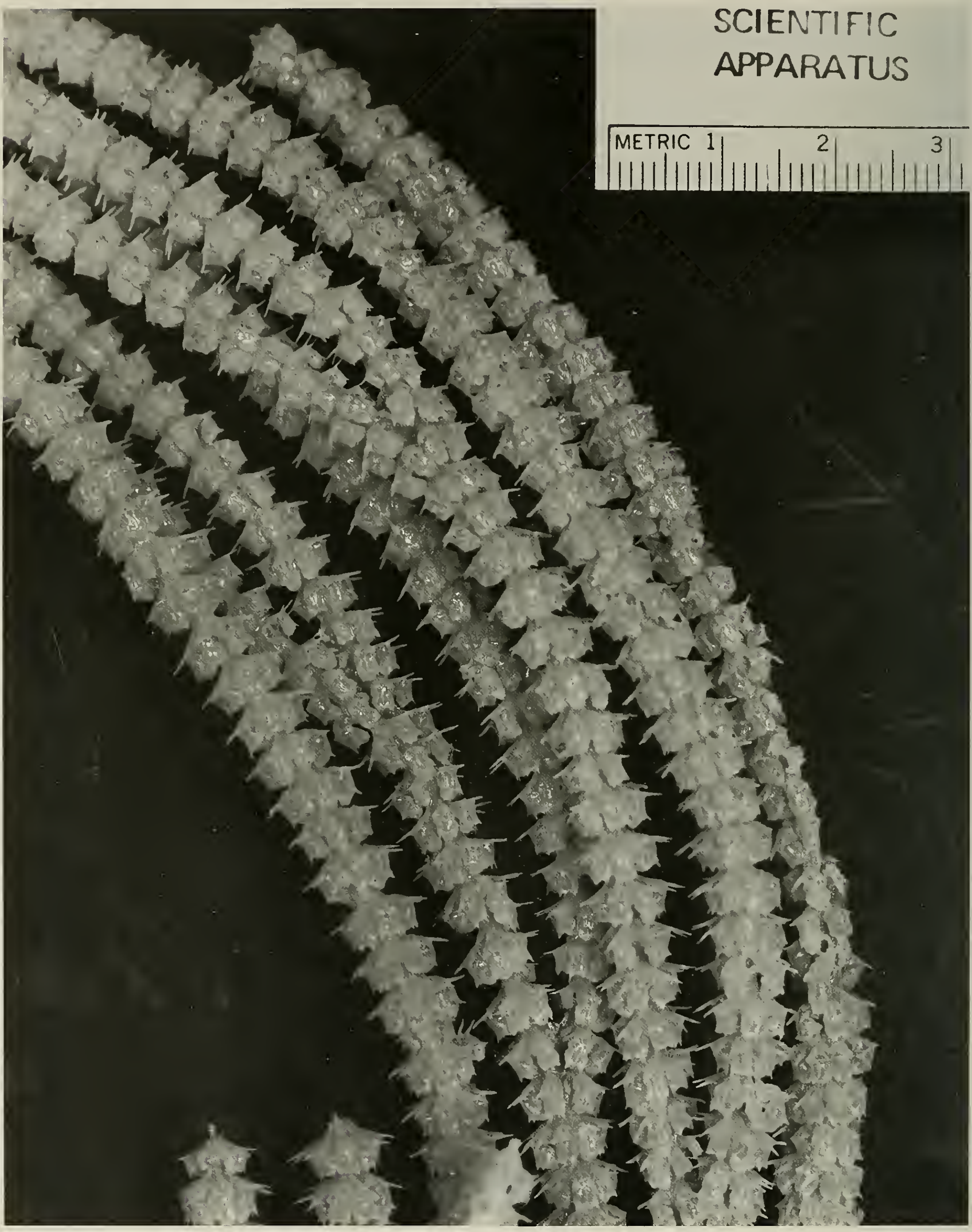


Fig. 6. *Arthrogorgia kinoshitai* from Near Islands, Aleutian Islands. Detail of branches.

The original type specimen (USNM 49978) obtained during the North Pacific cruise of USFC steamer *Albatross* in 1906 is in rather poor condition owing to inadequate curatorial maintenance. Consequently, the present material from this poorly known faunal region is a valuable addition to our National Collections.

Fig. 7. *Arthrogorgia kinoshitai* from Near Islands, Aleutian Islands. Whorls of polyps. SEM 2510. Stereo view.

The large, paired plates surrounding the polyps are prone to mechanical damage incurred owing to the rigors of the environment. In one polyp isolated and examined by SEM, one of the two buccal scales appears to have been broken and the fragments subsequently repaired individually, with elaborate spinous development of the margins (Fig. 11).

Some polyps are modified for brooding (Fig. 10) and contain a single planula larva, the largest sufficiently advanced as to have clearly visible mesenteries densely packed with minute, elongate flat rodlets with scalloped margins, the longest 0.145 mm in length and 0.04 mm in overall width. In brooding polyps, the body wall between the buccal scale pair and the operculars is conspicuously enlarged to accommodate the contained larva and is packed with abundant small scales. The closed operculum projects conspicuously from the enlarged brood chamber (Fig. 10, top) and the adaxial body wall is covered by numerous small, irregular scales (Fig. 10, bottom); no evidence was found to suggest that the opercular scales are lost when the polyp expels the contained larva, as appears to be the case in *Tokoprimno maia* Bayer (Bayer 1996:514, fig. 3).

Although until now this species has not been reported since the original description, there can be no doubt that the three large fragments from the Okhotsk Sea reported by

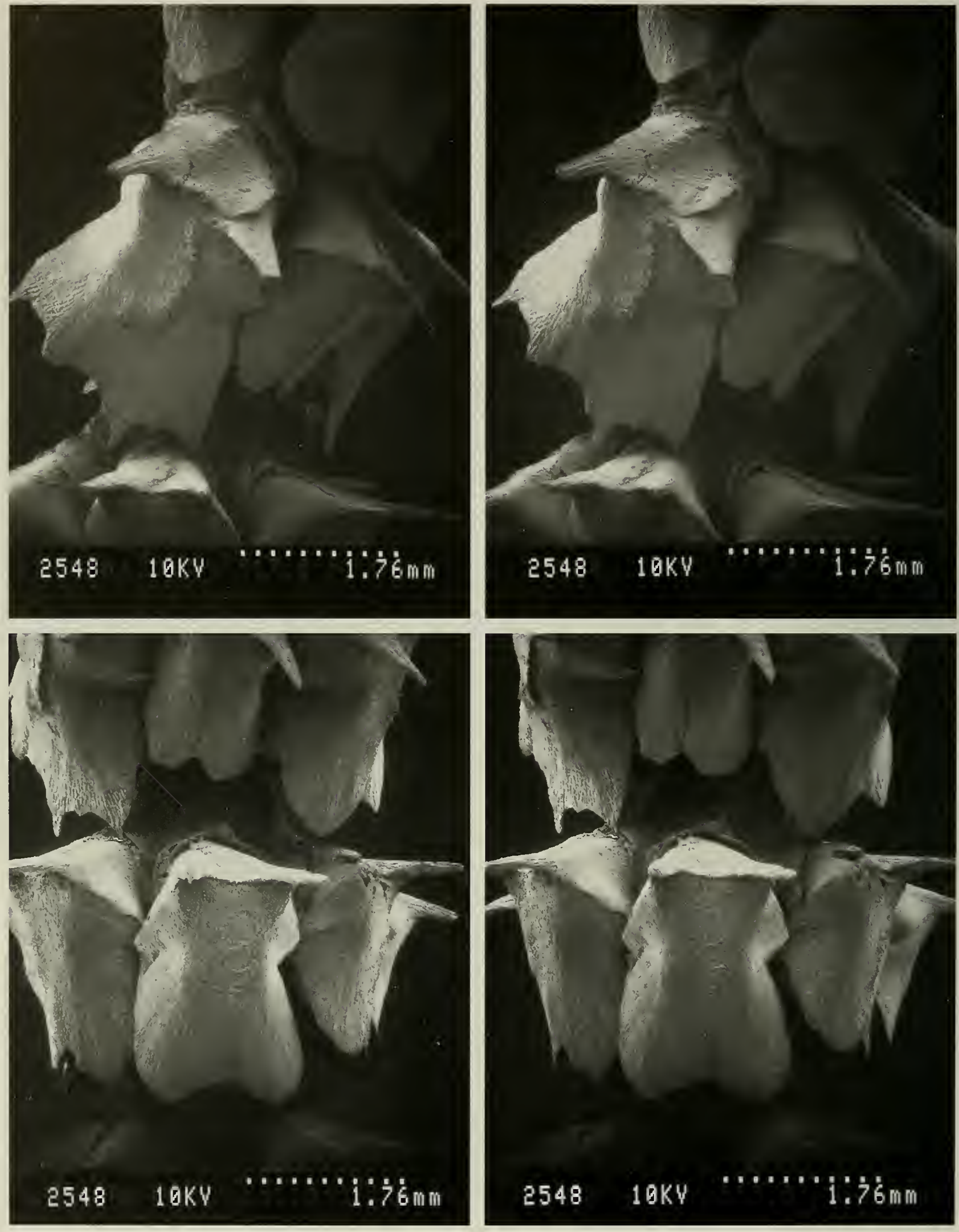


Fig. 8. *Arthrogorgia kinoshitai* USNM 49978, holotype from vicinity of Aggatu, Aleutian Islands. Whorls of polyps. SEM 2548. Stereo views.

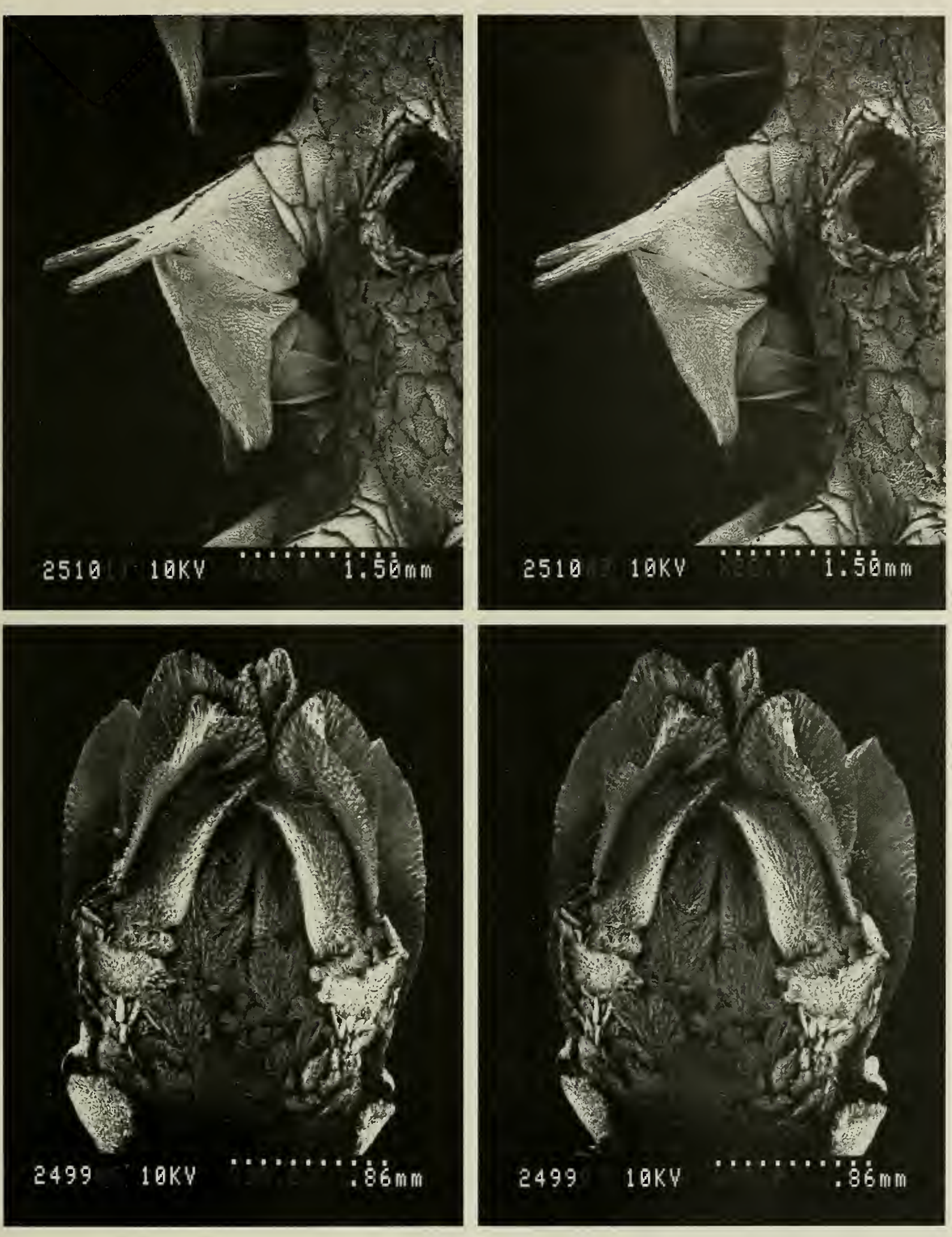


Fig. 9. *Arthrogorgia kinoshitai* from Near Islands, Aleutian Islands. Top: Lateral view of polyp *in situ,* showing multiple infrabasal scales, SEM 2510; Bottom, Opercular view of isolated polyp showing numerous small adaxial scales below the adaxial operculars, SEM 2499. Stereo pairs.

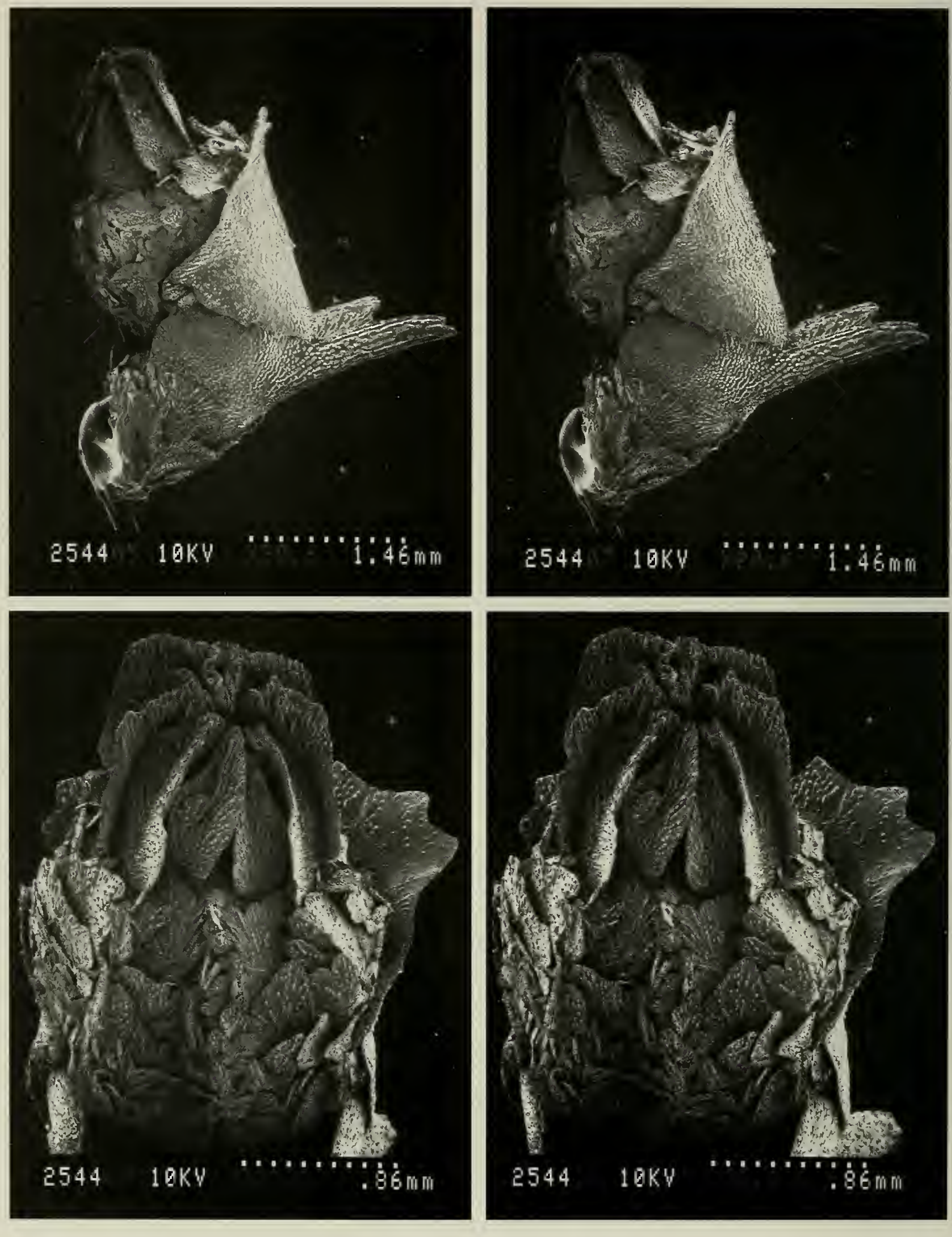


Fig. 10. *Arthrogorgia kinoshitai* from Near Islands, Aleutian Islands. Brood polyp, lateral and adaxial aspects. SEM 2544. Stereo pairs.

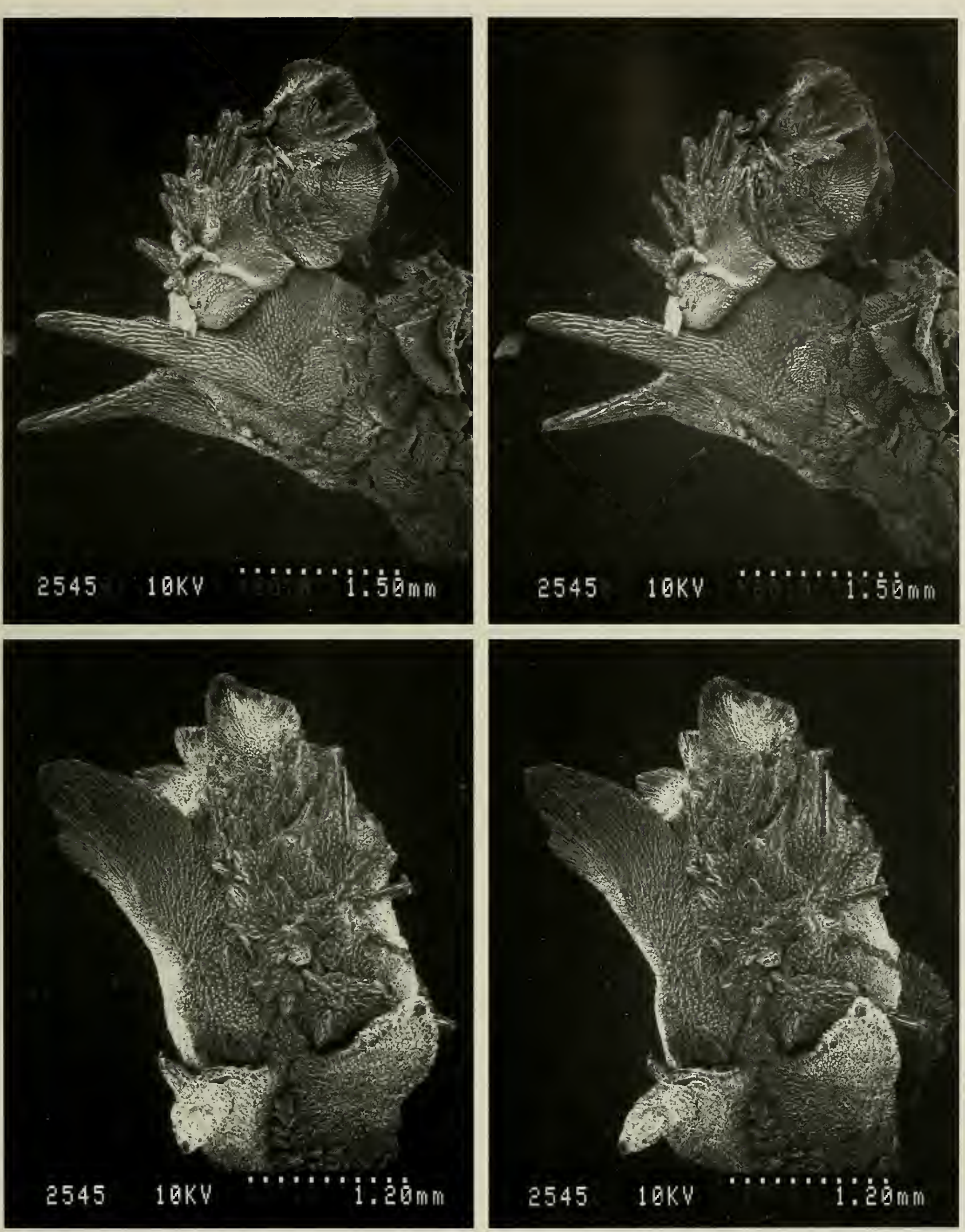


Fig. 11. *Arthrogorgia kinoshitai* from Near Islands, Aleutian Islands. Abnormal polyp with one buccal scale subdivided into several smaller, spinose scales, and the associated operculars with unusually spinose margins. SEM 2545. Stereo pairs.

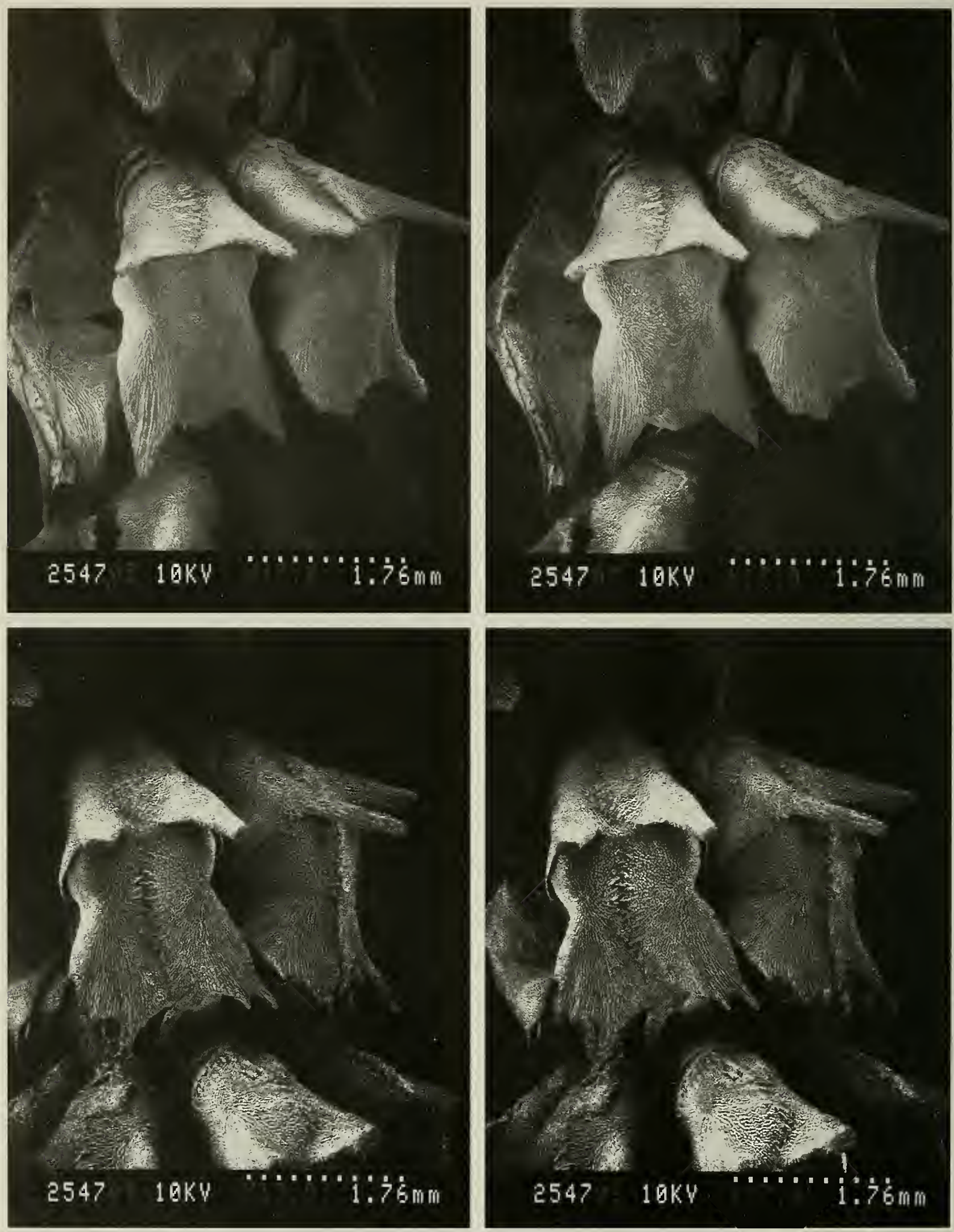


Fig. 12. *Arthrogorgia kinoshitai* from Near Islands, Aleutian Islands. Whorls of polyps showing variation of buccal margins. SEM 2547. Stereo pairs. Compare with Fig. 8.

Broch (1935:26) as *A. ijimai* (Kinoshita) are in fact *A. kinoshitai. A. ijimai* has been reported only from the vicinity of the Japanese main islands in depths of 728–1123 m, but has not been obtained in dredging and trawling stations by the then U.S. Fish Commission or subsequently by the present National Marine Fisheries Service of the U.S. Fish & Wildlife Service. Colonies of *A. ijimai* are small, pinnately branched, with very slender, flexible lateral branchlets (Nutting 1912: pl. 16, fig. 2), which is not consistent with "3 große Bruchstücke" reported by Broch, who provided no further particulars about colonial form. Moreover, his illustrations of polyps (Broch 1935:27, figs. 15a, 16) agree in general aspect with *A. kinoshitai* (Bayer 1952: pl. 2, figs. 1–3; figs. 8, 12 herewith), but not with *A. ijimai* (Kinoshita 1908b: pl. 6, fig. 54f; figs. 1, 2 herewith). The present specimens show variation in the margins of the buccal scales (SEM 2547, 2548) similar to that illustrated by Broch.

Arthrogorgia utinomii, new species
Figs. 13–20

Material.—Alaska. Aleutian Islands SSW of Attu I.: 52°28′N, 172°30′E, 234 m, R/V *Starlight* cruise 84-1, haul 36, 13 Jul 1984. One large colony lacking holdfast, otherwise in good condition, holotype, USNM (SEM 2504-2506, 2540, 2562). Aleutian Islands SE of Agattu, Aleutian Islands: 52°14′30″N, 174°13′E, 482 fathoms (=882 m), USFC steamer *Albatross* sta. D-4781, 7 June 1906. One incomplete colony lacking holdfast, USNM 58168 (SEM 1398, 2502, 2503, 2564–2566). Aleutian Islands S of Yunaska I.: 52°18.16′N, 170°41.96′W, 163 m, R/V *Harvester* cruise 802, sta. VH-80-42, 8 Aug 1980. Two branches of a large colony, USNM 80829 (SEM 1418–1422, 1428).

Diagnosis.—Stout, dichotomously branched *Arthrogorgia.* Margin of buccal scales of polyps not widely extending around operculars, with at most a blunt marginal angle not produced as a strong spine; one or more accessory infraopercular scales below abaxial, outer lateral and inner lateral opercular scales, visible beyond margin of buccal scales; margin of basal scales usually with a stout marginal spine, projecting strongly in some polyps, less so in others. Outer surface of scales with sharply prickly sculpture.

Description.—The colony (Fig. 13) is dichotomously branched, roughly in one plane, with undivided terminal branches up to 30 cm long. The bifurcations enclose rather narrow angles of 30°–35° and the branches are nearly straight and nearly parallel. The polyps are arranged in regular whorls of 7 or 8 (Fig. 14), predominantly directed downward (Fig. 15) but with a few individuals facing upward, especially just above branch dichotomies. From seven to nine whorls occur in 3 cm of branch length. The axis is brown or dark brown, with a bronze-colored metallic luster; narrow longitudinal grooves follow an irregular spiral course on the large branches, becoming essentially vertical on the narrow terminal branches.

The contracted polyps (Figs. 15–18) are 3.0–3.5 mm long measured parallel with the branch; they are protected by two pairs of large abaxial body scales, basal and buccal, and three or more pairs of infrabasals, which may be rather irregular. The basal scales have a strongly projecting marginal spike (Figs. 15, 16 top, 18 top). The free margin of the buccal scales scarcely extends beyond the base of the operculars (Figs. 16–18), sometimes forming rounded lobes (Fig. 17, bottom), sometimes a broad, projecting angle (Fig. 15, bottom). The operculum projects strongly beyond the buccal margin (Figs. 16, top; 17, top). The large buccal scales may be subdivided into several smaller, irregular scales, apparently by breakage and repair (Fig. 15 top). The operculum consists of eight tall scales, the abaxials largest, decreasing in size adaxially, the adaxial pair distinctly smaller and overlapped by the inner laterals; opercular scales with an inner longitudinal keel and corresponding external

Fig. 13. *Arthrogorgia utinomii,* holotype. Nearly complete colony.

groove, most strongly developed on the abaxial and lateral scales. One or two pairs of small adaxial buccal scales (Fig. 16, bottom) lie below the adaxial operculars, followed by one or more pairs of small adaxial body scales. In fully developed polyps, accessory infraopercular scales are present below the abaxial, outer lateral and inner lateral oper-

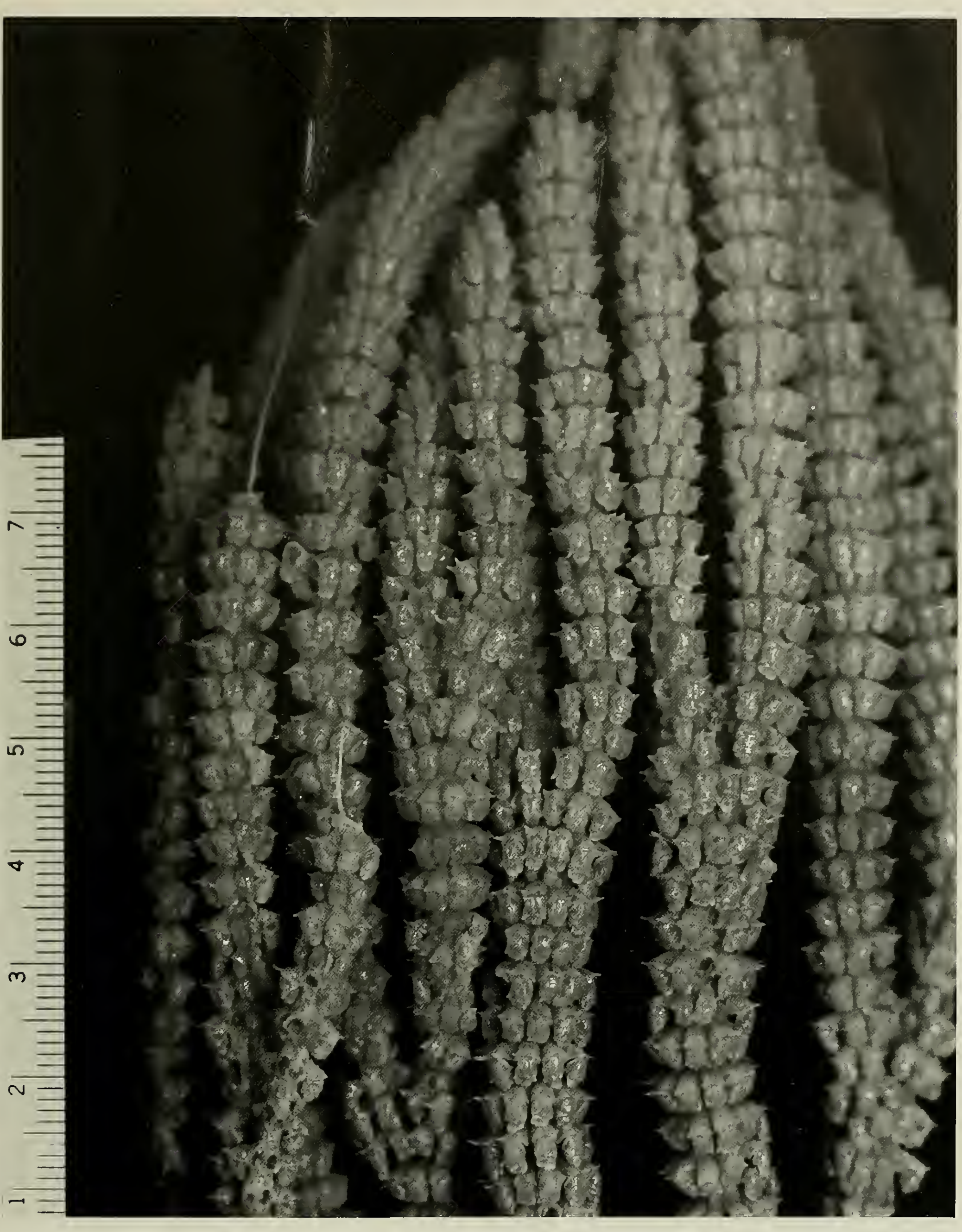


Fig. 14. *Arthrogorgia utinomii,* holotype. Detail of branches.

culars, sometimes below all. These accessory scales are visible beyond the margin of the buccal scale pair (Figs. 16, top; 17, top; 18, top) and are developed already in very young polyps (Fig. 18, bottom). These scales were called "marginal" in the case of *A. kinoshitai* and *A. otsukai* (Bayer 1952). The tentacles contain numerous small, flat, blunt

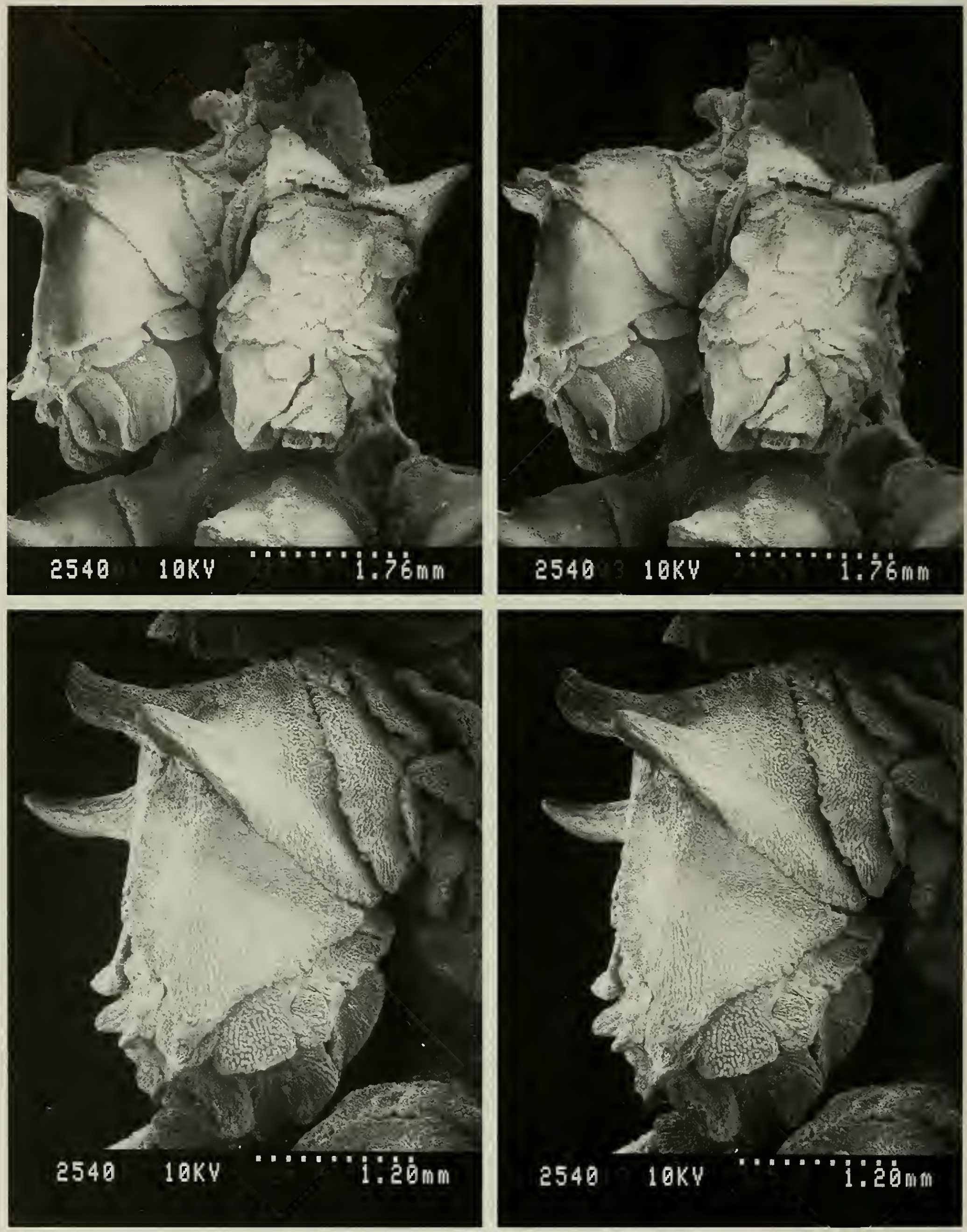


Fig. 15. *Arthrogorgia utinomii*, holotype. Top, Two polyps of distalmost whorl of terminal branch, one with medial scales subdivided by breakage and repair; Bottom, Lateral view of polyp showing infraopercular scales and angular projection of buccal margin. SEM 2540. Stereo pairs.

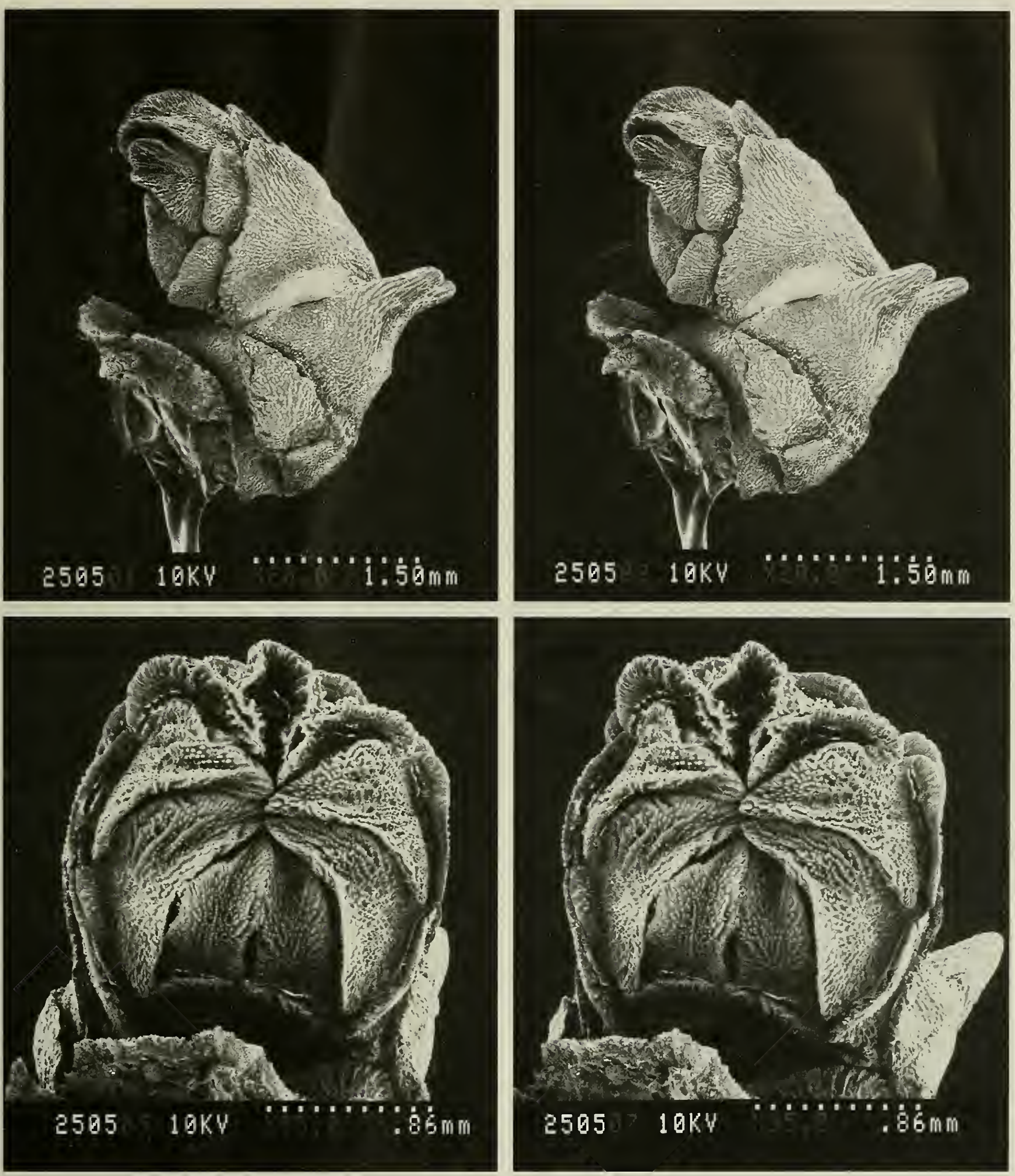


Fig. 16. *Arthrogorgia utinomii,* holotype. Lateral and opercular views of isolated polyp. SEM 2505. Stereo pairs.

rodlets with scalloped margins, about 0.085 mm long and 0.03 mm wide.

All of the body sclerites of the polyps are covered externally by sharp prickles arranged in lines radiating outward from the depositional center of the scale, ending at the margins as fine serrations; internally they are covered with complex tubercles.

The coenenchyme is filled with small, thorny or tuberculate spheroids, which become wider, flattened, and more scalelike in form where they merge with the infrabasals at the base of the polyps. In the angle of bifurcations, the coenenchyme extends as a narrow, membranous expansion possibly analogous with the coenenchymal mem-

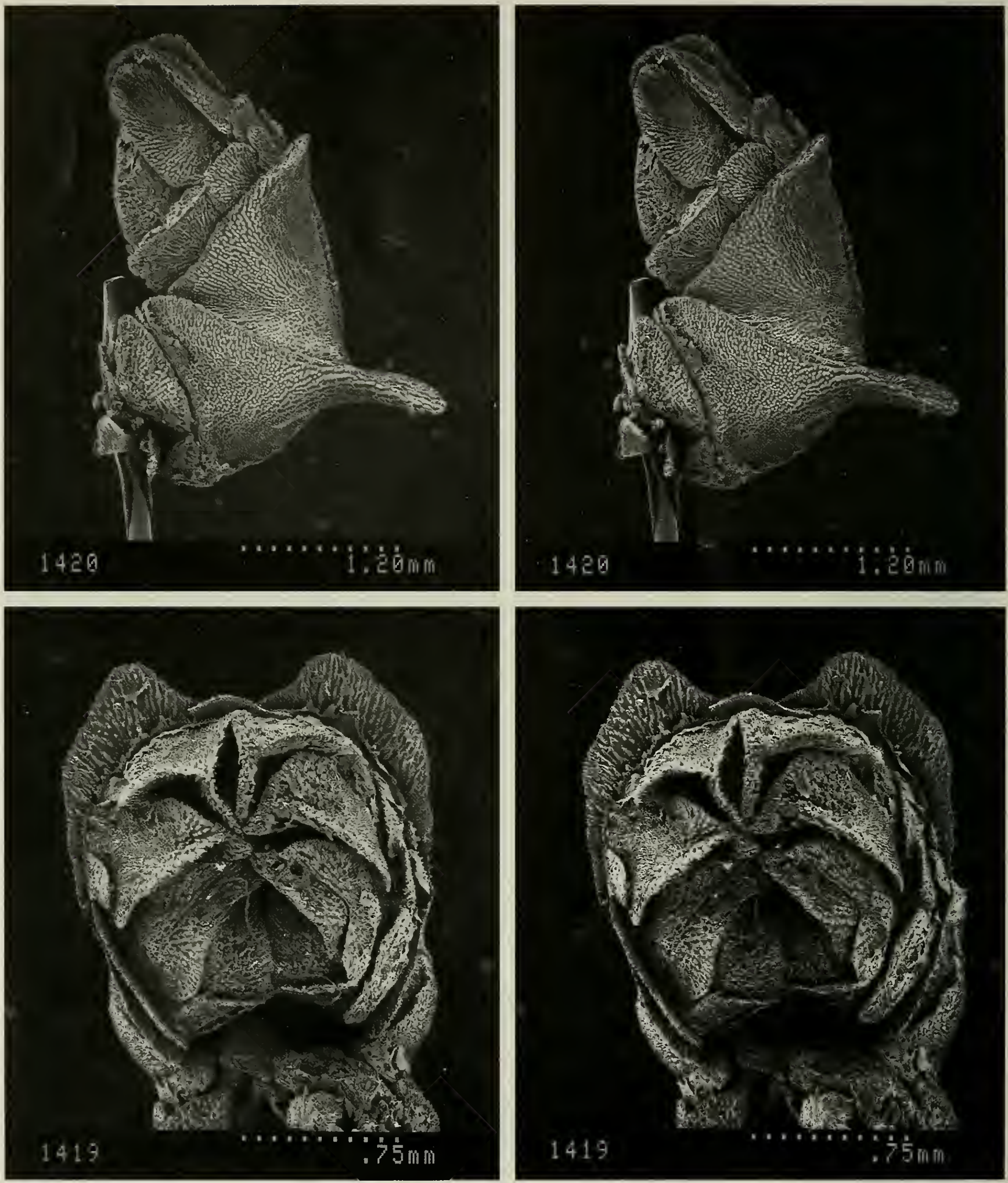


Fig. 17. *Arthrogorgia utinomii,* USNM 80829. Top, Lateral view of isolated polyp, SEM 1420; Bottom, Opercular view of isolated polyp, SEM 1419. Stereo pairs.

branes of *A. ijimai,* but not demonstrably associated with the presence of any commensal polychaete.

Most of the polyps of the colony from southeast of Attu I. (USNM 58168) have strongly developed infraopercular scales (Fig. 19, top), a condition apparently related to brooding, as several polyps dissected contain what appear to be a fully developed planula. The adaxial body wall of such individuals is protected by numerous small, irregular scales (Fig. 19, middle), small

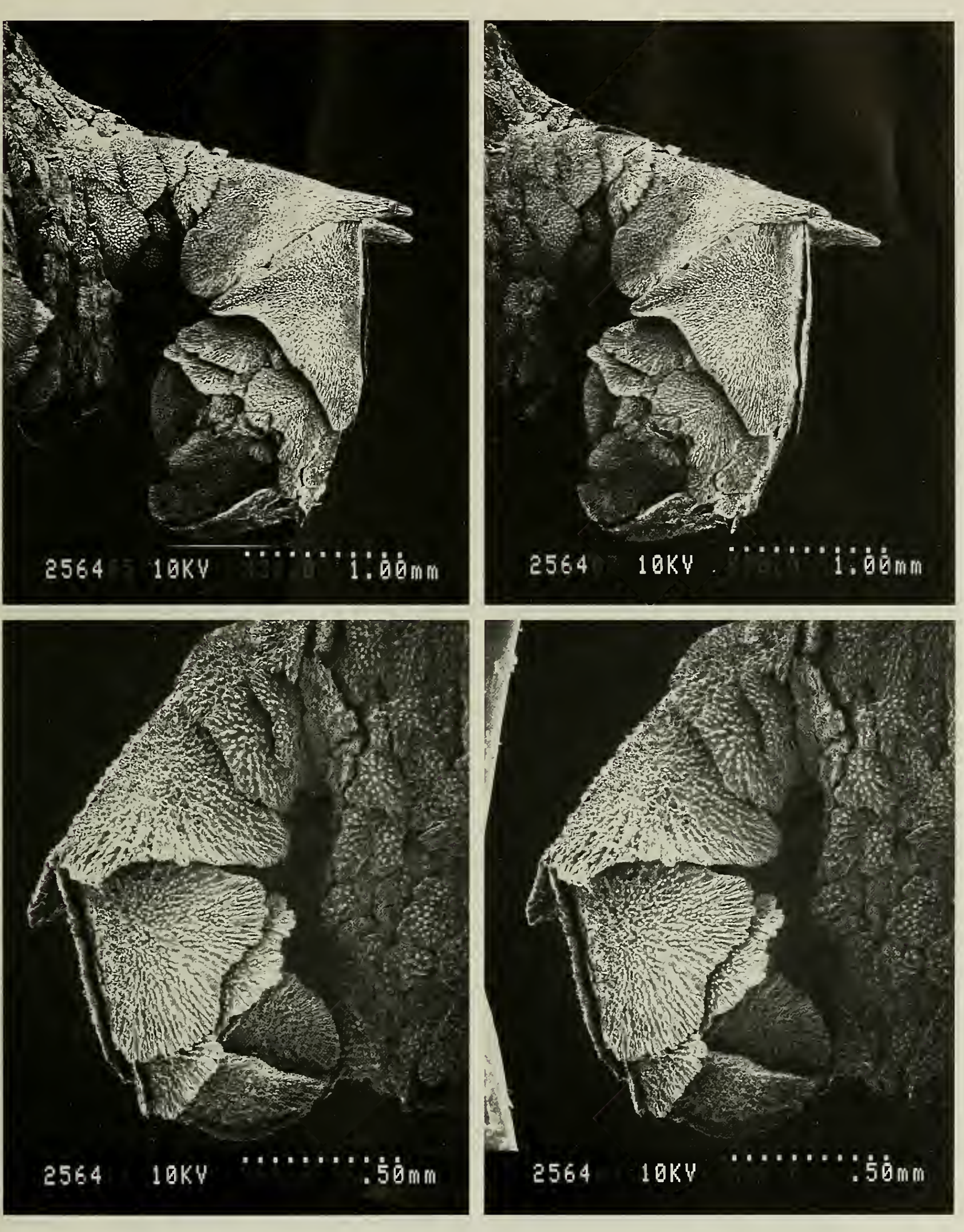
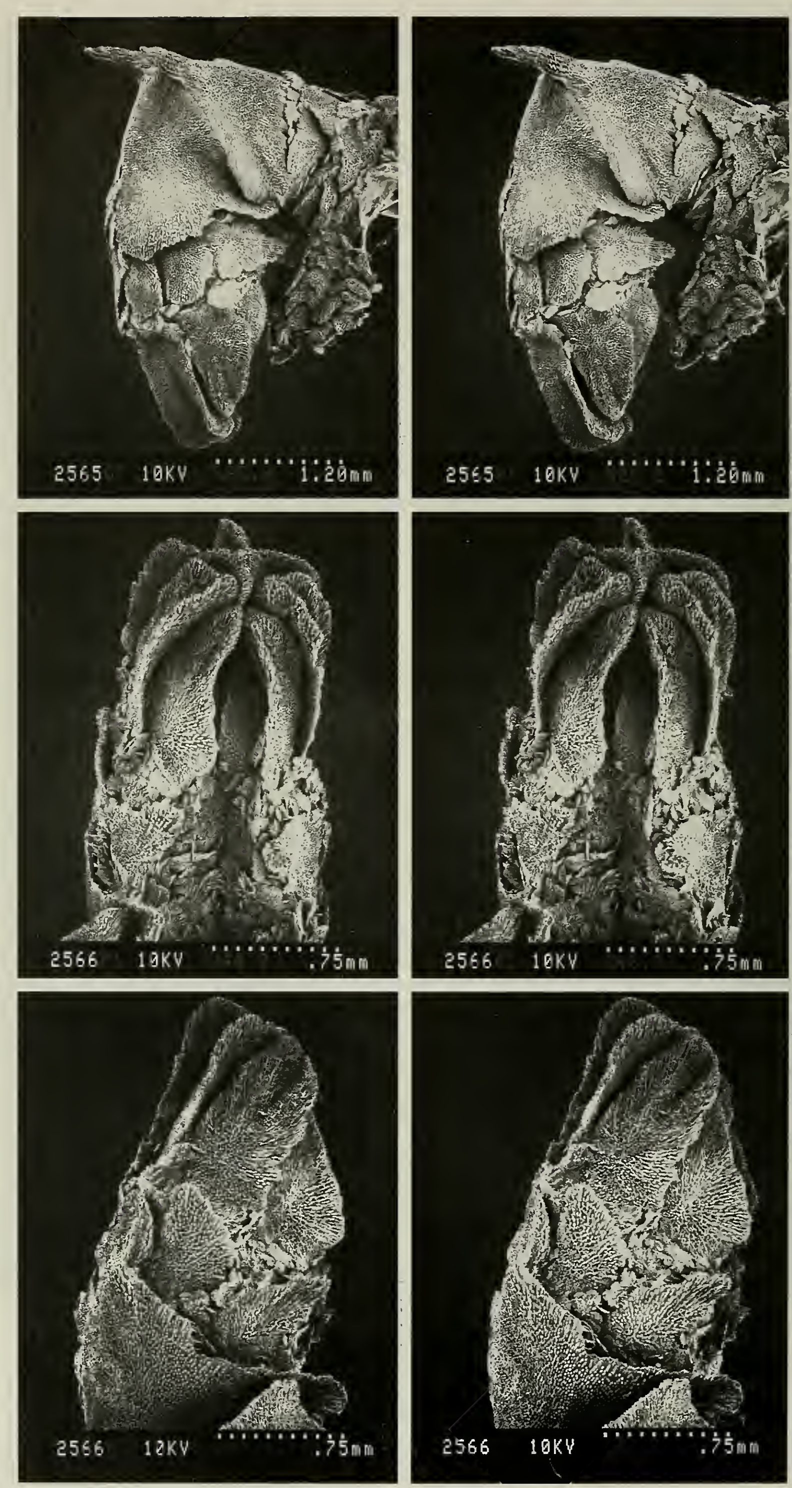


Fig. 18. *Arthrogorgia utinomii,* USNM 56168. Top, Lateral view of fully developed polyp in situ; Bottom, Lateral view of young polyp in situ. SEM 2564. Stereo pairs.

scales are present between the large infraoperculars (Fig. 19, bottom), and the opercular scales protrude conspicuously beyond the buccals and infraoperculars (Fig. 19, top, bottom). These brood polyps are similar to those of *A. kinoshitai* (cf. Fig. 10).

Etymology.—Named in memory of the late Dr. Huzio Utinomi, long-time friend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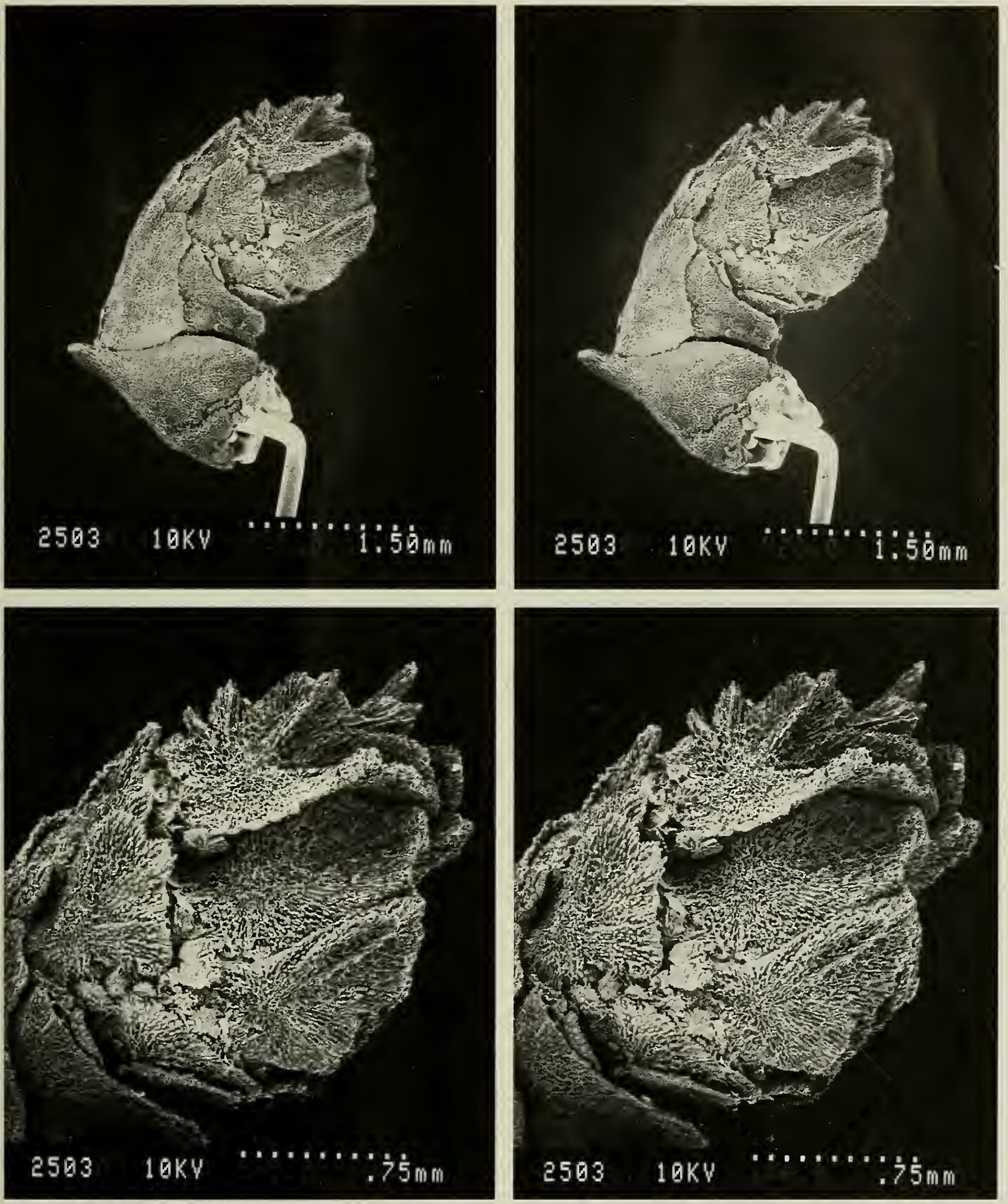

Fig. 20. *Arthrogorgia utinomii,* USNM 58168. Lateral and opercular views of polyp having elaborately developed opercular scales, SEM 2503. Stereo pairs.

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Fig. 19. *Arthrogorgia utinomii,* USNM 56168. Top, Lateral view of brooding polyp, SEM 2565; Middle, Adaxial view of operculum of brooding polyp, SEM 2566; Bottom, Lateral view of operculum of brooding polyp, SEM 2566. Stereo pairs.

and colleague whose descriptions of primnoids enhanced the scientific knowledge of the Gorgonacea of Japanese waters.

Comparisons.—Colonies of this species grossly resemble those of *A. kinoshitai* and *A. otsukai* but differ conspicuously from the delicate, pinnate colonies of *A. ijimai* (Kinoshita 1908: pl. 4, fig. 28; Nutting 1912: pl. 16, fig. 2). They differ from both in the development of accessory scales between the buccal pair and the operculars of the polyps, from *kinoshitai* by the negligible free margin of the buccal pair, and from *otsukai* by the larger size of the polyps and the development of a strong marginal spine on the basal scales.

Acknowledgments

I here extend my thanks to Dr. Manfred Grasshoff of the Natur-Museum Senckenberg, Frankfurt, Germany, for his useful and constructive suggestions of the manuscript. Most of the scanning electron micrographs were made by Mr. Walter R. Brown, chief of the SEM Laboratory, National Museum of Natural History, and the remainder under his supervision. Indispensable curatorial tasks related to integrating the material here described with the permanent collections of the National Museum of Natural History were carried out by Mr. T. E. Coffer, Museum Specialist, Department of Invertebrate Zoology.

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109(4):629–644. 1996

Revision of the scaleworm genera *Acholoe* Claparède, *Arctonoella* Buzhinskaja, and *Intoshella* Darboux (Polychaeta: Polynoidae) with the erection of the new subfamily Acholoinae

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Abstract.—Four genera and five species of polynoids are reviewed and revised, including *Acholoe* Claparéde, 1870, for *A. astericola* (Delle Chiaje, 1841), commensal with asteroids; *Arctonoella* Buzhinskaja, 1964, for *A. sinagawaensis* (Izuka, 1912); new genus *Paractonoella,* for *P. indica* (Day, 1973). n. comb., and *P. aphthalma* (Gallardo, 1968), n. comb., with ophiuroid (both as *Intoshella*); and *Intoshella* Darboux, 1900, for *I. euplectellae* (McIntosh, 1885), with glass sponge. All species are referred to the new subfamily Acholoinae, characterized by arctonoid type of prostomium and biramous parapodia with neuropodia deeply notched dorsally and ventrally, shorter rounded postsetal lobes and longer presetal acicular lobes, bifid distally, with longer supraacicular processes.

Covered in this report are five species and three synonyms: *Acholoe* Claparède, 1870, with *A. astericola* (Delle Chiaje, 1841) and synonyms: *Polynoe malleata* Grube, 1855, *Polynoe asterinae* Carrington, 1865, and *Acholoe orbiculata* Treadwell, 1921; *Arctonoella* Buzhinskaja, 1967, with *A. sinagawaensis* (Izuka, 1912); *Pararctonoella,* new genus, with *P. aphthalma* (Gallardo, 1968), n. comb. (as *Intoshella*), *P. indica* (Day, 1973), n. comb. (as *Intoshella*); *Intoshella* Darboux, 1900, with *I. euplectellae* (McIntosh, 1885).

The species have been variously included in Aphroditidae: Polynoinae by Day (1967); in Lepidonotinae by Hartman (1959) and Fauchald (1977); in Harmothoinae by Gallardo (1968), Uschakov (1974), and Fauchald (1977); and "arctonoid" type of prostomium by Uschakov (1982).

Based on the prostomium of the arctonoid type, the species of Acholoinae are more similar to the new subfamily Arctonoinae Hanley, 1989, who also included a detailed review of the subfamilies of Polynoidae. The neuropodia of the parapodia, with deeply notched anterior and posterior rounded lobes, resemble the new subfamily Lepidastheniinae Pettibone, 1989, and also lacking the elongate presetal acicular processes, as in Harmothoinae.

In addition to the collections in the National Museum of Natural History, Smithsonian Institution (USNM), the specimens covered herein are deposited in the following Museums; American Museum of Natural History, New York (AMNH): Natural History Museum, London (BMNH): Natural History Museum of Los Angeles County (LACM-AHF); Rijksmuseum van Natuurlijke Historie, Leiden (RNHL); Zoological Institute Academy of Sciences, Leningrad (ZIASL); and Zoologisches Museum, Berlin (ZMB).

Family Polynoidae Kinberg, 1856
Acholoinae, new subfamily

Diagnosis.—Body elongate, with numerous segments (more than 100) or moderate in number (up to 50). Elytra and bulbous elytrophores numerous pairs (more than 40) or fewer, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32, then variable in number and arrangement. Elytra orbicular, smooth, without fringes of papillae, with or without some microtubercles or some nodular papillae on surfaces. Dorsal cirri, on non-elytrigerous segments, with cylindrical cirrophores posterodorsal to notopodia, with distal styles; dorsal tubercles, in line with elytrophores, bifurcate, bulbous, or indistinct. Prostomium bilobed, with lobes rounded, without cephalic peaks, with paired palps and three antennae with distinct ceratophores; median antenna with large ceratophore in anterior notch of prostomium, with distal style; lateral antennae with distinct ceratophores inserted terminoventrally, converging midventrally, with short styles; usually two pairs of eyes. First or tentacular segment not visible dorsally; tentaculophores lateral to prostomium, with acicula, achaetous or with few setae, and dorsal and ventral tentacular cirri, similar to median antenna. Second or buccal segment with or without nuchal fold, with first pair of elytra and elytrophores, biramous parapodia, and ventral buccal cirri, longer than following ventral cirri. Parapodia biramous, smaller notopodia subconical with acicular processes on anterodorsal sides of larger neuropodia; neuropodia deeply notched dorsally and ventrally, with rounded postsetal lobes and slightly longer presetal acicular lobes, bifid distally, with variable development of supraacicular and subacicular processes. Notosetae few to numerous, variable. Neurosetae moderate in number to numerous, variable, all with entire tips. Ventral cirri short, subulate. Pygidium with pair of anal cirri. Pharynx with nine pairs of papillae and two pairs of jaws. Commensal with asteroids, ophiuroids, and glass sponges.

Remarks.—Members of the Acholoinae differ from the Lepidonotinae, where some of the newly proposed acholoinin species have previously been referred, by the position of the lateral antennae on the prostomium, where the lateral antennae are attached terminally on anterior extensions of the prostomium and without distinct ceratophores. The Acholoinae differ from the Harmothoinae, where the bilobed prostomium has cephalic peaks and the lateral antennae are inserted ventral to the ceratophore of the median antenna. Members of the Acholoinae have an "arctonoid" type of prostomium, as in the subfamily Arctonoinae, established by Hanley (1989). The bilobed prostomium, without cephalic peaks, has three antennae with distinct ceratophores. The ceratophore of the median antenna is inserted in the anterior notch of the prostomium and the ceratophores of the lateral antennae are inserted terminoventrally and converging midventrally.

The parapodia of the Acholoinae and the subfamilies Lepidastheniinae and Arctonoinae are similar in having subbiramous or biramous parapodia with the neuropodia deeply cut dorsally and ventrally, with anterior and posterior subequal rounded lobes but without projecting presetal acicular lobes, as in Harmothoinae. In the Acholoinae the slightly longer presetal acicular lobes are bifid distally, and with longer supraacicular processes.

Key to the Genera of Acholoinae

1. Segments numerous (more than 100). Elytra and elytrophores numerous pairs, continuing to posterior end of body. Elytra with microtubercles on anterior part (Fig. 1K). Dorsal tubercles on cirrigerous segments forming bifurcate T-shaped ciliated processes (Fig. 1H). Notosetae few (4–9), slender, with spinous rows and rounded tips (Fig. 1G, I). Neuropodium with bilobed presetal acicular lobe with deep notch and projecting aciculum and subequal rounded supraacicular and subacicular processes (Fig. 1G) .... *Acholoe* Claparède

– Segments moderate in number (up to 50). Elytra and elytrophores 16–23 pairs, not continuing to end of body. Elytra without microtubercles (Figs. 2H, 3J, 5F). Dorsal tubercles small, nodular or

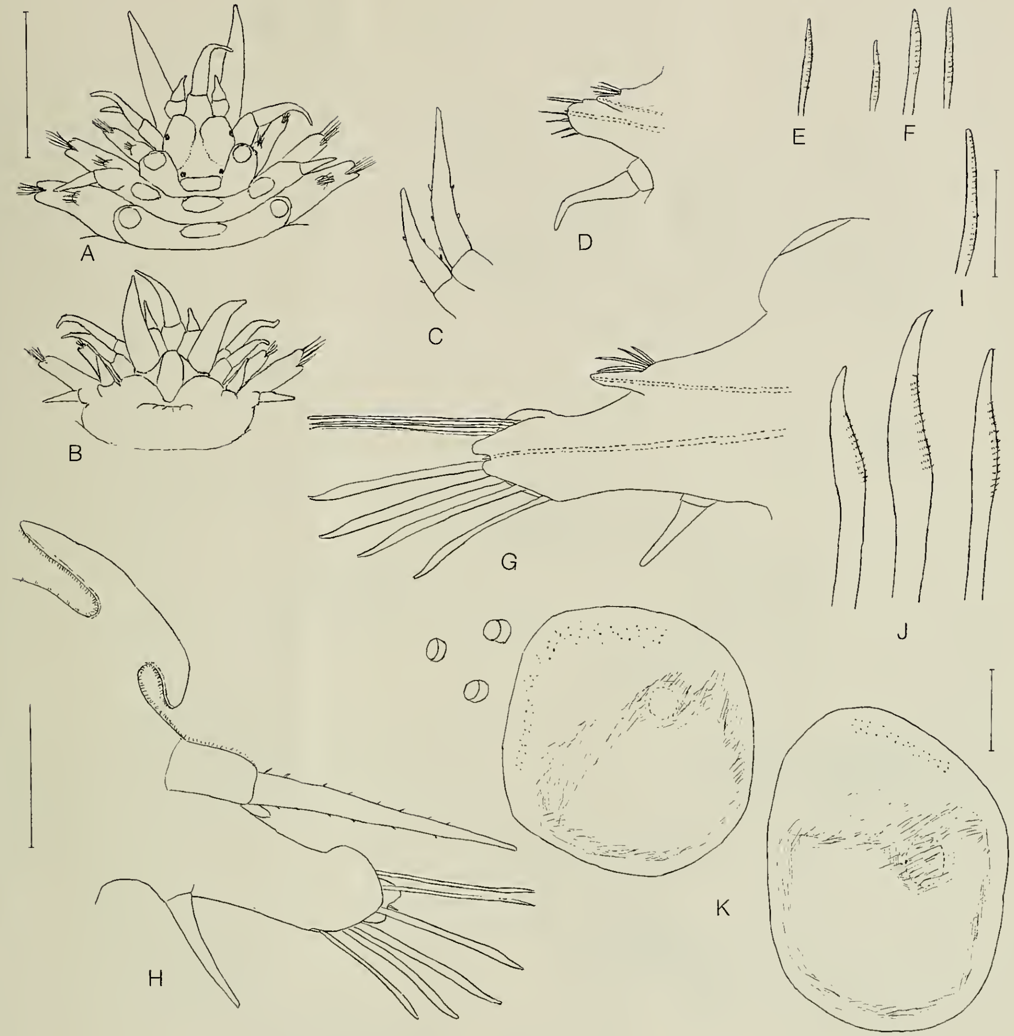

Fig. 1. *Acholoe astericola,* specimen from Naples (USNM 33626): A, Dorsal view of anterior end; B, Ventral view of anterior end; C, Tentaculophore of segment I, inner view; D, Right elytrigerous parapodium of segment II, anterior view, acicula dotted; E, Notoseta from same; F, Lower, middle & upper neurosetae from same; G, Right middle elytrigerous parapodium, anterior view, acicula dotted; H, Right middle cirrigerous parapodium, posterior view, with T-shaped dorsal tubercle; I, Notoseta from same; J, Lower, middle & upper neurosetae from same; K, Two right elytra, with detail of microtubercles. Scales = 1.0 mm for A, B; 0.5 mm for C, D, G, H; 0.1 mm for E, F, I, J; 0.5 mm for K.

bulbous. Notosetae numerous, variable. Neuropodium with bilobed presetal acicular lobe without wide notch, with longer supraacicular process (Figs. 2D, 3E, 4A, 5B) 2

2. Neuropodial presetal acicular lobe with longer subconical supraacicular process and shorter rounded subacicular process (Figs. 2D, 3E, 4A). Notosetae and neurosetae of single kind or of two kinds 3

– Neuropodial presetal acicular lobe with digitiform supraacicular process, without subacicular process (Fig. 5B). Both notosetae (Fig. 5D) and neurosetae (Fig. 5E) of single type, both glassy, with very faint spinous rows . . . . *Intoshella* Darboux

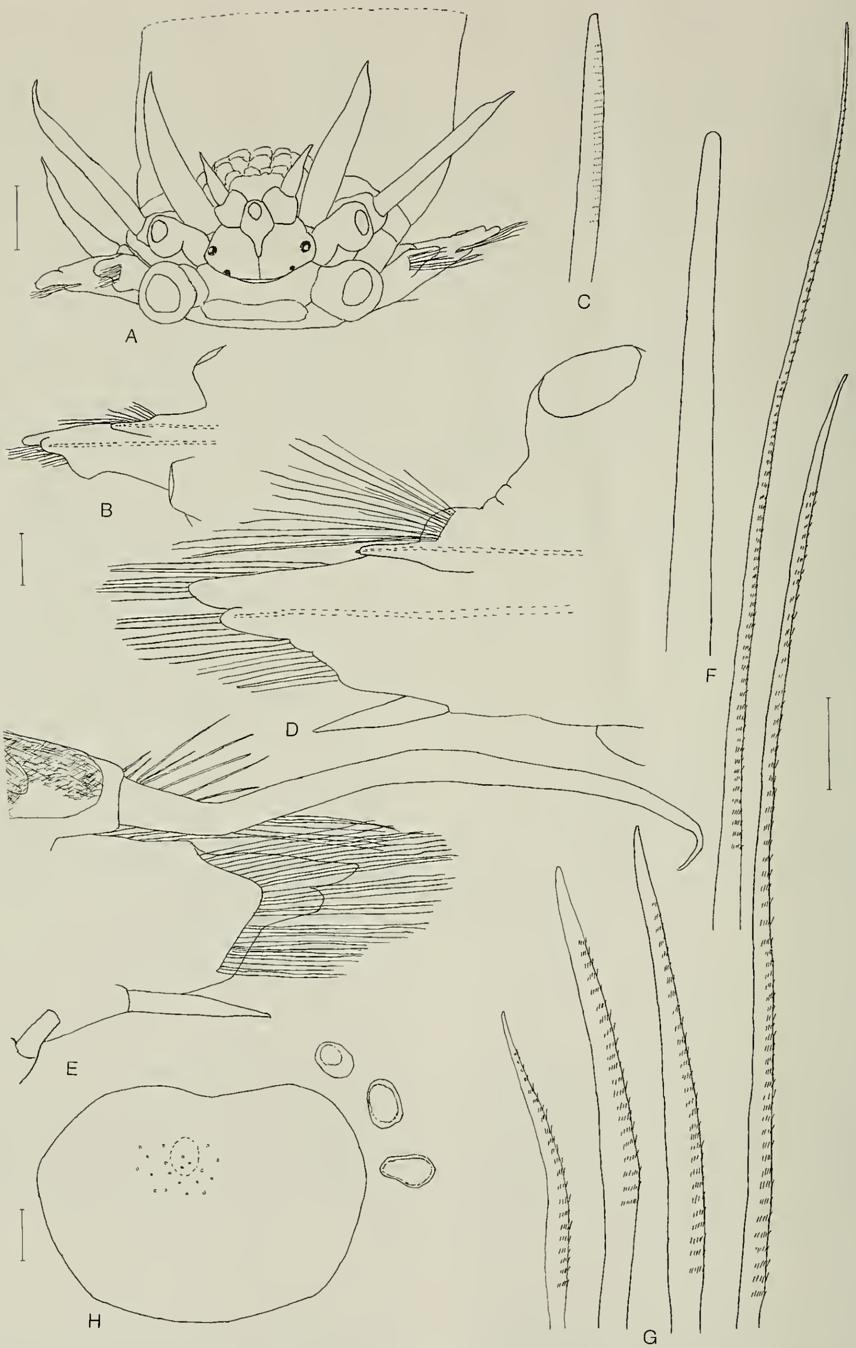

Fig. 2. *Arctonoella sinagawaensis,* specimen from Possjet Bay (ZIASL 17056): A, Dorsal view of anterior end, pharynx completely extended, distal part not shown; styles of median antenna, right and left dorsal tentacular cirri, and elytra missing; B, Right elytrigerous parapodium from segment II, anterior view, acicula dotted, ventral buccal cirrus missing; C, Short notoseta from same; D, Right middle elytrigerous parapodium, anterior view, acicula dotted; E, Right cirrigerous parapodium, posterior view, showing ventral nephridial papilla; F, Upper stout and lower slender notosetae from same; G, Lower, two middle, and upper neurosetae from same; H, Left middle elytron, with detail of central papillae. Scales = 1.0 mm for A; 0.5 mm for B, D, E; 0.1 mm for C, F, G; 1.0 mm for H.

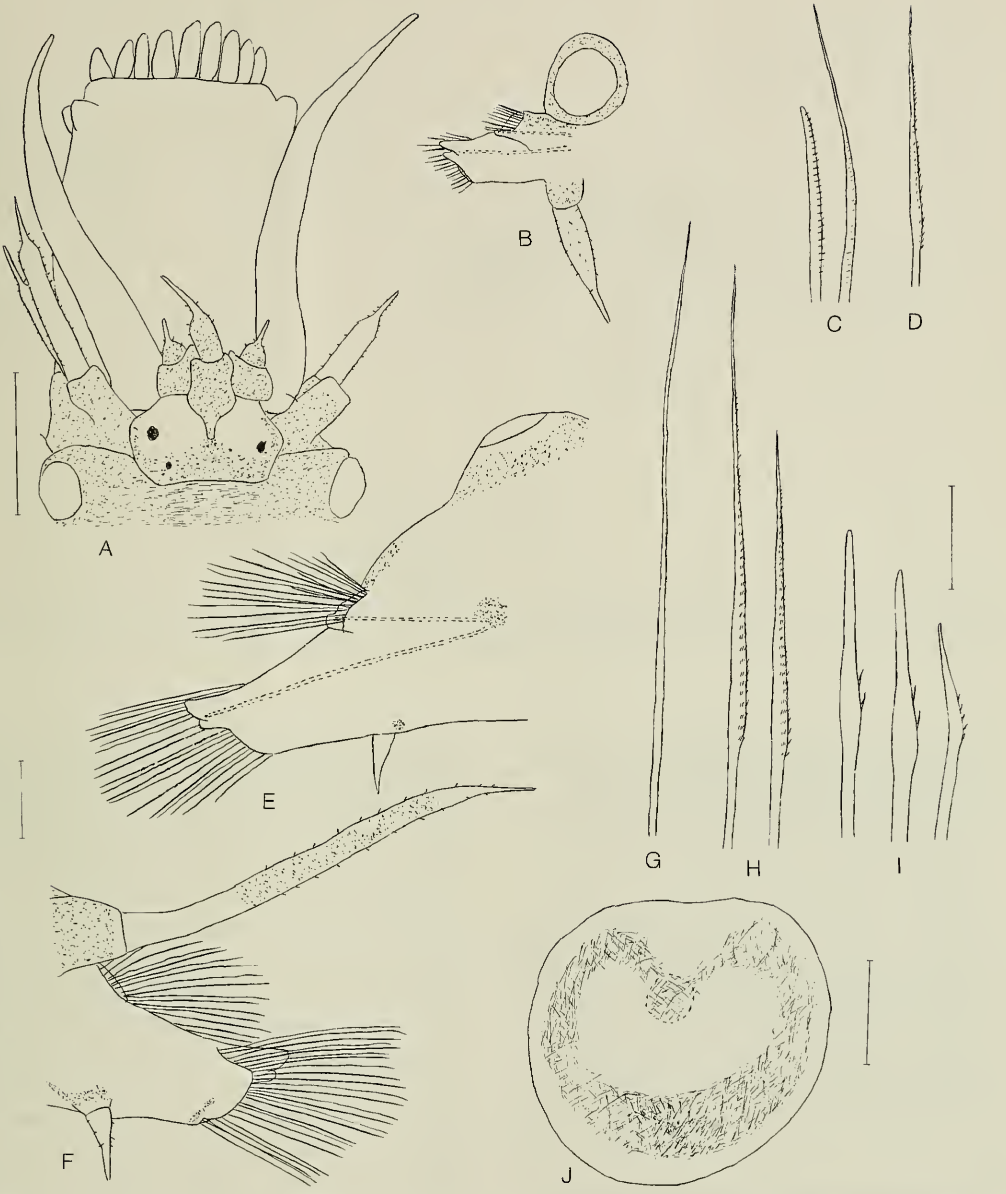

Fig. 3. *Pararctonoella indica,* holotype of *Intoshella indica* (BMNH 1972.51): A, Dorsal view of anterior end, pharynx fully extended, right dorsal tentacular cirrus missing, right eyes defective, only single one present, parapodia of segment II not shown; B, Right elytrigerous parapodium from segment II, anterior view, acicula dotted; C, Short and longer notosetae from same; D, Neuroseta from same; E, Right elytrigerous parapodium, anterior view, acicula dotted; F, Right cirrigerous parapodium, posterior view; G, Notoseta from same; H, Upper and lower supraacicular neurosetae from same; I, Middle and lower subacicular neurosetae from same; J, Left elytron. Scales = 1.0 mm for A; 0.5 mm for B, E, F; 0.1 mm for C, D, G–I; 1.0 mm for J.

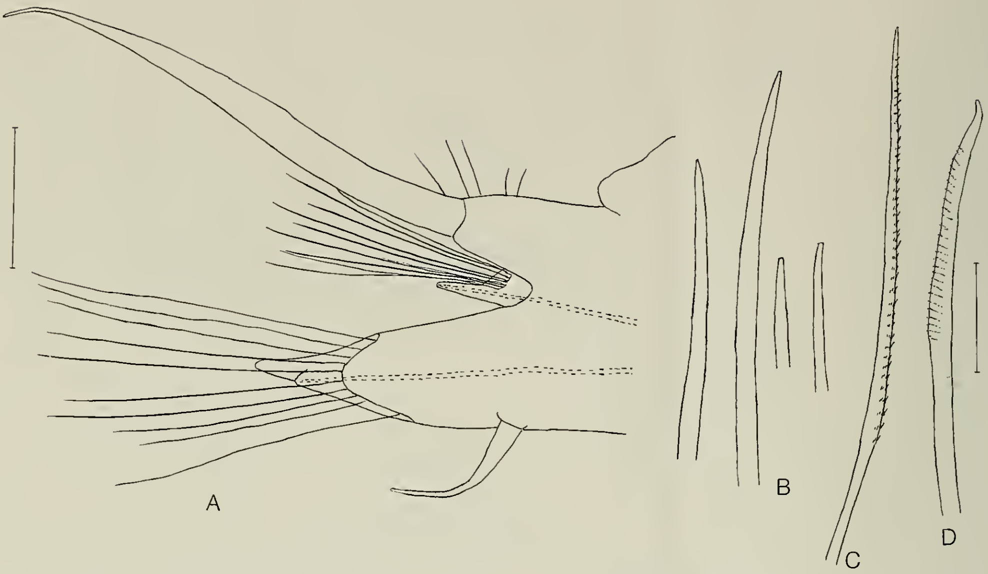

Fig. 4. *Pararctonoella aphthalma,* holotype of *Intoshella aphthalma* (USNM 45565, from LACM-AHF 296): A, Right cirrigerous parapodium, posterior view, acicula dotted; B, Notosetae from same; C, Supraacicular neuroseta from same; D, Subacicular neuroseta from same. Scales = 0.3 mm for A; 0.1 mm for B–D.

3. Elytra with nodular papillae on surface (Fig. 2H). Both notosetae and neurosetae of 2 kinds: notosetae stout, smooth, rod-like and long, spinous, with capillary tips (Fig. 2F); neurosetae shorter, with spinous rows and very long, with spinous rows, both with long bare tips (Fig. 2G) .... *Arctonella* Buzhinskaya
– Elytra without nodular papillae. Notosetae of single kind, slender, capillary (Fig. 3G) or acicular, clear (Fig. 4B). Neurosetae of 2 kinds: slender, long, with spinous regions, and shorter, stouter, with few spines (Figs. 3H, I; 4C, D) .... *Pararctonella,* new genus

Genus *Acholoe* Claparède, 1870

Type species.—*Polynoe astericola* Delle Chiaje, 1841, by monotypy. Gender: feminine.

Diagnosis.—Body elongate, vermiform, segments numerous (more than 100), tapering posteriorly. Elytra and prominent elytrophores numerous pairs (more than 40), on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32, continuing on every third segment to end of body. Elytra orbicular, smooth, without fringes of papillae, with scattered microtubercles on anterior part. Dorsal cirri on non-elytrigerous segments, with cylindrical cirrophores and distal styles; dorsal tubercles forming bifurcated T-shaped ciliated branchial processes. Prostomium bilobed, with 2 palps and 3 antennae with distinct ceratophores; median antenna inserted in anterior notch; ceratophores of lateral antennae inserted terminoventrally, converging midventrally (arctonoid type), with two pairs of eyes. First or tentacular segment not distinct dorsally, with tentaculophores lateral to prostomium, achaetous, with dorsal and ventral tentacular cirri, without conical facial tubercle. Second or buccal segment with subrectangular nuchal lobe, first pair of elytrophores, biramous parapodia, and ventral buccal cirri, longer than following ventral cirri. Parapodia biramous; notopodia short, subconical; neuropodia deeply cut dorsally and ventrally, with slightly longer bifid presetal acicular lobes and rounded postsetal lobes. Notosetae few, slender, short, curved, spinous, with blunt tips. Neurosetae stout,

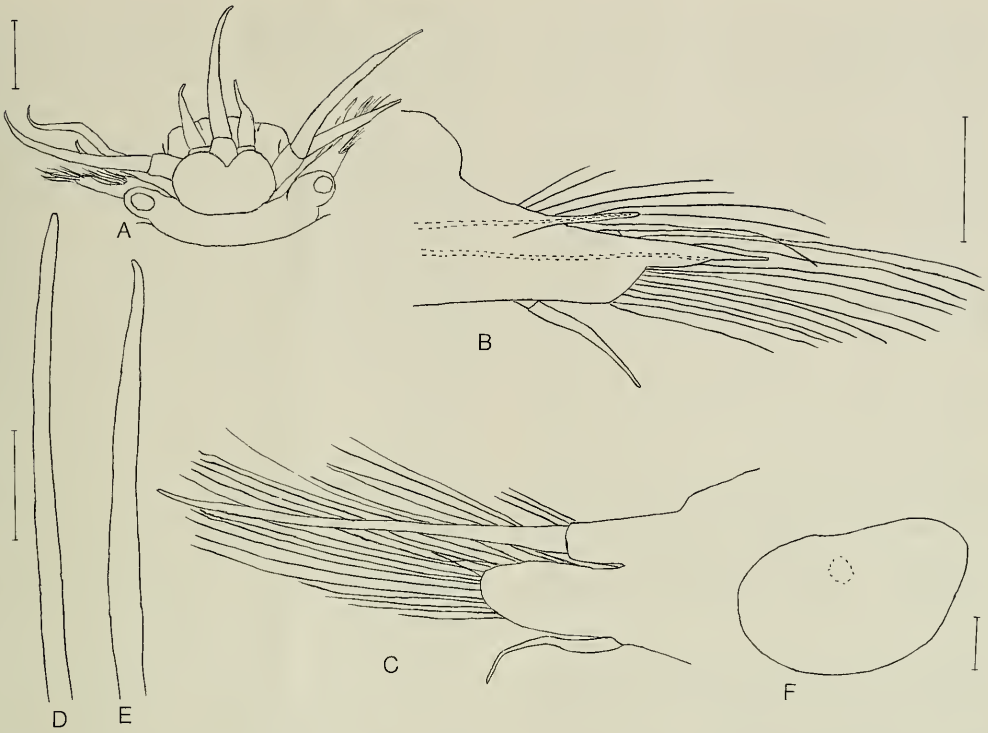

Fig. 5. *Intoshella euplectellae* syntype (BMNH 1921.5.1.548): A, Dorsal view of anterior end, pharynx partially extended, eyes faded, palps and elytra missing; B, Left elytrigerous parapodium, anterior view, acicula dotted; C, Left cirrigerous parapodium, posterior view; D, Notoseta from same, faint serrations not shown; E, Neuroseta from same, faint serrations not shown; F, Left elytron. Scales = 0.5 mm for A; 0.5 mm for B, C; 0.1 mm for D, E; 0.5 mm for F.

falcate, spinous, with entire tips. Ventral cirri short, subulate. Pharynx with nine pairs of papillae and two pairs of jaws. Nephridial papillae inconspicuous. Pygidium with pair of anal cirri. Commensal with asteroids.

Remarks.—There has been some confusion regarding the type species of *Acholoe* Claparède, 1870. In her Catalogue, Hartman (1959:59) listed: "Genotype: *Acholoe squamosa* (Delle Chiaje) 1828. Remarks: *Nereis squamosa* Delle Chiaje, 1828, predates *Polynoe astericola* Delle Chiaje, 1841, and both are here regarded as identical." However, Delle Chiaje (1841:106) lists: 1) *Polynoe squamosa* Savigny; 2) *Polynoe astericola* Delle Chiaje (*Nereis squamosa* Mem.su gli anim.s.vert. II 368, t. XIX 7) [1825:368, pl. 19:fig.7]. Thus *Nereis squamosa* Delle Chiaje (1825) was distinct from *Polynoe squamosa* Savigny and was referred to *Polynoe astericola,* not to be confused with Savigny's name of *squamosa.* This is confirmed by McIntosh (1900) in his synonymy of *Acholoe astericola.* Claparède (1870) chose *Polynoe astericola* as the type species of his new genus *Acholoe,* an appropriate name for the species commensal with asteroids, and has been widely used. Following Hartman (1959), some authors, such as Day (1967), and others, have incorrectly used *Acholoe squamosa* (Delle Chiaje).

Acholoe astericola (Delle Chiaje)
Fig. 1

Nereis squamosa Delle Chiaje, 1825:368. [Referred to *Polynoe astericola* by Delle Chiaje, 1841:106.]

Polynoe astericola Delle Chiaje, 1841:57, 62, pl. 129:fig. 7.

Polynoe malleata Grube, 1855:81, pl. 1: fig. 1.

Polynoe asterinae Carrington, 1865:177.

Acholoe astericola.—Claparède, 1870:382, pl.2:fig. 1, 1A, B.–McIntosh, 1900:397, pl.27:fig. 17, pl. 31:fig.4; pl. 33:fig. 15, pl. 41:figs. 13, 14.—Fauvel, 1923:94, fig. 36d–h.–Tebble, 1955:78.—Hartman, 1956:247, 271.—Cazaux, 1968:520, figs. 12, 13 (Development).

Acholoe orbiculata Treadwell, 1921:1, figs. 1–8.–Lopez-Garcia & San Martin-Peral, 1992:162, fig. 1a–f.

Acholoe squamosa.—Hartman, 1959:60 (Catalogue).—Day, 1967:52, fig. 1.5.g–k.—Barel & Kramers, 1977:49, fig. 9F.—Campoy, 1982:75.—Kirkegaard, 1983: 187.

Material examined.—Mediterranean: Naples, G. Skiasuy, collector, 2 specimens (RNHL 376; USNM 33626). Naples, collector P. Fauvel, 1 specimen (BMNH 1928.4.26.211). Off Camarque, Faraman, Beauduc, 10 m, 3 Jun 1959, H. Zibrowius, collector, 7 specimens (USNM 47171). Gulf of Kassandra, Kassandra Peninsula, North Aegean Sea, in ambulacral groove of sea-star *Astropecten aurantiacus,* 2 m, in sand, H. Lessios, collector, 6 Aug 1971, 1 specimen (USNM 50552).

Adriatic: Trieste, Lesia, Porto Ré, Grube, collector, 5 syntypes of *Polynoe malleata* (ZMB 1149–1151).

West Africa: St. Paul de Loanda, Belgian Congo, 22 Sep 1915, H. Lang & J. Chapin, collectors, holotype and 3 paratypes of *Acholoe orbiculata* (AMNH 1364, 1367). Off Accra, Gold Coast, R. Bassindale, collector, 1 specimen (BMNH 1953.3.1.619–620).

Type material.—The types of Delle Chiaje from Naples are not known to exist. Specimens from Naples (RNHL 376, USNM 33626) were examined and used to supplement the description of the species. Claparède (1870) reported a length of 45 mm and width of 4 mm, with about 120 segments. Syntypes of *Polynoe malleata* Grube (ZMB 1149–1151) from Trieste, Adriatic, were examined. A complete syntype of about 100 segments measured 40 mm in length and 5 mm in width, including setae. The species was referred to *A. astericola* by McIntosh (1900:397). The holotype and paratypes of *Acholoe orbiculata* Treadwell (AMNH 1364, 1367) from the Belgian Congo were examined. The complete holotype of about 145 segments measured 50 mm in length and 5 mm in width, including setae. The types were examined by Hartman (1956:147) and referred to *A. astericola.* No types are known for *Polynoe asterinae* Carrington (1865:177), from Southport Sands, England, commensal with *Asterias aurantiaca.* The latter incompletely described species was referred to *Acholoe squamosa* by Hartman (1959:99; Catalogue).

Description.—Body elongated, depressed, tapering slightly anteriorly and more so posteriorly, with numerous segments (up to 120 or more). Elytra on large bulbous elytrophores covering dorsum. Elytra large, oval, without papillae, with scattered microtubercles on anterior part, and with yellow brown to blackish pigmentation in central part and near external borders (Fig. 1K; McIntosh 1900, pl. 33:fig. 15). Dorsal cirri, on non-elytrigerous segments, with short cylindrical cirrophores and tapering papillate styles extending to tips of neurosetae; dorsal tubercles, in line with elytrophores, modified and forming large, flattened, T-shaped ciliated branchial processes (Fig. 1H; Claparède 1870, pl. 2: fig. 1A; McIntosh 1900, pl. 31:fig. 4).

Bilobed prostomium with lobes rounded, without cephalic peaks; median antenna with large ceratophore in anterior notch of prostomium, with style rather short, with tapering tip; lateral antennae with distinct ceratophores inserted terminoventrally, converging midventrally, with styles short, subulate; palps stout, tapering, longer than median antenna; eyes rather small, larger anterior pair anterolateral, smaller posterior pair near posterior border; tentaculophores lateral to prostomium, achaetous, with dorsal and ventral tentacular cirri similar to median antenna (Fig. 1A–C; McIntosh 1900, pl. 27:fig. 17).

Segment 2, with rectangular bulbous area or nuchal fold between first pair of elytrophores; similar lobes on segments 3 and 4 (Fig. 1A). Small biramous parapodia with ventral buccal cirri longer than following ventral cirri; notosetae and neurosetae similar to following segments, only more slender (Fig. 1D–F).

Biramous parapodium with smaller notopodium on anterodorsal side of large neuropodium, in form of short, digitiform acicular lobe; well developed neuropodium with presetal bilobed acicular lobe with acicular notch and projecting aciculum, slightly longer than rounded postsetal lobe (Fig. 1G, H; McIntosh 1900, pl. 31:fig. 4). Notosetae few (4–8), forming small bundle, short, extending to tips of notopodial lobe, slender, curved, with spinous rows and blunt bare tips (Fig. 1I). Neurosetae few (7–8), stout, thicker than notosetae, with short spinous regions and entire hooked tips, upper ones slightly more slender (Fig. 1J). Ventral cirri short, tapered (Fig. 1G, H). Pygidium with pair of anal cirri.

Development.—Cazaux (1968:520–524, Figs. XII–XIII) followed the pelagic development of *Acholoe astericola* in Arcachon, France, from the Trochophore to the Nectochaete II stage (30 days), with nine segments and five pairs of elytra.

Habitat.—*Acholoe astericola* has been reported as commensal with various species of star-fish of the genus *Astropecten,* including *A. aurantiacus, A. bispinosus, A. platyacanthus, A. pentacanthus, A. irregularis, A. hupferi,* and the star-fish *Luidia ciliaris.* The polynoids occupy the ambulacral grooves of the asteroids.

Distribution.—Atlantic Ocean, English Channel, France, Spain, Mediterranean, Adriatic, West Africa, in shallow depths.

Remarks.—A unique feature in *Acholoe astericola* is the development of the dorsal tubercles on the cirrigerous segments, forming bifurcate T-shaped ciliated branchial structures. The more numerous segments and elytra, continuing to the posterior end of the body, differs from the other shorter species of Acholoinae. Middorsal subrectangular bulbous areas, found on segments 2, 3, & 4, of *A. astericola,* are also found on segment 2 of *Arctonoella sinagawaensis.* The neuropodial presetal acicular lobes have wider acicular notches than in the other species of Acholoinae.

Genus *Arctonoella* Buzhinskaja, 1967

Type species.—*Harmothoe sinagawaensis* Izuka, 1912, by original designation and monotypy. Gender: feminine.

Diagnosis.—Body elongate, with segments up to 41, tapering posteriorly. Elytra and prominent elytrophores 16 pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32, 33 (or 35). Elytra orbicular, without fringe of papillae or tubercles, with nodular papillae in central area. Dorsal cirri on non-elytrigerous segments, with cylindrical cirrophores and long distal styles; dorsal tubercles small, nodular. Prostomium bilobed, with two palps and three antennae with distinct ceratophores; median antenna inserted in anterior notch of prostomium; ceratophores of lateral antennae inserted terminoventrally, converging midventrally (arctonoid type), with two pairs of eyes. First or tentacular segment not distinct dorsally, with tentaculophores lateral to prostomium, achaetous, with dorsal and ventral tentacular cirri; without conical facial tubercle. Second or buccal segment without nuchal fold, with first pair of elytrophores, biramous parapodia, and long ventral buccal cirri. Parapodia biramous; shorter notopodia with projecting acicular lobe; larger neuropodia deeply cut dorsally and ventrally, longer presetal acicular lobe bifid distally, with longer supraacicular process and shorter rounded postsetal lobe. Notosetae numerous, of two kinds: upper ones smooth, rod-like, stouter than neurosetae;

lower ones slender, serrated, tapering to fine tips. Neurosetae with long to shorter spinous regions, all with rather long bare entire tips. Ventral cirri short, subulate. Pharynx with nine pairs of papillae and two pairs of jaws. Nephridial papillae prominent, beginning on segment 6. Pygidium with pair of long anal cirri.

Arctonoella sinagawaensis (Izuka)
Fig. 2

Harmothoe sinagawaensis Izuka, 1912:57: pl. 6:figs. 8–12.—Fauvel, 1933:10.

Not ? *Harmothoe sinagawaensis.*—Fauvel, 1932:23; 1953:48 [=*Pararctonoella indica* (Day, 1973), new combination].

Gattyana sinagawaensis.—Hartman, 1959: 71, 78.—Imajima & Hartman, 1964:32.

Hesperonoe (?) *sinagawaensis.*—Uschakov & Wu, 1965:172.

Arctonoella sinagawaensis.—Buzhinskaja, 1967:83, fig. 1A–E.—Uschakov, 1982: 39, pl. 39:1–8.

Material examined.—Sea of Japan: Possjet Bay, A. N. Golikov, collector, Aug 1962, 1 specimen (ZIASL 17056).

Type material.—The types of Izuka from the Gulf of Tokyo, Japan are not known to exist. Fauvel (1933) described two specimens from the Gulf of Pei Tcheu Ly in the Yellow Sea. The specimen from Possjet Bay in the Sea of Japan, deposited in ZIASL, was received on loan from P. V. Uschakov. The specimen was described and figured by G. N. Buzhinskaja (1967) and referred to the new genus *Arctonoella.*

Description.—Body flattened, tapering slightly anteriorly and more so posteriorly. Segments up to 41, length 58 mm, width 18 mm, with setae. Elytra large, oval, covering dorsum, smooth, with or without group of soft rounded papillae in central area (Fig. 2H). Dorsal cirri with short cylindrical cirrophores and bulbous lobe on posterior side; style long, extending far beyond tips of neurosetae; dorsal tubercles small, nodular (Fig. 2E).

Bilobed prostomium with lobes rounded, without cephalic peaks, broader than long; median antenna with large ceratophore in anterior notch, style longer than lateral antennae; lateral antennae with large ceratophores inserted terminoventrally, converging midventrally; styles short subulate; palps stout, long, tapering; larger anterior eyes in region of greatest width of prostomium, smaller posterior eyes near posterior border; tentaculophores large, achaetous, with long dorsal and ventral tentacular cirri (Fig. 2A).

Segment 2 with rectangular raised area between first pair of large elytrophores, biramous parapodia, and long ventral buccal cirri (Fig. 2A, B). Notosetae similar to following, except stout notosetae showing faint indications of spinous rows (Fig. 2C); neurosetae similar to following, all with slender bare tips. Biramous parapodia with smaller notopodia with projecting acicular lobes on lower sides; larger neuropodia with shorter subconical postsetal lobes and longer presetal acicular lobes, bifid distally, with longer subconical supraacicular processes (Fig. 2D, E). Notosetae numerous, of two kinds: upper ones radiating, stout, acicular, smooth, tapering to rounded tips and lower ones slender, very finely denticulate, tapering to fine tips (Fig. 2D, F). Neurosetae numerous, with long (lower ones) to very long (upper ones) spinous regions, all with rather long, bare, entire tapered tips (Fig. 2D, G). Ventral cirri short, smooth, subulate (Fig. 2D, E). Pygidium with pair of long anal cirri. Nephridial papillae beginning on segment 6, small at first, then long, cylindrical (Fig. 2E).

Distribution.—North Pacific, Japan Sea, Yellow Sea, in shallow depths.

Remarks.—*A. sinagwaensis* agrees with *A. astericola* in having segment 2 with rectangular raised areas between the first pair of elytrophores. The notopodia, with two kinds of notosetae: stout, rodlike, smooth, and slender, spinous, with capillary tips, differs from the other members of the Acholoinae, in having notosetae of a single kind.

Paractonoella, new genus

Type species.—*Intoshella indica* Day, 1973. Gender: feminine.

For: *Pararctonoella indica* (Day, 1973), new combination *Pararctonoella aphthalma* (Gallardo, 1968), new combination.

Diagnosis.—Body elongate, with segments up to 48, tapering posteriorly. Elytra and prominent elytrophores 18–20 or more pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32/35, 37, 39 (*P. indica*) or 36, 37, 40, 41 (*P. aphthalma*). Elytra large, oval, smooth, without papillae or tubercles. Dorsal cirri on non-elytrigerous segments, with cylindrical cirrophores and long styles; dorsal tubercles indistinct or bulbous. Prostomium bilobed, with lobes rounded, without cephalic peaks, with two palps and three antennae with distinct ceratophores; median antenna inserted in anterior notch of prostomium; ceratophores of lateral antennae inserted terminoventrally, converging midventrally (arctonoid type); with (*P. indica*) or without (*P. aphthalma*) two pairs of eyes. First or tentacular segment not distinct dorsally; tentaculophores lateral to prostomium, each with single seta and dorsal and ventral tentacular cirri; without conical facial tubercle. Second or buccal segment without nuchal fold, with first pair of elytrophores, biramous parapodia, and long ventral buccal cirri. Parapodia biramous, shorter notopodia with projecting acicular lobes, larger neuropodia deeply cut dorsally and ventrally, with shorter rounded postsetal lobes and longer presetal acicular lobes, bilobed distally, with longer conical supraacicular and shorter rounded subacicular processes. Notosetae of single kind: slender, capillary (*P. indica,* except segment 2), or stouter, acicular (*P. aphthalma*). Neurosetae of two kinds: supraacicular ones with long spinous regions and fine tips; subacicular ones stouter, with fewer spinous rows and long bare tips. Ventral cirri short, subulate. Pharynx with nine pairs of papillae and two pairs of jaws. Nephridial papillae beginning on segment 6. Pygidium with pair of anal cirri. Commensal with ophiuroid (*P. aphthalma*).

Etymology.—*Para,* near, plus *Arctonella,* indicating the similarity of the two genera.

Remarks.—Day (1973) assigned his new species of *indica* to *Intoshella* "with considerable hesitation". The same could be said for Gallardo (1968) when he assigned his new species of *aphthalma* to *Intoshella.* Both species are referred herein to the new genus *Pararctonella.* The new genus differs from *Arctonella* Buzhinskaya by having notosetae of one kind: slender, capillary (*P. indica*) or acicular (aphthalma), instead of two kinds, as in *A. sinagawaensis. Arctonella* has 16 pairs of elytra; *Pararctonella,* with 18–20 or more pairs.

Pararctonoella indica (Day),
new combination

Fig. 3

??*Harmothoe sinagawaensis.*—Fauvel, 1932:23, pl. 1:figs. 1, 2, text-fig. 3a–d. Not Izuka, 1912.

?*Harmothoe sinagawensis* [sic].—Fauvel, 1953:48, fig. 21a, b (Incertae sedis]. Not Izuka, 1912.

Intoshella indica Day, 1973:338, fig. 1A–F (genus doubtful).—Uschakov, 1982:140 (Key).

Material examined.—Indian Ocean: Mirkar wada, Ratnagiri, South of Bombay, India, muddy stones, 4 Jul 1969, U. D. Gaikwad, collector, holotype (BMNH 1972.51).

Description.—Body flattened ventrally, slightly arched dorsally, tapering anteriorly and posteriorly, with 40 segments, last one minute, 24 mm long, 8 mm wide with setae. Elytra and elytrophores 18 pairs (not 16, as indicated by Day), on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32, 35, 37, 39. Elytra large, oval, smooth, without papillae or tubercles, with blackish pigmentation concentrated on places of attachment to elytrophores and outer circular areas (Fig. 3J; Fauvel 1932, pl. 1:fig. 1; Day 1973, fig. 1A). Dorsal cirri with thick cylindrical cirrophores and long styles, extending far beyond neurosetae, with short papillae, pigmented on middle part and on cirrophores; dorsal tubercles inflated, indistinct (Fig. 3F; Day 1973, fig. 1F).

Bilobed prostomium with lobes rounded, without cephalic peaks; median antenna with large inflated ceratophore in anterior notch, with short style and long filamentous tip; lateral antennae with large inflated ceratophores inserted terminoventrally and converging midventrally, with styles similar to median antenna but smaller, both with few micropapillae; palps very long, tapered, smooth; eyes rather small, anterior dorsolateral pair larger than posterior pair (right side defective on holotype, only one eye in intermediate position); tentaculophores (segment 1) lateral to prostomium, each with single stout seta and dorsal and ventral tentacular cirri, similar to but longer than median antenna (Fig. 3A; Day 1973, fig. 1B).

Segment 2 without nuchal fold, with first pair of large elytrophores, biramous parapodia, and long ventral buccal cirri, similar to tentacular cirri (Fig. 3A, B); notosetae differing from following segments, of two kinds; shorter, with distinct spinous rows and blunt tips and longer, with indistinct spinous rows and fine tips (Fig. 3C); neurosetae similar to lower supraacicular neurosetae of following segments (Fig. 3D). Biramous parapodia with notopodia short, subconical, with short rounded acicular processes on anterodorsal faces of larger neuropodia; neuropodia with shorter rounded postsetal lobes and longer presetal acicular lobes, bilobed distally, with longer conical supraacicular and shorter rounded subacicular processes (Fig. 3E, F; Fauvel 1932, pl. 1:fig. 2; Day 1973, fig. 1F). Notosetae numerous, forming fan-shaped bundle, extending to near distal tips of neuropodia, finer than neurosetae, finely serrated and appearing smooth, with fine hairlike tips (Fig. 3E, G); Fauvel 1932, fig. 3a; Day 1973, fig. 1C). Neurosetae numerous, of two kinds: supraacicular long, slender, with numerous spinous rows and tapering to fine capillary tips (Fig. 3H; Fauvel 1932, fig. 2B; Day 1973, fig. 1D); subacicular shorter, stouter, with 2 (upper) to 5 (lower) large spines on enlarged basal parts and long, bare, blunt tips (Fig. 3I; Fauvel 1932, fig. 3c, d; Day 1973, fig. 1E). Ventral cirri short, subulate, with few micropapillae (Fig. 3E, F). Pharynx (extended) with nine pairs of papillae and two pairs of jaws (Fig. 3A). Nephridial papillae minute. Pygidium with anus medial to parapodia of segment 39, with pair of anal cirri.

Distribution.—Indian Ocean, off Bombay, India, intertidal.

Remarks.—As Uschakov (1982:190) pointed out, Day's species of *indica* is distinguished from *Arctonella* by the absence of large acicular notosetae and replaced by slender notosetae with hairlike tips. In *P. indica,* the neurosetae are of two kinds: slender, with long spinous regions, tapered capillary tips, and shorter, stouter, with few spines (2–5) and long bare tips. Eyes are present (absent in *P. aphthalma*).

Paractonoella aphthalma (Gallardo), new combination
Fig. 4

Intoshella aphthalma Gallardo, 1968:47, pl. 2:figs. 1–6, pl. 3:figs. 1, 2.—Uschakov, 1982:141, pl. 46:1–8 (after Gallardo).

Material examined.—South China Sea: South Viet Nam, Bay of Nha Trang, NAGA Exped. Sta 285, 23 Mar 1960, 19 m, mud, on ophiuroid, holotype (LACM-AHF 296; parapodium, USNM 45565).

Description.—Body long, narrow, flattened, tapering posteriorly, with 44 segments (incomplete), 11+ mm long, and 4 mm wide with setae. Elytra and elytrophores 20+ pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32, 36, 37, 40, 41, 44. Elytra large, oval, smooth, without papillae or tubercles (Gallardo 1968, pl. 2:fig. 2) Dorsal cirri with cylindrical cirrophores and long, smooth, tapering styles, extending about to tips of neurosetae; dorsal tubercles bulbous (Fig. 4A; Gallardo 1968, pl. 2:fig. 4).

Prostomium bilobed, slightly longer than wide, lobes rounded, without cephalic peaks, with scattered pigmentation; median antenna with bulbous ceratophore in anterior notch of prostomium, style slightly longer than prostomium; lateral antennae with bulbous ceratophores inserted terminoventrally and converging midventrally, with styles half as long as median antenna; palps stout, tapered, longer than median antenna; eyes absent (faded or hidden by pigmentation?); tentaculophores (segment I) lateral to prostomium, each with small acicular lobe, slender seta, and dorsal and ventral tentacular cirri longer than palps (Gallardo 1968, pl. 2:fig. 1).

Segment 2 without nuchal fold, with first pair of large elytrophores, biramous parapodia, and long ventral buccal cirri on distinct cirrophores and extending to tips of neurosetae; notosetae and neurosetae similar to following segments (Gallardo 1968, pl. 2:figs. 1, 3). Biramous parapodia with notopodia short, subconical, with projecting acicular processes on anterodorsal faces of larger neuropodia; neuropodia with shorter rounded postsetal lobes and longer presetal acicular lobes, bilobed distally, with longer conical supraacicular and shorter rounded subconical processes (Fig. 4A; Gallardo 1968, pl. 2:fig. 4). Notosetae numerous, forming fan-shaped bundles, extending to distal tips of neuropodia, about equal in thickness to neurosetae, slightly curved, smooth, with or without very fine denticulations, tapering to rounded tips (Fig. 4B; Gallardo 1968, pl. 2:fig. 5). Neurosetae numerous, of two kinds; supraacicular ones long, slender, with long spinous regions, tapering to slender bare tips (Fig. 4C; Gallardo 1968, pl. 3:fig. 1); subacicular ones stouter, with shorter spinous regions and slightly hooked bare tips (Fig. 4D; Gallardo 1968, pl. 2:fig. 6, pl.3:fig. 2). Ventral cirri short, subulate, smooth (Gallardo 1968, pl. 2:fig. 4). Nephridial papillae cylindrical, turned dorsally between parapodia, beginning on segment 6. Pharynx (?, not extended). Pygidium (?, incomplete).

Distribution.—North Pacific Ocean, South China Sea, South Viet Nam, 19 meters, on ophiuroid.

Remarks.—In *P. aphthalma,* the single available specimen was incomplete posteriorly, with 44+ segments and 20+ pairs of elytrophores. There is the possibility that the elytra continue to the posterior end of a longer body. Eyes were absent, as the species name indicates, with the possibility that they were just faded. The neurosetae are of two kinds, as in *P. indica.* Here they are long, slender, with numerous spinous rows, tapering to slender tips, and stouter, with fewer spinous rows and slightly hooked bare tips.

Genus *Intoshella* Darboux

Type species.—*Polynoe* (*Langerhansia*) *euplectellae* McIntosh, 1885 by monotypy.

Intoshella Darboux, 1900, new name for *Langerhansia* McIntosh, 1885, preoccupied by Czerniavsky, 1881, in Syllidae.

Diagnosis.—Body long, slender, flattened, tapering posteriorly. Segments up to 50. Elytra up to 23 pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32, 33, 36, 38, alternate segments to end of body. Elytra large, covering dorsum, without fringes of papillae or tubercles. Dorsal cirri with cylindrical cirrophores and long styles; dorsal tubercles bulbous. Prostomium bilobed, rounded anteriorly, without cephalic peaks, with pair of palps and three antennae with distinct ceratophores; median antenna with ceratophore in anterior notch, lateral antennae with ceratophores inserted terminoventrally, with two pairs of eyes; tentaculophores of segment I lateral to prostomium, each with seta and dorsal and ventral tentacular cirri; without facial tubercle. Buccal segment (2) without nuchal lobe, with first pair of elytrophores, biramous parapodia, and long ventral buccal cirri. Biramous parapodium with small subconical notopodium with long digitiform acicular process; larger neuropodium with shorter, rounded postsetal lobe and larger, subconical presetal acicular lobe with long digitiform supraacicular extension. Both notosetae and neurosetae of about equal width, transparent, with faint serrations, notosetae tapering to blunt tips, neurosetae with tips slightly falcate. Ventral cirri short, tapered. Pygidium (?, incomplete). Pharynx (?, not extended). Nephridial papillae inconspicuous. Commensal with glass sponges.

Intoshella euplectellae (McIntosh)
Fig. 5

Polynoe (*Langerhansia*) *euplectellae* McIntosh, 1885:108, pl. 15:fig. 6, pl. 19:fig. 7, pl. 9A:figs. 8, 9.

Intoshella euplectellae.—Hartman, 1959:82 (Catalogue).—Uschakov, 1982:140 (Key).

Material examined.—Pacific Ocean, off Philippines, *Challenger* sta, 183 meters, with glass sponge, *Euplectella,* syntype, female with eggs (BMNH 1921.5.1.548).

Description.—Body long, slender, flattened, tapering slightly anteriorly and more so posteriorly, very fragile, delicate, translucent, with two dorsal ciliated bands per segment, extending on to dorsal tubercles and elytrophores. Length about 21 mm, width 7 mm, segments up to 50. Elytra large, oval, covering dorsum, up to 23 pairs, on segments 2, 4, 5, 7 alternate segments to 23, 26, 29, 32, 33, 36, 38, alternate segments to end of body. Elytra delicate, translucent, smooth, without tubercles or fringes of papillae, with or without translucent micropapillae near posterior borders (Fig. 5F; McIntosh 1885, pl. 19:fig. 7). Dorsal cirri on non-elytrigerous segments with short cylindrical cirrophores and long smooth styles, tapering to slender tips and extending beyond tips of neurosetae; dorsal tubercles bulbous (Fig. 5C; McIntosh 1885, pl. 15:fig. 6).

Bilobed prostomium with rounded lobes, without cephalic peaks; median antenna with ceratophore in anterior notch, style tapered, small, longer than prostomium; lateral antennae with distinct ceratophores inserted terminoventrally, with short tapered styles; palps stout, tapered, as long as median antenna; 2 pairs of small eyes on posterior half of prostomium, closely approximated on each side of prostomium; tentaculophores lateral to prostomium, each with single seta and dorsal and ventral tentacular cirri, longer than median antenna (Fig. 5A; McIntosh 1885, pl. 15:fig. 6). Without facial tubercle.

Segment 2 without nuchal fold, with first pair of large elytrophores, biramous parapodia and long ventral buccal cirri, extending anteriorly (Fig. 5A; McIntosh 1885, pl. 15:fig. 6). Biramous parapodia long, translucent; notopodia small lobes on anterodorsal sides of larger neuropodia, with long digitiform acicular processes; larger neuropodia with shorter, rounded postsetal lobes and longer, subconical presetal acicular lobes with digitiform supraacicular extensions (Fig. 5B, C). Notosetae moderate in number (ca. 15), pale, translucent, short to longer, some extending beyond tips of neuropodia, similar to neurosetae in width and appearance, smooth or with faint transverse striations, slightly curved and tapering to blunt tips (Fig. 5B, D; McIntosh 1885, pl. 9A:fig. 8). Neurosetae moderate in number (ca. 30), extra long, fragile, similar to notosetae in width and appearance, with tips slightly falcate (Fig. 5B, E; McIntosh 1885, pl. 9A:fig. 9). Ventral cirri short, tapering to slender tips and extending beyond basal tips of neuropodia (Fig. 5B, C). Pharynx (?, not extended). Pygidium (?).

Distribution.—Pacific Ocean, off Philippines, 184 meters, commensal with glass sponge *Euplectella asperigillum*

Remarks.—The type species of *Intoshella* Darboux, 1900, *Polynoe* (*Langerhansia*) *euplectella,* was incompletely described and figured by McIntosh (1885) and Darboux (1990). Even though a questionable genus, it was incorrectly used for a number of species, including the two species covered herein: *I. aphthalma* Gallardo, 1968, and *I.*

indica Day, 1973, and referred to the new genus *Pararctonella.* At present, *Intoshella* should be considered to be monotypic.

In *I. euplectella,* the neuropodial subconical presetal acicular lobes have digitiform supraacicular extensions and lack subacicular extensions, as found on the other genera of Acholoinae.

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Presence of *Micronereis* in Antarctic waters and description of a new species, *M. antarctica* (Polychaeta: Nereididae: Notophycinae)

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Abstract.—A new species of Nereididae, *Micronereis antarctica* from Antarctic waters (South Shetland Islands and the Palmer Archipelago), is described. The species was collected on the sea-bed from the intertidal zone to 30 m deep. This represents the first record of the genus in Antarctic waters. Of the eight known species in this genus, *M. antarctica* is most similar to *M. nanaimoensis* Berkeley & Berkeley, 1953 distributed along the western coast of North America; the two species can be distinguished by morphological differences of the peristomium and mouth, the parapodia and setae, and coloration of integument and eggs.

The systematics of *Micronereis* Claparède, 1863 was reviewed recently by Paxton (1983). *Micronereis* is the only genus in the Notophycinae, one of the four subfamilies in the Nereididae. The Notophycinae show the greatest divergence from the basic nereidid plan by the absence of antennae, presence of small palps lacking palpostyles, a very short peristomium, a proboscis that is not fully eversible, two types of very slightly sclerotized paragnaths, parapodia without dorsal cirri on the first two setigers, and biramous parapodia with widely separated notopodia and neuropodia (Banse 1977, Paxton 1983). The taxonomic status of the genus has been reviewed by Reish (1961), Banse (1977), Buzhinskaya (1981) and Paxton (1983); reproduction and development of some of its species have been studied by Racovitza (1893, 1894), Berkeley & Berkeley (1953) and Rullier (1954).

With eight species described, *Micronereis* has a wide geographical distribution. Its species have been found on the coasts of Europe (*M. variegata* Claparède, 1863), the Pacific coast of North America (*M. nanaimoensis* Berkeley & Berkeley, 1953), the Atlantic coast of North America (*M. picola* Paxton, 1983), the Kurile Islands, Sea of Okhotsk (*M. ochotensis* Buzhinskaya, 1981), the Marshall Islands, Western Pacific (*M. eniwetokensis* Reish, 1961), Australia (*M. halei* Hartman, 1954), Australia and Suez Canal, Egypt (*M. bansei* (Hartmann-Schröder, 1979)), and Snares Island, New Zealand (*M. minuta* (Knox & Cameron, 1970)). Villalba & Viéitez (1988) have reported the presence of *Micronereis* in NW of Spain through a specimen from the intertidal zone of an area in the ría Pontevedra, which could represent a new species. Until now no species of *Micronereis* has been found south of the Antarctic Convergence. In studies undertaken in the intertidal and subtidal zones of Robert Island, South Shetland Islands and Doumer Island, Palmer Archipelago as part of the "Antarctic intertidal ecology" and "Herbivorous fish of the Antarctic rocky sublitoral" projects, numerous *Micronereis* specimens were found. These differed from the other known species reported for the genus and consequently are described as a new species.

Type specimens of the new species are deposited in the National Museum of Natural History, Smithsonian Institute, Washington D.C. (USNM); Sala de Sistemática, Departamento de Ecología, Pontificia Universidad Católica de Chile (SSUC); and Museo de Zoología, Universidad de Concepción (UCCC).

Materials and Methods

Specimens were collected at Robert Island, South Shetland Islands (62°24′S, 59°30′W), in January 1978 and 1979, and in South Bay, Doumer Island, Palmer Archipelago (64°52′S, 63°36′W), in January 1993 and 1995. In Robert Island, samples were taken from a rocky shore ("Roquerío Gaviota") overlooking the Estrecho Inglés, about mid-way between Cabo Morris and Caleta Copper Mine; samples were taken during low tide, in the lower intertidal fringe, from among the alga *Gigartina skottsbergii* Setchell & Gardner, 1936. In South Bay, samples were taken from the subtidal seabed by diving; samples were collected from 1 m^2 areas along a bathymetric transect at six depths (3, 7, 12, 20, 30 and 40 m) with four replicate samples taken at each depth. Polychaetes were fixed in 10% formalin and preserved in 70% ethanol. Small specimens, oocytes and eggs were measured by microscopic observation and the use of a calibrated micrometer eyepiece in the stereoscopic and compound microscopes. To examine paragnaths and jaws, it was often necessary to make a ventrolateral incision and dissect out the complete pharynx and buccal tube, which were opened by cutting laterally. Figures were prepared with a drawing tube on a Wild M-5 stereoscopic microscope and a Leitz compound microscope. For scanning electron microscopic observations (SEM), specimens were treated with ultrasound in an aqueous medium to detach particles adhering to the setae and body surface, dehydrated in acetone, critical point dried in CO_2, mounted on bronze stubs with double-coated tape, sputter-coated with gold-palladium (≈40 Å) and examined and photographed with a JEOL JSM-25SII microscope using an accelerating voltage of 30 kV.

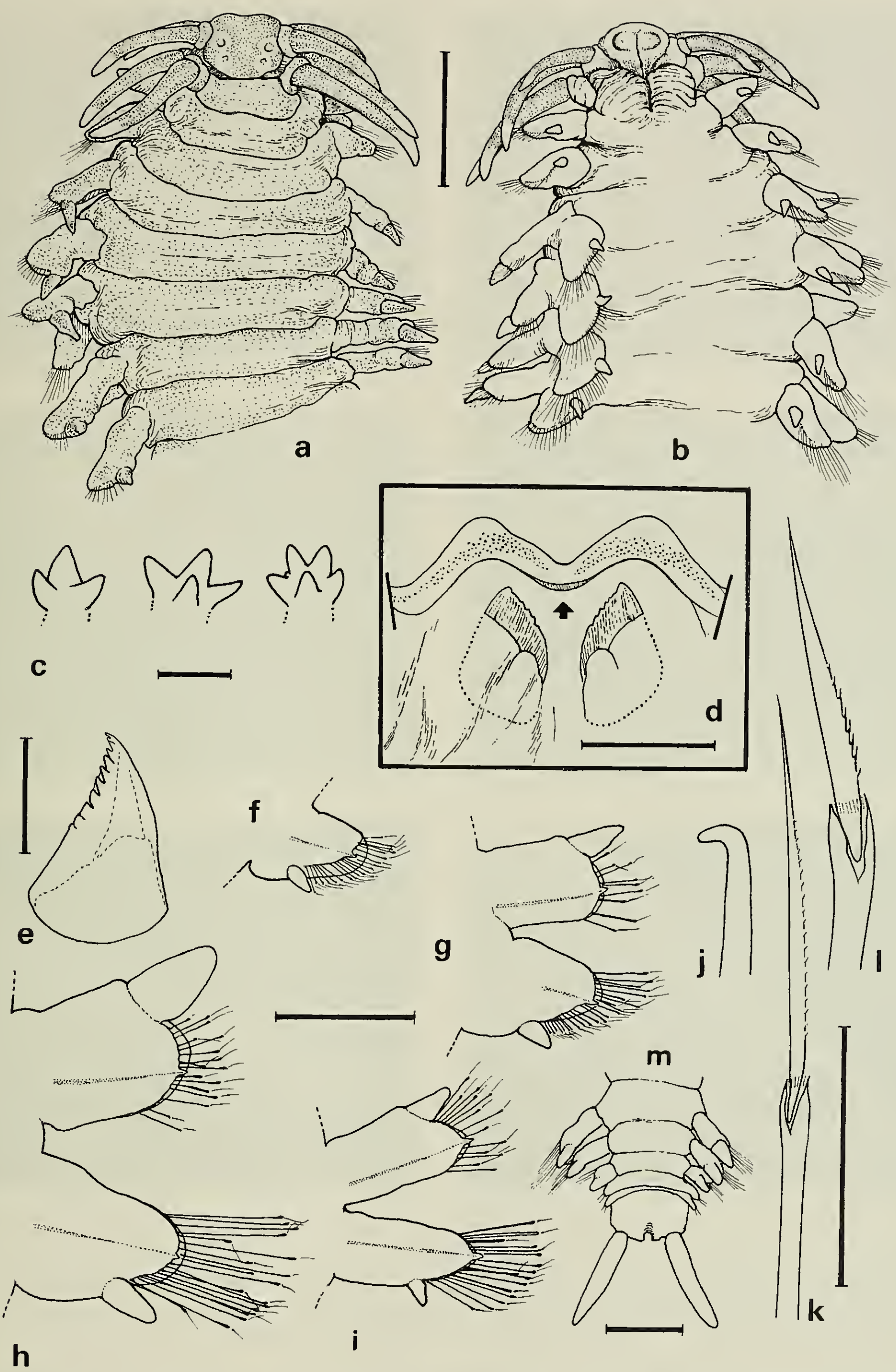
Micronereis antarctica, new species
Figs. 1, 2

Material examined.—Antarctica: Palmer Archipelago, Doumer Island, South Bay, 64°52′S, 63°36′W, J. M. Fariña & A. Palma, coll., 26 Jan 1993, female holotype (USNM 174067, 12 m; 4 sex indeterminate paratypes (USNM 174068, 7-20 m; 11 sex-indeterminate paratypes (USNM 174069), 12-20 m; 3 female paratypes (USNM 174070, 1 small female paratype (USNM 174071); 2 small sex-indeterminate paratypes (USNM 174072), 14 Jan 1995, 12 m, J. M. Fariña & B Broitman, coll.; 1 female paratype (SSUC 6791) and 10 sex-indeterminate paratypes (SSUC 6792), 26 Jan 1993, 12-20 m, J. M. Fariña & A. Palma, coll.; 1 female paratype (SSUC 6793), 14 Jan 1995, 12 m; 3 female and 1 sex-indeterminate paratypes (UCCC 24038–24041), 14 Jan 1995, 12 m, J. M. Fariña & B. Broitman, coll. South Shetland Islands, Robert Island, Copper Mine Peninsula, 62°24′S, 59°30′W, N. Rozbaczylo, coll., 12 Jan 1978, intertidal, 2 small sex-indeterminate paratypes (USNM 174073).

Diagnosis.—Prostomium rounded to subquadrangular. Peristomium well developed, approximately half the length of prostomium. Peristomial cirri subulate. Mouth with long mid-ventral fissure. Oral paragnaths with 3–5 conical cusps circularly disposed. One median maxillary paragnath bar-shaped. Jaws of adults of shortened type. Compound homogomph spinigers with serrated blades, shaft without internal

→

Fig. 1. *Micronereis antarctica,* new species, holotype; a, anterior end, dorsal view; b, anterior end, ventral view; c, oral paragnaths showing different numbers of cusps, side view; d, scheme of buccal tube and pharynx



dissected ventrally showing the two groups of oral paragnaths, the maxillary paragnath (indicated by the arrow) and the jaws; e, jaw from a specimen 4.9 mm in length; f, parapodium from setiger 1, posterior view; g, parapodium from setiger 3, posterior view; h, parapodium from setiger 13, posterior view; i, parapodium from setiger 26, posterior view; j, tip of a notopodial acicula from setiger 26; k, thin homogomph spiniger from notopodium of setiger 12; l, broad homogomph spiniger from notopodium of setiger 12; m, posterior end. Scales = 1 mm for a, b; 0.5 mm for d–i, m; 0.05 mm for k, l; 0.01 mm for c, j.

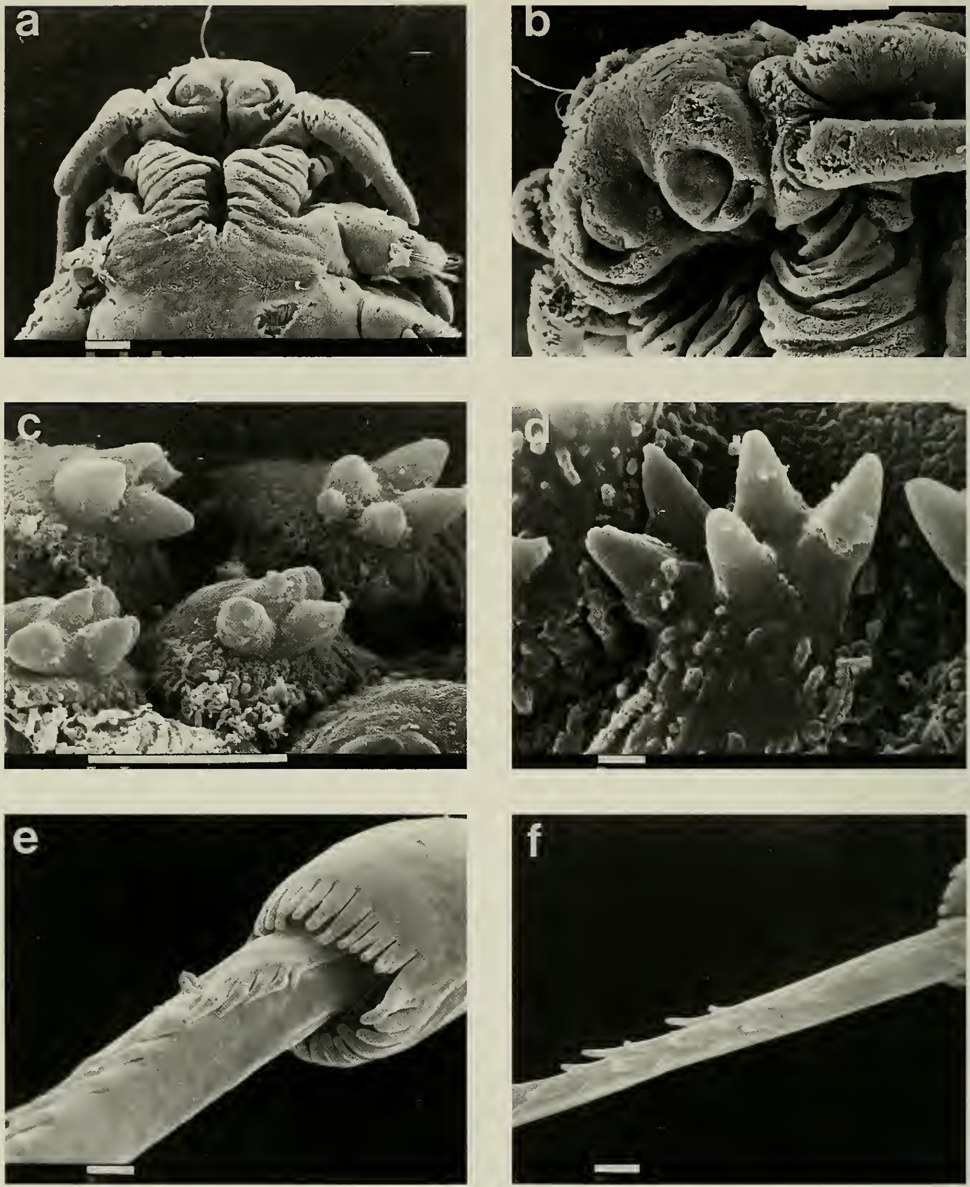


Fig. 2. *Micronereis antarctica,* new species, SEM micrographs: a, anterior end, ventral view; b, anterior end, ventrolateral view showing form and position of palps; c, oral paragnaths with short base; d, detail of an oral paragnath with long base; e, broad homogomph spiniger from neuropodium of setiger 5, detail of the articulation showing crenulations of the shaft; f, thin homogomph spiniger from notopodium of setiger 7 showing detail of the blade. Scales = 0.1 mm for a, b; 0.01 mm for c; 0.001 mm for d–f.

transversal septa, with crenulated distal end. Notopodial and neuropodial aciculae with bent tips. Parapodia without ciliation. Accessory parapodial cirri absent.

Description.—Holotype female, complete with 40 setigers, measuring 14.5 mm long, 1.9 mm wide without and 2.7 mm with parapodia. Smallest specimens (Paratypes USNM 174071 and USNM 174072 and 174073) 2.5–4.2 mm long for 14–17 setigers; width 0.3–0.8 mm without and 0.7–1.2 mm with parapodia, without setae. Largest specimen (Paratype SSUC 6793) 36 mm long for 46 setigers, width 2.4 mm without parapodia at setigers 4–5 and 3.9 mm with parapodia, without setae. In specimens conserved in alcohol body colour varying from light to dark brown more or less uniform; distal ends of peristomial cirri with little or no pigmentation; in some specimens the prostomium and first setigers have more pigmentation; in some light-brown specimens the notopodia and dorsal parapodial cirri are dark brown; in a few specimens the body has darkish brown transversal stripes of different lengths that cover the full width of the segment against a light-brown background.

Prostomium (Fig. 1a) rounded to subquadrangular, slightly wider than long, with weakly bilobed anterior margin; rounded in the smallest specimens. Two pairs fuchsia-coloured eyes with lenses, in trapezoidal arrangement; anterior pair larger and further apart than smaller posterior pair. In smallest specimens eyes in a nearly transverse row. A pair of small, rounded, ventral palps (Figs. 1b, 2a, b), with external lateral margins delimited by a slight half-moon shaped depression and separated from each other by a more or less narrow gap; tips of palps slightly bent towards middle ventral line of body, with brown-coloured spots.

Peristomium (Fig. 1a), seen dorsally, a clearly visible segment approximately half the length of prostomium; anterior margin narrower than posterior margin; anterolateral edges oblique at level of second dorsal pair of peristomial cirri; ventrally (Figs. 1b, 2a), the peristomium is only slightly longer than in dorsal view; mouth extending lengthwise with a long mid-ventral groove extending almost the entire length of peristomium and reaching nearly the anterior border of the first setiger; 2 to 10 furrows on either side of the groove around mouth; in smallest specimens there is no groove so that anterior margin of peristomium is entire with few furrows and U- or V-shaped or slightly concave.

Four pairs long, subulated tentacular cirri of different lengths; the anterior two pairs, arising slightly in front of the first pair of eyes and the posterior two pairs at level of second pair of eyes or slightly posterior; the anterior ventral pair is the shortest, approximately 1.5 to 2 times the length of prostomium; anterior dorsal pair longer than anterior ventral pair, measuring over twice the length of prostomium; posterior ventral pair somewhat longer than anterior dorsal pair; posterior dorsal pair longest, measuring approximately three times length of prostomium and in most of the larger specimens, when extended backwards, reaching near to the posterior border of setiger 3 and in few cases anterior margin of setiger 5. In most smaller specimens posterior ventral pair of peristomial cirri is the shortest; posterior dorsal pair, extended backwards, reaching setigers 2–3. Dorsally both the first and second setigers segments are only slightly longer than peristomium, but they are wider than it.

Buccal tube with up to 180 oral paragnaths and with one mid-dorsal maxillary paragnath. Oral paragnaths (Figs. 1c, 2c, d) caramel-coloured, with 3 to 5 conical cusps of varying sizes, arranged circularly with tips facing outwards; cusps simple or bifid. In general, paragnaths with four cusps in the form of a cross are most common. In both large (over 13.5 mm) and smaller specimens (4.9–5.7 mm) there are small and large paragnaths, whose distal diameters vary between 4.6 and 11.5 μm and whose bases are also of variable length (Fig. 2c, d). Oral paragnaths, 176–180 in large specimens and 132–154 in specimens of smaller size, arranged (Fig. 1d) in rows which are more or less parallel, alternate, distributed in two fusiform bands which surround almost the entirety of the buccal tube, with the wider central parts in lateral position and the narrow ends in dorsal and ventral position; the dorsal and ventral ends of both bands approximate towards the middle line of the buccal tube taking up a V shape; in the widest parts there are 3–4 rows of predominately large paragnaths (with greater diameter and long base); towards the narrow ends the number of rows diminishes from 2 to 1, being continuous only between the ventral ends of both areas (so constituting the vertex of a V). The rows are discontinuous dorsally; here the paragnaths tend to be small (with smaller diameter and short base). Maxillary paragnath located in mid-dorsal region of buccal tube (Fig. 1d), shaped like a thick bar, with anterior margin slightly concave; light caramel-coloured in large specimens and unpigmented in small specimens. Pharynx with two jaws (Fig. 1d, e), caramel-coloured; of prolonged type in small specimens, in large of shortened type; with 10 teeth on cutting edge distributed as follows: 2–3 incipient teeth in the basal part, then 4–6 prominent teeth and distally one to two small teeth close to the apex. Posterior edge of invaginated pharynx generally reaching back to setiger 4–5 in larger specimens and setiger 2–3 in smaller ones.

First and second pair of parapodia uniramous (Fig. 1f); first pair shortest, directed anteriorly or laterally; presetal lobe longer than postsetal; ventral cirri conical, slightly smaller than those of following parapodia, and located closer to base of parapodia. Setae are homogomph spinigers; shaft without internal transversal septa, distal ends weakly crenulated; blades finely serrated but serration not always visible under 40× magnification; usually setae becoming slightly wider towards acicula; first of supra-acicular dorsal setae thinnest and longest.

From setiger 3 onwards parapodia biramous with conical dorsal cirrus larger than ventral cirrus; presetal lobe longer than postsetal in both rami; notopodial and neuropodial aciculae with bent tips (Fig. 1j) extending slightly beyond the distal margin of the presetal lobe, covered by epidermis; aciculae dark brown with colourless tips. In anterior biramous parapodia (Fig. 1g) notopodial ramus similar in length and width to neuropodial ramus; towards middle of body notopodia becoming slightly wider (Fig. 1h), diminishing again and similar to neuropodia in posterior setigers (Fig. 1i). Setae homogomph spinigers, similar to those in anterior uniramous parapodia (Fig. 2e, f), of two types: one, with blades gradually tapering towards tip, with fine serrations uniformly distributed along almost entire length of blade (Fig. 1k); and, two, with blades widened at base, with more conspicuous, wider based serrations ending in fine extensions (Fig. 1l). Narrower setae located in dorsal- and ventralmost positions of each fascicle, wider ones in middle of each fascicle, next to aciculae; under SEM 2–3 longitudinal rows of spines can be observed as more or less fingerlike extensions bent slightly outwards (Fig. 2f), or bent towards the central axis (Fig. 2e). Pygidium short, with terminal anus, without accessory lobes (Fig. 1m), with pair of subulate cirri approximately 1.5–3 times as long as pygidium.

Geographical distribution.—South Shetland Islands, Robert Island, intertidal to 6 m deep and Palmer Archipelago, Doumer Island, 3–30 m.

Remarks.—None of the specimens examined presented the characteristics in the male described for other species of *Micronereis* (setiger 3 with neuropodial copulatory hooks, accessory parapodial cirri, pygidium with a pair of lateral lobes between the cirri and the anus, additional simple setae or spinigers) or clearly recognizable male gametes. Specimens having eggs or containing oocytes were determined to be female. In the light of the uncertainty present in identifying male specimens, it was decided to consider those specimens in which oocytes were not observed, to be of indeterminate sex. Oocytes are located in the coelemic cavity and in various cases also in the region adjacent to the parapodial rami. In a specimen of 4 mm in length and 16 setigers the oocytes measured 54 μm in diameter and in larger specimens (14.5–26 mm in length, 40 and 38 setigers respectively) measured 194 and 266 μm in diameter; the larger oocytes are light brown. Jaws of females are of shortened type; jaws of a small specimen (4 mm long) are of prolonged type with distal prolongation and 5 proximal teeth. Accessory parapodial cirri absent. In general in the larger female the body is of uniform dark brown colour, of inflated appearance, with bulbous lobe at base of dorsal cirri. In many specimens the parapodia of middle region of the body have openings on the dorsal surface of the base of the notopodial lobes through which a hyaline mucous substance can be seen to have passed; apparently this would serve to keep the oocytes attached to the body of the female. Some specimens also present openings in the neuropodia. In specimens having few openings in parapodia, up to two circular areas, one proximal and the other distal, with thin more or less translucent walls, can be seen in the dorsal region of intact notopodia. A female, 21 mm in length, with 41 setigers, was collected with its mucous egg cocoon in the lower intertidal fringe of Robert Island attached by mucous to the algae *Gigartina skottsbergii*; the mucous egg cocoon preserved in alcohol measures 3 mm in diameter and contains at least two layers of eggs; 143 dark brown eggs, 261–360 μm in diameter, were counted in the outer layer.

Taxonomical remarks.—The new species *Micronereis antarctica* is most similar to *M. nanaimoensis* Berkeley & Berkeley, 1953 distributed along the west coast of North America; in both species individuals reach large sizes (over 10 mm); they are similar in the form of prostomium (anteriorly rounded and slightly bilobed), the form of peristomial cirri (subulate), absence of accessory parapodial cirri, and distally bent tips of noto- and neuropodial aciculae. *M. antarctica* is distinguished from *M. nanaimoensis* by the following characteristics present in the latter species: peristomial segment shortened, mouth with conical lateral lips, parapodia strongly ciliated with dorsal and ventral subulate cirri, setae with internal transversal septa in the shaft, tips of aciculae only slightly bent, different body colour pattern for females (a closely set of fine, transverse, dark red or red-brown lines on a cream ground), and differences in egg size and colour (green and 200 μm for *M. nanaimoensis* and brown and 360 μm for *M. antarctica*). It also resembles *M. variegata* Claparède, 1863 in the form of prostomium (rounded with anterior edge slightly bilobed), form of peristomial cirri (subulate), absence of accessory parapodial cirri, and absence of internal transversal septa in the shaft of spinigers. It is distinguished from *M. variegata* by the following characteristics of the latter species: all the peristomial cirri are of equal length or with the posterior dorsals only slightly longer than the rest, oral paragnaths diadem-shaped with a flat base and a side having 4 cusps, and two median maxillary paragnaths. It is distinguished from *M. piccola* Paxton, 1983, *M. bansei* (Hartmann-Schröder, 1979), *M. eniwetokensis* Reish, 1961, and *M. ochotensis* Buzhinskaya, 1981 because in all of these the peristomial segment is very short and the shaft of spiniger has internal transversal septa; and in the first three species there are two median maxillary paragnaths rather than one. Moreover, *M. piccola* has cirriform peristomial cirri, extended notopodial lobes above the dorsal cirrus with several setae, and long and cirriform dorsal and ventral parapodial cirri. *Micronereis bansei* has ciliated parapodia, and mature females have enlarged dorsal cirri with lamellar extensions. *Micronereis eniwetokensis* has peristomial cirri broadest near the point of attachment and tapered distally, and the inner margin between notopodium and neuropodium is ciliated; *M. ochotensis* has larger palps, ciliated parapodia, and subulate parapodial cirri of similar size. *M. antarctica* is distinguished from *M. minuta* (Knox and Cameron, 1970) and *M. halei* Hartman, 1954 by the accessory parapodial cirri of both of these species; *M. minuta* also has peristomial cirri terminating in short fingerlike projections and two median maxillary paragnaths; further, *M. halei* lacks paragnaths.

Etymology.—This new species has been named *antarctica* since this is the first species of *Micronereis* known for Antarctic waters.

Ecological remarks.—Micronereis antarctica, new species, occurs from the intertidal down to 30 m deep in the subtidal zone off South Bay, Doumer Island. The highest densities of this polychaete were found between 12 and 20 m depth, which corresponds to a zone dominated by species of the red algal genera *Iridaea, Plocamium, Ptilonia* and *Callophyllis. Micronereis antarctica* was the most abundant polychaete species in the benthic samples taken in 1995 (26% of the total number of individuals), while in 1993 samples was the second most important polychaete species (9%) after *Neanthes kerguelensis* (McIntosh, 1885).

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A review of the taxonomic nomenclature and a checklist of the species of the Branchiobdellae (Annelida: Clitellata)

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Abstract.—The taxonomic nomenclature of the branchiobdellidans is reviewed. This includes the higher rankings and the numerous generic names assigned during the first half of the 19th century, particularly the use of *Branchiobdella* for species of the marine leech, *Branchellion.* The current taxonomic situation is summarized to high light where inconsistencies and omissions exist in the data. The class Branchiobdellae consists of one order, Branchiobdellida, with five families containing a total of 21 genera and 149 species. The binomia are given with any junior synonyms, and these are followed by the citation in which the rank was reduced to junior status. In addition, the valid taxon *Sinodrilus heterorchis* has been placed in *incertae sedis* until the entry point of the sperm ducts into the glandular atrium can be determined, two species are considered *nomen inquirenda* and three others *nomen nudem.*

Branchiobdellidans are leech-like symbionts found mainly on astacid crayfish in the Holarctic. The taxon is monophyletic and is considered to be independent of, and equivalent in rank to, the clitellate Oligochaeta and Hirudinea (Holt 1989a, Gelder & Brinkhurst 1990, Brinkhurst & Gelder 1991). Currently, the Clitellata is considered to be a subphylum, and so the three taxa just mentioned have the assigned rank of class. Thus, the higher taxonomic rankings of the branchiobdellidans are, the class Branchiobdellae Kasprzak, 1984, which consists of one order, Branchiobdellida Holt, 1965a, with five families (Holt 1986), Branchiobdellidae, Bdellodrilidae, Cambarincolidae, Caridinophilidae, and Xironodrilidae.

Historical review of the higher ranks.—The branchiobdellidans were raised to family rank by Grube (1851) with the name Branchiobdellea. Subsequently, Vejdovský (1884) reduced "Branchiobdellidae aut." to a junior synonym of his proposed Discodrilidae. Ludwig (1886:786) did not accept Vejdovský's recommendation, but changed the suffix used by Grube (1851) to read Branchiobdellidae. This spelling has continued to be accepted as it conforms to the recommendations of the International Code of Zoological Nomenclature for constructing a family name.

The taxonomy of the branchiobdellidans has undergone a number of revisions, and this has resulted in some of the names and ranks becoming superfluous. The list below gives all of the names and their ranks as they have appeared in the literature.

Higher Taxonomic Ranks and Names Proposed for Branchiobdellidans

Class Branchiobdellae Kasprzak, 1984:217
Subclass Branchiobdellida Stuart, 1982:43
Branchiobdellidea Sawyer, 1986:647
Order Branchiobdellida Holt, 1965a:30
Superfamily Branchiobdelloidae Hall, 1914:190
Family Branchiobdellea Grube, 1851:114
Discodrilidae Vejdovský, 1884:38
Branchiobdellidae Ludwig, 1886:782
Bdellodrilidae Holt, 1986:668

Cambarincolidae Holt, 1986:692
Caridinophilidae Holt, 1986:692
Xironodrilidae Holt, 1986:691
Subfamily Branchiobdellinae Goodnight, 1940:27
Cambarincolinae Goodnight, 1940:29

"Branchiobdell-" for non-branchiobdellidans.—The stem "branchiobdell-" was used by Rudophi in an unpublished collection name for a marine leech with paired, external gills, *Branchiobdellion Torpedinis.* The new species was described and named *Branchellion torpedinis* Savigny, 1820. Unfortunately three junior synonyms were then created, *Hirudo* (*Branchiobdella*) *Rudolphii* Blainville, 1827, *Branchiobdella torpedinis* Blainville, 1828, and *Hirudo* (*Branchiobdella*) *torpedinis* Gervais, 1836. These misuses of "*Branchiobdella*" for *Branchellion* ceased with Diesing (1850) and the synonym status of *B. torpedinis* was reviewed by Blanchard (1894). Other suffixes to the stem have been found in the literature by the author, however, they have not been cited or discussed as this would have added nothing to the presented clarification of these misuses.

Historical review of genera and species.—The first report of a worm that can be recognized as a branchiobdellidan was made by Roesel (1755) when he reported a worm living on the surface of the crayfish, *Astacus Fluviatilis.* Although the Roesel reference has often been cited in historical reviews of branchiobdellidans (Sawyer 1986, and others), no tangible information has been reported, and the page and figure numbers cited were usually incorrect. Therefore, a translation of the anatomical description and location of the symbiont on the host is given (Roesel 1755:327, tab. LIX, figs. 19–22).

"25. With regard to the remaining figures in tab. LIX, particularly [figs] 19, 20, 21, 22. They show us a kind of worm that receives its nourishment from the "river crab" especially in December and January. Figure 19 depicts them [the worms] in their natural maximum size [about 8mm long] — smaller versions can also be found. Their movement corresponds to the movement of a leech. Here [Fig. 19] I portray them in the positions they take up. Their basic color is a shiny brownish yellow; the head is their most supple member, it is a little pointed in shape and has a pair of black eye-spots. The remaining joints following the head get progressively thicker — right to the last joint [segment] — the sections [segments] as well as the dividing points between the sections are more round than wide. On the back of the third, fourth and fifth segment — counting from the rear — one notices a black spot discernible through the skin. It is simply feces in the rectum. These worms can be found anywhere under the breast plate of the "river crab", particularly at the two sides from the head to the tail; especially where they occur in considerable numbers. Roesel's figures 20, 21, 22 show these worms in the same position as in [Fig.] 19, but greatly enlarged [about 5×]. Whether these [worms] originate within the body of the "river crab" or outside of it, I cannot say, but I have observed that the "river crabs" are covered with many small eggs that stick together in clumps, at the time when they harbor these worms."

Roesel's figures 20 to 22 have been redrawn (Fig. 1a–c) and show branchiobdellidans in typical fixed positions. Figure 1a depicts the "head" followed by 11 segments with the posterior disc or "sucker" forming the 11th. The other two specimens are sufficiently contracted to hide the posterior segments. The reported and drawn "pair of eye-spots" are precisely where the dark jaws should be in a branchiobdellidan. Due to the fragile condition of this rare book, the author was supplied with photocopies of only a few requested pages. It is possible that Roesel (1755) made additional references to branchiobdellidans in other parts of this volume that were not available to the author. Reason for this belief comes from a subsequent work by Moquin-Tandon (1846) who refers to Roesel's finding very

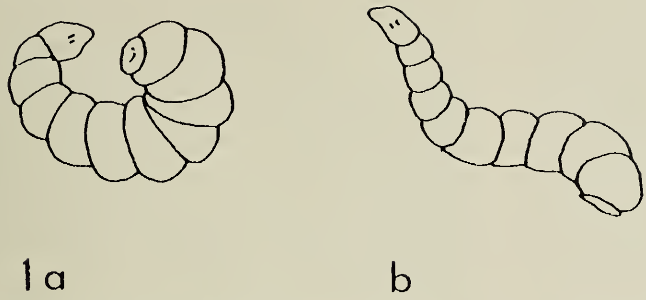

Fig. 1. Three preserved worms from the "river crab," redrawn from Roesel (1755: Tab. LIX, figs. 20, 21, and 22, respectively) at approximately 6.5×.

small hirudineans, *Branchiobdella astaci,* which were parasitic in the gills of crawfish.

An improved description of a "crab worm," *Hirudo parasita* was made by Braun (1805), followed by a second species, *Hirudo astaci* Müller, 1806. However, it was the detailed observations on *Branchiobdella astaci* Odier, 1823, and presumably the same name as used by Roesel that resulted in this being accepted as the type species for the newly created genus. For completeness, it should be noted that Vejdovský (1884) did not agree with Odier and recognized *B. parasita* Braun, 1805, as the type species.

Unfortunately, in the early 1800's, Blainville was already incorrectly using *Branchiobdella* for the gilled leeches, as noted earlier. Therefore, to accommodate the branchiobdellidans, he created a new generic name *Microbdella* Blainville, 1827. This name was modified to *Hirudo* (*microbdella*) *astaci* by Gervais (1836:628), and later (Gervais 1845) to *Microbdella astaci.* The problem of consistency with the genus name continued when Vallot (1840) proposed *Astacobdella branchiale* for *B. parasita.* In his checklist of worms, Diesing (1850) accepted the former generic name for his two new species, *Astacobdella Roeseli* Diesing, 1850, and *Astacobdella Abildgaardi* Diesing, 1850. Continuing this trend, *Astacobdella Philadelphica* Leidy, 1851, became the first reported branchiobdellidan in North America. After 1851, all branchiobdellidans were placed in the genus *Branchiobdella,* until Moore (1895a) recognized that specimens found in North America were sufficiently different from *Branchiobdella* to warrant forming a number of additional genera. The century closed with Voigt (1885) arguing that the four know species of *Branchiobdella* in Europe were variants of a single species, *B. varians.* Although a few of his contemporaries used the name, it was not generally accepted.

The last monograph on the branchiobdellidans was produced by Pierantoni (1912). Since then a number of reviews, checklists, and keys to species have been produced, but they have been restricted to one of the three geographical regions in the Holarctic where the symbionts are found. These regions are North America, from Panama to southern Canada inclusive (Hoffman 1963; Holt 1965a, 1968a, 1973a, 1974a, 1986), Europe, from the Atlantic coast to the Ural Mountains (Moszyński 1938, Pop 1965, Boshko 1983), and eastern Asia, which include southeastern Russia, Korea, Japan, and China (Yamaguchi 1934; Liu 1964, 1984; Subchev 1986; Gelder 1987; Timm 1991). Therefore, a single checklist for the taxon is long overdue.

The largest contribution to branchiobdellidan taxonomy has been made by Holt (see Holt & Opell 1993), whose primary focus was on North American species. His philosophy (Holt pers. comm.) was that if a group of individuals has a recognizable anatomical structure, or a structure with a different relative proportion to that in a described species, then the new group should be described as a new species. This philosophy was also shared by Yamaguchi (1934). However, European workers such as Moszyński (1938), Pop (1965), and Karaman (1967) recognized that such a level of difference warranted only subspecies rank. Therefore, this dichotomy in what constitutes a species in the branchiobdellidans needs to be addressed in the future.

This checklist contains the binomial names and junior synonyms of all branchiobdellidans with the author and date of the original description. The endings of a number of species binomen have been changed since the type descriptions were published (see Holt 1973a, Holt & Opell 1993). However, Holt & Opell (1993) changed the specific name endings of three species of *Cambarincola* from "us" back to the original "a" without supporting the change. These reversals have not been accepted in this checklist. The change of *Cambarincola osceola* to *osceolia* by Holt (1973:10) is not supported by the current International Code of Zoological Nomenclature (ICZN, 1985) in the opinion of F. M. Bayer (pers. comm.), and so the former spelling is accepted. In order to make this checklist more user-friendly, some species citations are followed by an author's name and a date. This citation indicates the paper in which the preceding name was modified or changed. Researchers studying type descriptions will become aware of the occasional anomaly where information in the checklist differs from the original paper. Two of these are explained to prevent confusion. The description of *Branchiobdella balcanica sketi* Karaman, 1967, was republished as a new subspecies by Karaman (1970), but the former is the authentic citation. Some papers have a year printed at the head of the pages, but due to delays, the journals were actually published a year later than stated. The date of publication is the only correct one, for example; Moore (1894) has the previous year imprinted on its pages. Ellis (1918) reported a number of branchiobdellidans on Michigan crawfishes, and a number of the species cited were followed by, "*in ed.*" The type descriptions of these new genera and species were published in Ellis (1919). The discrepancy in time was caused by an editorial delay of the manuscript with the new taxa, which did not effect the publication or distribution of the paper. The correct type citations for these taxa are Ellis (1919).

Taxonomic keys require a number of external and internal anatomical characters to be observed before the specimen can be identified. Many of the characters are not easy to observe, so there has been a temptation to use only the obvious characters of the external body shape, body length, and jaw structure. Such an approach invariably ignores the differing effect that fixation anomalies can produce on a soft body, and the apparently different morphology of the jaws when seen from various aspects. As a result of the variability of these few characters, 33 new species were described by Georgevitch (1955, 1957) that have since been reduced to junior synonyms of four species by Pop (1965).

Sinodrilus heterorchis (Liu & Zhang, 1983) has a pair of separately opening anterior nephridiopores which makes it a member of either the Branchiobdellidae or the Xironodrilidae. However, the type description did not state where the vas deferens enters the glandular atrium; without this information, it is not possible to assign this genus to a family. Therefore, the valid genus and species of *Sinodrilus heterorchis* has been placed in incertae sedis until the missing information is obtained. In addition, two species are considered nomen inquirenda and three other species nomen nudem in the checklist.

Checklist

Class Branchiobdellae Kasprzak, 1984
Order BRANCHIOBDELLIDA Holt, 1965a
Family Branchiobdellidae (Grube, 1851)

Ankyrodrilus Holt, 1965b
  Ankyrodrilus koronaeus Holt, 1965b
  Ankyrodrilus legaeus Holt, 1965b

- *Branchiobdella* Odier, 1823
  - *Branchiobdella astaci* Odier, 1823
    - = *Astacobdella Roeseli* (Diesing, 1850)
    - = *Branchiobdella astaci fluviatilis* (Ostroumoff, 1883)
    - = *Branchiobdella astaci leptodactyli* (Ostroumoff, 1883)
    - = *Branchiobdella varians* var. *astaci* (Voigt, 1885) Pierantoni, 1912
    - = *Hirudo astaci* (Müller, 1806) Vejdovský 1884
    - = *Hirudo (Microbdella) astaci* (Gervais, 1836) Vejdovský, 1884
    - = *Malacobdella (Hirudo) Astaci* (Gervais, 1836) Diesing 1850
    - = *Microbdella astaci* (Gervais, 1845) Vejdovský 1884
  - *Branchiobdella balcanica balcanica* Moszyński, 1938
    - = *Branchiobdella pentodonta orientalis* (Pop, 1965) Karaman 1967
    - = *Xironogiton dolicoderos* (Georgevitch, 1957) Pop 1965
  - *Branchiobdella balcanica sketi* Karaman, 1967
  - *Branchiobdella cheni* Liu, 1964
  - *Branchiobdella digitata* Pierantoni, 1906
  - *Branchiobdella domina* Timm, 1991
  - *Branchiobdella hexodonta* Gruber, 1883
    - = *Branchiobdella dubia* (Pierantoni, 1912) Pop 1965
    - = *Branchiobdella ochridensis* (Georgevitch, 1957) Pop 1965
    - = *Branchiobdella varians* var. *hexodonta* (Voigt, 1885) Pierantoni 1912
    - = *Cambarincola pluridentata* (Georgevitch, 1957) Pop 1965
  - *Branchiobdella italica* Canegallo, 1928
    - = *Branchiobdella insolita* (Moszyński, 1938) Pop 1965
    - = *Branchiobdella pentodonta* var. *italica* (Canegallo, 1928) Pop 1965
  - *Branchiobdella kobayashii* Yamaguchi, 1934
  - *Branchiobdella kozarovi* Subchev, 1978
  - *Branchiobdella macroperistomium* Liu & Zhang, 1983
  - *Branchiobdella minuta* Pierantoni, 1912
  - *Branchiobdella monodontus* Liu & Zhang, 1983
  - *Branchiobdella orientalis* Yamaguchi, 1934
  - *Branchiobdella parasita* Henle, 1835
    - = *Astacobdella branchialis* (Vallot, 1840) Vejdovský 1884
    - = *Branchiobdella anatis* (Pierantoni, 1912) Pop 1965
    - = *Branchiobdella bidens* (Georgevitch, 1955) Pop 1965
    - = *Branchiobdella decidonta* (Georgevitch, 1957) Pop 1965
    - = *Branchiobdella tridens* (Georgevitch, 1955) Pop 1965
    - = *Branchiobdella varians* var. *parasita* (Voigt, 1885) Pierantoni 1912
    - = *Cambarincola cylindrica* (Georgevitch, 1957) Pop 1965
    - = *Cambarincola odontias* (Georgevitch, 1955) Pop 1965
    - = *Hirudo Parasita* (Braun, 1805) Henle 1835
    - = *Pterodrilus aliata* (Georgevitch, 1957) Pop 1965
    - = *Pterodrilus bidens* (Georgevitch, 1955) Pop 1965
    - = *Pterodrilus dentata* (Georgevitch, 1957) Pop 1965
    - = *Pterodrilus karamani* (Moszyński, 1938) Pop 1965
    - = *Pterodrilus megas* (Georgevitch, 1955) Pop 1965
    - = *Pterodrilus megodont* (Georgevitch, 1955) Pop 1965
    - = *Pterodrilus prion* (Georgevitch, 1955) Pop 1965
    - = *Xironogiton bidens* (Georgevitch, 1955) Pop 1965
  - *Branchiobdella pentodonta* Whitman, 1882
    - = *Bdellodrilus hexadonta* (Georgevitch, 1957) Pop 1965
    - = *Branchiobdella capito* (Georgevitch, 1955) Pop 1965
    - = *Branchiobdella cordis* (Georgevitch, 1955) Pop 1965
    - = *Branchiobdella karamani* (Georgevitch, 1957) Pop 1965
    - = *Branchiobdella segmentata* (Georgevitch, 1957) Pop 1965
    - = *Branchiobdella septadonta* (Georgevitch, 1957) Pop 1965
    - = *Branchiobdella unidonta* (Georgevitch, 1957) Pop 1965
    - = *Branchiobdella varians* var. *pentodonta* (Voigt, 1885) Pierantoni 1912
    - = *Cambarincola dojranensis* (Georgevitch, 1955) Pop 1965
    - = *Cambarincola gastrax* (Georgevitch, 1955) Pop 1965
    - = *Cambarincola hamata* (Georgevitch, 1957) Pop 1965
    - = *Cambarincola odontias* (Georgevitch, 1955) Pop 1965
    - = *Xironodrilus crassus* (Georgevitch, 1955) Pop 1965
    - = *Xironodrilus tetradonta* (Georgevitch, 1955) Pop 1965
    - = *Xironogiton dilatatus* (Georgevitch, 1955) Pop 1965
    - = *Xironogiton dolicoderos* (Georgevitch, 1955) Pop 1965
    - = *Xironogiton latus* (Georgevitch, 1957) Pop 1965

= *Xironogiton tridens* (Georgevitch, 1957) Pop 1965
Branchiobdella teresae Subchev, 1986

Cirrodrilus Pierantoni, 1905
Cirrodrilus aequiannulus (Liu, 1984)
= *Stephanodrilus aequiannulus* Liu, 1984
Cirrodrilus anodontus (Liu, 1964)
= *Stephanodrilus anodontus* Liu, 1964
Cirrodrilus aomorensis (Yamaguchi, 1934)
= *Stephanodrilus* (*St.*) *aomorensis* Yamaguchi, 1934
Cirrodrilus breviformis (Liu & Chang, 1964)
= *Stephanodrilus breviformis* Liu & Chang, 1964
Cirrodrilus chosen (Yamaguchi, 1934)
= *Stephanodrilus* (*St.*) *chosen* Yamaguchi, 1934
Cirrodrilus cirratus Pierantoni, 1905
= *Ceratodrilus cirratus* (Yamaguchi, 1932a) Holt 1967a
= *Stephanodrilus* (*Ceratodrilus*) *cirratus* (Pierantoni, 1905) Yamaguchi 1934
Cirrodrilus ezoensis (Yamaguchi, 1934)
= *Stephanodrilus* (*St.*) *ezoensis* Yamaguchi, 1934
Cirrodrilus fimbriatus Timm, 1991
Cirrodrilus heteroglandularis (Liu & Chang, 1964)
= *Stephanodrilus heteroglandularis* Liu & Chang, 1964
Cirrodrilus homodontus (Yamaguchi, 1932b)
= *Cambarincola homodontus* Yamaguchi, 1932b
Cirrodrilus inukaii (Yamaguchi, 1934)
= *Stephanodrilus* (*St.*) *inukaii* Yamaguchi, 1934
Cirrodrilus japonicus (Pierantoni, 1912)
= *Stephanodrilus japonicus* Pierantoni, 1912
Cirrodrilus kawamurai (Yamaguchi, 1934)
= *Stephanodrilus* (*St.*) *kawamurai* Yamaguchi, 1934
Cirrodrilus liaoningensis (Liu & Chang, 1964)
= *Stephanodrilus liaoningensis* Liu & Chang, 1964
Cirrodrilus makinoi (Yamaguchi, 1934)
= *Stephanodrilus* (*St.*) *makinoi* Yamaguchi, 1934
Cirrodrilus megalodentatus (Yamaguchi, 1934)
= *Stephanodrilus* (*St.*) *magalodentatus* Yamaguchi, 1934
Cirrodrilus minimus (Liu, 1964)
= *Stephanodrilus minimus* Liu, 1964
Cirrodrilus nipponicus (Yamaguchi, 1932c)
= *Carcinodrilus nipponicus* Yamaguchi, 1932c
Cirrodrilus peristomalis (Liu & Chang, 1964)
= *Stephanodrilus peristomalis* Liu & Chang, 1964
Cirrodrilus pugnax Timm, 1991
Cirrodrilus quadritentacularis (Liu, 1984)
= *Stephanodrilus quadritentacularis* Liu, 1984
Cirrodrilus sapporensis (Pierantoni, 1906)
= *Stephanodrilus sapporensis* Pierantoni, 1906
Cirrodrilus suzukii (Yamaguchi, 1934)
= *Stephanodrilus* (*St.*) *suzukii* Yamaguchi, 1934
Cirrodrilus uchidai (Yamaguchi, 1932a)
= *Ceratodrilus Uchidai* Yamaguchi, 1932a
= *Stephanodrilus* (*Ceratodrilus*) *uchidai* (Yamaguchi, 1932a) Yamaguchi, 1934

Xironogiton Ellis, 1919
Xironogiton cassiensis Holt, 1974a
Xironogiton fordi Holt, 1974a
Xironogiton instabilis (Moore, 1894) Holt 1974a
= *Bdellodrilus instabilis* (Moore, 1894) Pierantoni 1912
= *Branchiobdella instabilia* (Moore, 1894) Ellis 1919
= *Xironogiton instabilius instabilius* (Goodnight, 1940) Holt 1974a
= *Xironogiton instabilius oregonensis* (Goodnight, 1940) Holt 1974a
= *Xironogiton oregonensis oregonensis* (Ellis, 1919) Holt 1974a
= *Xironogiton oregonensis pectinatus* (Ellis, 1919) Holt 1974a
Xironogiton kittitasi Holt, 1974a
Xironogiton occidentalis Ellis, 1919
Xironogiton victoriensis Gelder & Hall, 1990

Family Bdellodrilidae Holt, 1986

Bdellodrilus Moore, 1895b
Bdellodrilus illuminatus (Moore, 1894)
= *Branchiobdella illuminata* (Moore, 1894)

Cronodrilus Holt, 1968b
Cronodrilus ogygius Holt, 1968b

Hidejiodrilus Gelder & Brinkhurst, 1990
Hidejiodrilus koreanus (Pierantoni, 1912)
= *Stephanodrilus koreanus* (Pierantoni, 1912)

Uglukodrilus Holt, 1989b
Uglukodrilus hemophagus (Holt, 1977a)
= *Adenodrilus hemaphagus* Holt, 1977a

Family Caridinophilidae Holt, 1986

Caridinophilus Liang, 1963
Caridinophilus unidens Liang, 1963

Family Cambarincolidae Holt, 1986

Cambarincola Ellis, 1912
Cambarincola acudentatus Holt, 1973a
Cambarincola alienus Holt, 1963
Cambarincola barbarae Holt, 1981a
Cambarincola bobbi Holt, 1988a
Cambarincola branchiophilus Holt, 1954
Cambarincola carcinophilus Holt, 1973a
Cambarincola chirocephalus Ellis, 1919
= *Cambarincola* (*Coronata*) *chirocephala* (Ellis, 1919) Goodnight 1940
Cambarincola demissus Hoffman, 1963
Cambarincola dubius Holt, 1973b
Cambarincola ellisi Holt, 1973a

Cambarincola fallax Hoffman, 1963
Cambarincola floridanus Goodnight, 1941
Cambarincola goodnighti Holt, 1973c
Cambarincola gracilis Robinson, 1954
Cambarincola heterognathus Hoffman, 1963
Cambarincola hoffmani Holt, 1973a
Cambarincola holostomus Hoffman, 1963
Cambarincola holti Hoffman, 1963
Cambarincola illinoisensis Holt, 1982
Cambarincola ingens Hoffman, 1963
Cambarincola jamapaensis Holt, 1973a
Cambarincola leoni Holt, 1973b
Cambarincola leptadenus Holt, 1973b
Cambarincola macrocephalus Goodnight, 1943
Cambarincola macrodontus Ellis, 1912
  = *Cambarincola* (*Cambarincola*) *macrodontus* (Ellis, 1912) Goodnight 1940
Cambarincola manni Holt, 1973c
Cambarincola marthae Holt, 1973b
Cambarincola mesochoreus Hoffman, 1963
Cambarincola meyeri Goodnight, 1942
Cambarincola micradenus Holt, 1973a
Cambarincola montanus (Goodnight, 1940)
  = *Triannulata montana* (Goodnight, 1940) Holt 1974b
Cambarincola nanagnathus Holt, 1973a
Cambarincola olmecus Holt, 1973a
Cambarincola osceola Hoffman, 1963
Cambarincola ouachita Hoffman, 1963
Cambarincola pamelae Holt, 1984a
Cambarincola philadelphicus (Leidy, 1851)
  = *Astacobdella Philadelphica* (Leidy, 1851)
  = *Branchiobdella americana* (Pierantoni, 1912) Holt 1967a
  = *Cambarincola* (*Coronata*) *philadelphica* (Leidy, 1851) Goodnight 1940
Cambarincola restans Hoffman, 1963
Cambarincola serratus Holt, 1981a
Cambarincola sheltensis Holt, 1973b
Cambarincola shoshone Hoffman, 1963
Cambarincola smalleyi Holt, 1964
Cambarincola speocirolanae Holt, 1984b
Cambarincola steevesi Holt, 1973b
Cambarincola susanae Holt, 1973a
Cambarincola toltecus Holt, 1973a
Cambarincola virginicus Hoffman, 1963
Cambarincola vitreus Ellis, 1919
  = *Cambarincola* (*Cambarincola*) *vitrea* (Ellis, 1919) Goodnight 1940

Ceratodrilus Hall, 1914
  Ceratodrilus orphiorhysis (Holt, 1960a) Holt 1988b
  Ceratodrilus thysanosomus Hall, 1914
    = *Cirrodrilus thysanosomus* (Hall, 1914) Goodnight 1940

Ellisodrilus Holt, 1960b
  Ellisodrilus carronamus Holt, 1988a
  Ellisodrilus clitellatus Holt, 1960b
  Ellisodrilus durbini (Ellis, 1919)
    = *Pterodrilus durbini* (Ellis, 1919) Holt 1960b

Magmatodrilus Holt, 1967a
  Magmatodrilus obscurus (Goodnight, 1940)
    = *Stephanodrilus obscurus* (Goodnight, 1940) Holt 1967a

Oedipodrilus Holt, 1967b
  Oedipodrilus anisognathus Holt, 1988a
  Oedipodrilus cuetzalanae Holt, 1984b
  Oedipodrilus macbaini (Holt, 1955)
    = *Cambarincola macbaini* (Holt, 1955) Holt 1969
  Oedipodrilus oedipus Holt, 1967b

Pterodrilus Moore, 1895a
  Pterodrilus alcicornus Moore, 1895a
  Pterodrilus annulatus Gelder, 1996
  Pterodrilus cedrus Holt, 1968c
  Pterodrilus choritonamus Holt, 1968c
  Pterodrilus distichus Moore, 1895a
  Pterodrilus hobbsi Holt, 1968c
  Pterodrilus mexicanus Ellis, 1919
  Pterodrilus missouriensis Holt, 1968c
  Pterodrilus simondsi Holt, 1968c

Sathodrilus Holt, 1968b
  Sathodrilus attenuatus Holt, 1981b
  Sathodrilus carolinensis Holt, 1968b
  Sathodrilus chehalisae Holt, 1981b
  Sathodrilus dorfus Holt, 1977b
  Sathodrilus elevatus (Goodnight, 1940)
    = *Cambarincola elevatus* (Goodnight, 1940) Holt 1978
    = *Cambarincola* (*Cambarincola*) *elevatus* (Goodnight, 1940) Hoffman 1963
  Sathodrilus hortoni Holt, 1973c
  Sathodrilus inversus (Ellis, 1919)
    = *Cambarincola inversa* (Ellis, 1919)
    = *Cambarincola* (*Cambarincola*) *inversa* (Ellis, 1919) Goodnight 1940
    = *Sathodrilus virgiliae* (Holt, 1977b) Holt 1981b
  Sathodrilus lobatus Holt, 1977b
  Sathodrilus megadenus Holt, 1968b
  Sathodrilus nigrofluvius Holt, 1989b
  Sathodrilus norbyi Holt, 1977b
  Sathodrilus okaloosae Holt, 1973c
  Sathodrilus prostates Holt, 1973a
  Sathodrilus rivigeae Holt, 1988a
  Sathodrilus shastae Holt, 1981b
  Sathodrilus veracruzicus Holt, 1968b
  Sathodrilus villalobosi Holt, 1968b
  Sathodrilus wardinus Holt, 1981b

Tettodrilus Holt, 1968b
  Tettodrilus friaufi Holt, 1968b

Triannulata Goodnight, 1940
  Triannulata magna Goodnight, 1940

Family Xironodrilidae Holt, 1986

Holtodrilus Gelder & Brinkhurst, 1990

Holtodrilus truncatus (Liang, 1963)

Xironodrilus Ellis, 1919
  Xironodrilus appalachius Goodnight, 1943
  Xironodrilus bashariae Holt & Weigl, 1979
  Xironodrilus dentatus Goodnight, 1940
    = *Xironodrilus pulcherrimus dentatus* (Goodnight, 1940) Goodnight 1943
  Xironodrilus formosus Ellis, 1919
  Xironodrilus pulcherrimus (Moore, 1894)
    = *Branchiobdella pulcherrima* (Moore, 1894) Ellis 1919

Incertae sedis:
  Sinodrilus heterorchis (Liu & Zhang, 1983) Gelder & Brinkhurst 1990

Nomen inquirenda:
  Branchiobdella tetradonta Pierantoni, 1912 (Holt 1967a:7)
  Cambarincola okadai Yamaguchi, 1933 (Holt & Opell 1993:253)

Nomen nudem:
  Astocobdella Abildgaard Diesing, 1850:434—inadequate description.
  Bdellodrilus manus n. sp. cited in Moore 1895a: 454—no description.
  Branchiobdella chilensis Moquin-Tandon, 1846: 300—no description.
    = *Astacobdella chilensis* Diesing, 1850
  Branchiobdella auriculae Moquin-Tandon, 1846: 301—no description.

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Sericosura heteroscela and *S. cyrtoma*, new species, and other Pycnogonida from Atlantic and Pacific hydrothermal vents, with notes on habitat and environment

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Abstract.—The first new hydrothermal vent pycnogonid from the Mid-Atlantic Ridge, *Sericosura heteroscela,* new species, is described and illustrated from specimens taken in 1727 m south of the Azores and other nearby localities in similar depths from vent areas just west of the Azores. Males of this new species have extremely dimorphic anterior and posterior propodi. Another new species, *S. cyrtoma,* is described and figured from a hydrothermal vent at 13°N off the Pacific coast of Mexico, in 2563 m. A juvenile specimen of a possibly new third *Sericosura* species is discussed and compared with *S. venticola* Child. The specimen was taken from vents north of Easter Island, southeast Pacific, in 2578 m. The three species are compared with each other and with other known hydrothermal vent species in this genus, their distribution is discussed, and a *Sericosura* key is presented. Two known species in the genera *Callipallene* and *Colossendeis* are also listed from the same Mid-Atlantic vent areas. Descriptive remarks on the habitat and environment of the specimens are presented.

Sericosura species have been associated with the majority of pycnogonid captures from hydrothermal vent exposures. Most of them (70+%) are from recently discovered tectonic spreading zones of the north and south Pacific (Child 1987, 1989; Stock 1991) and more recently in Atlantic localities (Segonzac 1992). The type species of this genus, *Sericosura mitrata* (Gordon 1944:54–57, figs. 19a–e, 22b), was described before hydrothermal vents were known. It was collected from an Antarctic locality where no hydrothermal vent is known (219 m). It is now considered, if correct (Gordon questioned the validity of her data), as being too shallow to be a vent exposure, when compared with other *Sericosura* species collected from vent fields. This species was later collected in depths more consistent with known hydrothermal vents, in 2100 m on the Walvis Ridge off South Africa (Child 1982a:19–21, fig. 6). Whether or not the Walvis Ridge specimen was associated with hydrothermal vents was not recorded and remains unknown, although the Walvis Ridge is not known to have hydrothermal vents. A specimen of this species was also found and reported (Segonzac 1992:596) from the Snake Pit area at 23°N on the Mid-Atlantic Ridge.

Two other hydrothermal vent species have been described more recently as additional vents were discovered and their fauna examined. *Sericosura venticola* Child (1987:896–899, fig. 2), was collected from hydrothermal vent fields on the Juan de Fuca Ridge and other hydrothermal vent areas in the northeast Pacific, in 2200 m. *Sericosura cochleifovea* Child (1989:732–737, fig. 1), was collected from vent fields in the

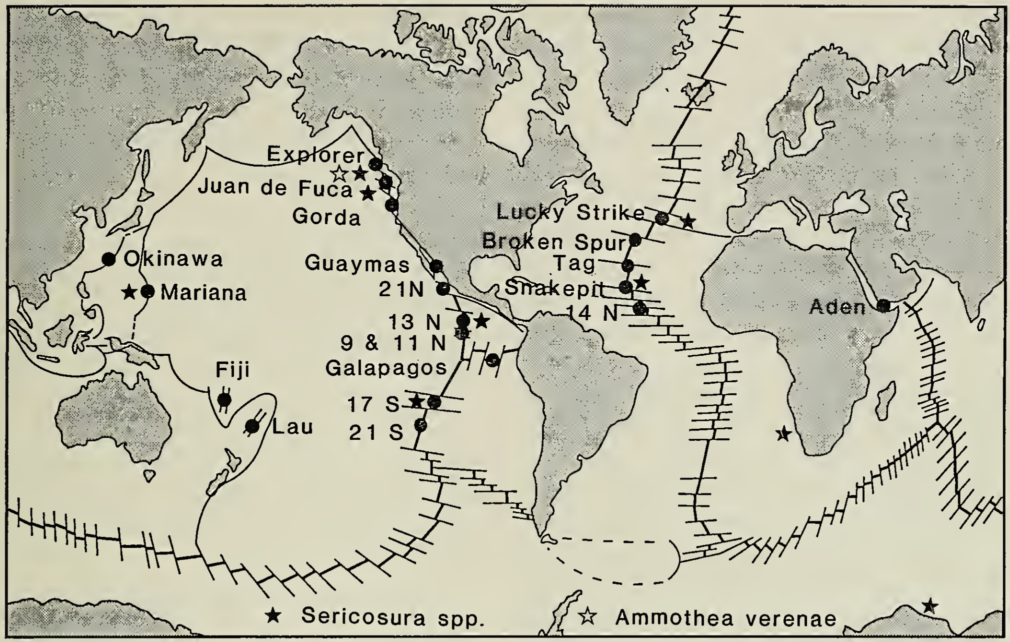

Fig. 1. Distribution of hydrothermal vent (black circles) with associated pycnogonids (except Walvis Ridge and Antarctic records) with locations for *Sericosura* (black stars) and *Ammothea* vent-associated species (white star).

Back-Arc Basin of the Mariana Islands in 3600 m. Stock (1991:158–160, figs. 24, 25) described *Sericosura bifurcata* from the New Caledonia basin, SW Pacific, in 3680–3700 m. *Sericosura bifurcata* could have been associated with hydrothermal vents, particularly at those collecting depths, although no vents are known in this area. I believe that Stock's proposed species is probably *S. cochleifovea* with variations rather than a separate species.

With the increasing efforts of many nations to discover and explore hydrothermal vent localities, it is not difficult to predict that more new species and additional localities for known species will be described in the near future.

Figure 1 shows the known distribution of the genus *Sericosura* (solid stars) and of *Ammothea verenae* Child (open star), the only hydrothermal *Ammothea* species known. The species concerned are predominantly but not exclusively found in areas of active hydrothermal vents. *Sericosura* has a cosmopolitan distribution and is a deep-water genus although it is not confined to abyssal depths. However, the distribution of these species is poorly known because of the small number of collections. Three species out of five are only known from their type locality, excluding the two new species presented herein. It is significant that in the distribution of *Sericosura* species, *S. mitrata* the first known species, has been collected from such diverse and widespread areas as the Walvis Ridge (Child 1982a), the Snake Pit hydrothermal area of the North Atlantic, and from the Antarctic (Gordon 1944). From this evidence, the distribution of this species possibly extends to sites along the Mid-Atlantic Ridge and it will be found at other Atlantic sites. It will be interesting to systematists to see if distributions of the other species will extend to other vents as more collections are made.

There appears to be no adaptation to hydrothermal vents (no adherent bacteria or sulphur deposits) by either *Callipallene producta* (Sars) or *Colossendeis macerrima* Wilson. These species were collected or photographed in depths at which they have been previously taken on other expeditions. There is no reason to believe that their occurrence at or near hydrothermal vents is anything but coincidence. There are no records of either species having been taken previously in association with these vents.

The known species of *Sericosura* are difficult to separate taxonomically. Females are particularly difficult, lacking femoral cement glands and with leg setation sometimes greatly dimorphic from setation of males. This genus is also sometimes difficult to separate from *Ammothea* which usually has palps of nine segments, but some have six- or seven-segmented palps, and others have eight. The single consistent difference is the placement and shape of the male femoral cement gland. In *Sericosura,* it is proximolateral with a tube extending in a dorsal or dorsolateral direction. In *Ammothea,* the gland and its orifice are dorsodistal, usually with only a pore and not a tube. It is difficult to describe a new species of *Sericosura* from a female lacking full diagnostic characters. *Sericosura cyrtoma* is described as new because the single specimen has palps of seven segments, a number common to *Sericosura* (four out of six known species), but only two *Ammothea* species in 32 have seven-segmented palps (the number of segments in one varies from six or seven and in the other from seven to nine).

The specimens are deposited primarily in the Museum national d'Histoire naturelle, Paris (MNHN), with surplus specimens deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH).

Systematics

Family Ammotheidae Dohrn, 1881

Genus *Sericosura* Fry & Hedgpeth, 1969

Diagnosis.—Ammotheidae, very similar to *Ammothea.* Trunk fully segmented, with transverse ridges, but lacking discrete dorsal tubercles, lateral processes only slightly separated. Proboscis large, ovoid and straight, tapering or curved. Short ocular tubercle, blind, tip sometimes bifurcate. Chelifores two-segmented, scape short, adult chelae reduced to buds. Palps more commonly seven- or less commonly nine-segmented, distal segments short. Oviger ten-segmented, strigilis weak, with plain or denticulate spines, without terminal claw. Legs sexually dimorphic, propodus *Achelia*-like, claw long, with auxiliary claws, anterior/posterior propodi dimorphic in males of one species. Male cement gland bulge and orifice proximolateral, single tube at oblique or right angle to femur.

Key to the Species of *Sericosura*

1). Palps with seven segments 2
Palps with nine segments 5
2). Terminal palp segment longest of distal three; trunk and lateral processes with many slender spines and setae; proboscis ovoid, straight, carried horizontally 3
Fifth palp segment longer than either of distal two; trunk and lateral processes with short broad spines, few setae; proboscis downcurved. (Female only) . .
. . . . *S. cyrtoma,* new species
3). Male and female tibiae setae dimorphic, propodi similar 4
Tibiae similar in both sexes, male coxae has many more setae; female propodi alike, male propodi dimorphic, anterior four normal, other four inflated . . . . .
. . . . *S. heteroscela,* new species
4). Female tibiae with long ventral setae mixed with short spines, male tibiae with few short ventral setae, no spines; male cement gland tube almost as long as femur diameter; palp second segment longest . . . . *S. mitrata* (Gordon)
Female tibiae with row of very long lateral setae, male's with short setae; cement gland tube short, inconspicuous; palp fourth segment longest . . . .
. . . . *S. venticola* Child
5). Abdomen with long setae; ocular tubercle tip rounded; lateral processes with

long dorso- and laterodistal spines, female propodi with long lateral setae
.... *S. cochleifovea* Child

Abdomen with two tiny setae; ocular tubercle tip bifurcate; lateral processes with one laterodistal spine or none; propodi without long lateral setae ......
.... *S. bifurcata* Stock

(*Scipiolus thermophilus* Turpaeva, 1988, is a junior synonym of *Ammothea verenae* Child, 1987, from hydrothermal vents on the Explorer and Juan de Fuca Ridges in the NE Pacific.)

Sericosura heteroscela, new species
Figs. 2, 3

Material examined.—The types were from the Lucky Strike hydrothermal vent area, Mid-Atlantic Ridge, southwest of the Azores Islands. Cruise DIVA 1, sta. DV 19, Nuno site, sulphur tubes at the foot of hydrothermal vent, 37°17.5′N, 032°16.9′W, 1727 m, 23 May 1994, 1 ♂ with eggs, holotype, MNHN, Paris, 1 ♀, 1 juvenile, paratypes, MNHN, Paris. Same station, 1730 m, 27 May 1994, 2 ♂, 10 ♀, 3 juveniles, paratypes, MNHN, Paris, 1 ♂, 2 ♀, 1 juvenile, paratypes, NMNH, Washington.

Other material.—The following material came from the Lucky Strike hydrothermal vent area, 37°17.3′N, 032°16.5′W, 1629–1727 m, May–Jun 1994; at Tour Eiffel, Nuno, Isabel and Pagode sites, 9 ♂ with eggs, 7 ♂, 12 ♀, 6 juveniles, and Menez-Gwen Site, 37°50.5′N, 031°31.4′W, 850 m, May–Jul 1994, 2 juveniles.

Mid-Atlantic Ridge, Microsmoke Vent, 14°45′N, depth unknown, sta. PL 20, 22 May 1995, 1 ♀, 1 juvenile.

Description.—Size moderately large, leg span 26.7 mm. Trunk glabrous, dorsal segmentation lines raised, swollen, without dorsomedian tubercles. Lateral processes closely spaced, separated by 0.25–0.3 times their diameters, with ring of distal spines, dorsal ones largest, ventral spines smaller. Neck with broad anterolateral expansion, elevated dorsally in lateral view, with one or two short anterolateral spines. Ocular tubercle a small anterior-leaning tube, blind, with bifurcate tip. Proboscis very large, inflated, longer than trunk, without constrictions, with flat oral surface. Abdomen downcurved, extending to midpart of second coxae of fourth leg pair, armed with three or four pairs of short dorsal spines.

Chelifores short, scape one-segmented, only about twice longer than wide, armed with five or six spines, two dorsodistal ones longer than segment diameters. Chelae atrophied to knobs, fingers reduced to tiny bumps.

Palps seven-segmented, major segments armed dorsally with row of erect spines subequal in length to segment diameters. First segment broad, a truncate cone, second longest, slightly longer than fourth, distal three segments very short, of decreasing diameters, and armed with many short distal and ventral setae.

Ovigers fairly small, typical for genus. Second segment slightly longer than fourth or fifth, third curved at right angle, fourth and fifth subequal, with short lateral setae. Sixth, seventh and eighth with lateral setae longer than segment diameters. Seventh lacking denticulate spines. Eighth, ninth and tenth with tiny blunt denticulate spines in formula 2: 1: 2, spines with tiny laterodistal serrations. Eggs carried in cemented groups of moderate size, egg size slightly less than diameters of oviger segments.

Legs dimorphic, posterior four differing from anterior four, mainly in propodus. Second coxae less than 1.5 times length of first and third, all coxae similar. Femora similar in size and spination, cement gland a small raised bulge with small anterior pointing cone with apical pore at proximal end. All tibiae with dorsal, lateral and ventral setae mostly shorter than segment diameters, length of tibiae of anterior two pairs of legs subequal. Tibiae of posterior two pairs of legs unequal to anterior two pairs, inflated. First tibia of posterior two pairs longer and more inflated than second tibia. Tarsus of all legs subequal. Propodus of anterior two leg pairs typical, a curved cylinder without

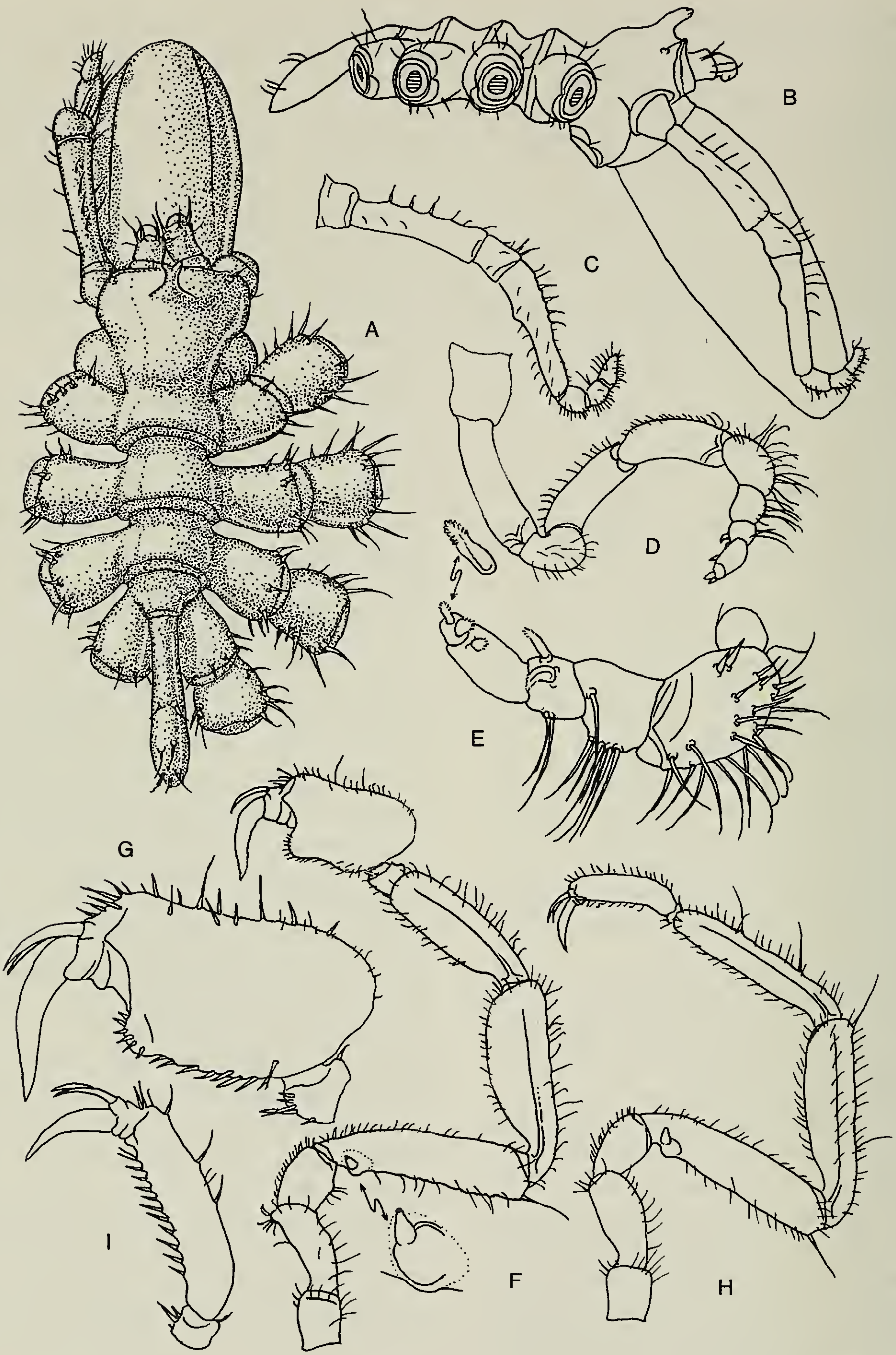

Fig. 2. *Sericosura heteroscela,* new species, holotype male: A, trunk, dorsal view; B, trunk, lateral view; C, palp; D, oviger; E, oviger distal segments and denticulate spine, enlarged; F, third leg; G, third leg distal segments, enlarged; H, second leg; I, second leg distal segments, enlarged.

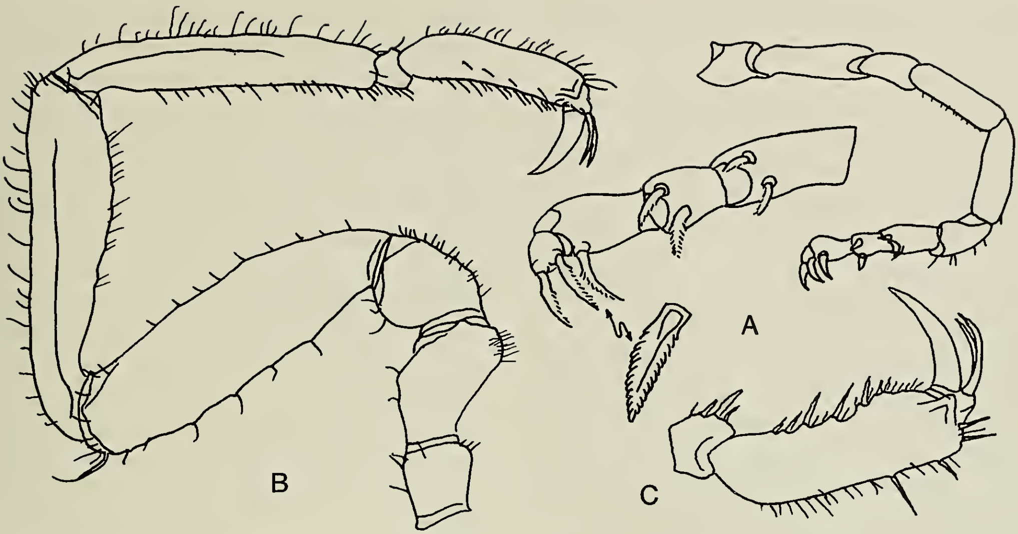

Fig. 3. *Sericosura heteroscela,* new species, paratype female: A, oviger with distal segments and denticulate spine, enlarged; B, third leg. Paratype juvenile: C, distal leg segments, enlarged.

heel, with row of short sole spines, few dorsal setae, a slender curved claw little more than half propodal length, auxiliaries little more than half main claw length. Propodi of posterior two pairs of legs grossly inflated, wider than any other leg segment, with few short sole spines, many short dorsal setae, and a distal sole bulge bearing row of six or seven short spines. Claw at tip of narrow anterior propodal extension, well curved, slightly recurved at tip, auxiliaries slightly longer than half main claw length.

Female and juvenile paratypes: Adult female with all legs alike, differing only slightly from anterior four legs of male. Second coxae slightly shorter in length, third coxae with dorsodistal swelling armed with many short setae. Femora of one female specimen are swollen more than those of other females and apparently recently contained eggs. First tibiae slightly longer than those of male. Distal leg segments like those of anterior legs of male. Female oviger much smaller, with more and larger denticulate spines having many more lateral lobes, in formula 2: 2: 1: 2. Seventh segment with two spines.

Juvenile males have incompletely formed posterior propodi which are only half as inflated, or less, as those of adult males. Inflation is more marked ventrodistally next to the claw insertion. At this stage, ovigers are not yet fully formed.

Measurements.—Holotype in mm: Trunk length from chelifore insertion to tip 4th lateral processes, 3.1; trunk width across 2nd lateral processes, 2.5; proboscis length, 3.6; abdomen length, 1.8; third leg, coxa 1, 0.58; coxa 2, 1.14; coxa 3, 0.80; femur, 2.4; tibia 1, 2.32; tibia 2, 1.82; tarsus, 0.37; propodus, 1.7; claw, 0.96; auxiliaries, 0.53.

Measurements of second leg distal segments: femur, 2.45; tibia 1, 2.4; tibia 2, 2.21; tarsus, 0.39; propodus, 1.25; claw, 0.56.

Distribution.—The Mid-Atlantic Ridge is the type locality for this new species, among sulfides and mussels at the base of hydrothermal structures at the Lucky Strike vent zone west of the Azores Plateau, in 1727–1730 m. Material came from other nearby Lucky Strike sites in 1685 m, and vents at Menez-Gwen area in 845–1685 m, and also from the 14°45′N site.

Etymology.—The specific name (Latin:

hetero = different, and *scela* = leg) refers to the dimorphic propodi in the male of this new species.

Remarks.—Differing leg morphology within the same specimen (intraspecific dimorphism) is fairly rare in pycnogonids. The most prevalent instance of this phenomenon is in the different propodal size and spination of some (but not all) species of the predominantly Antarctic genus *Ammothea.* The propodi of the anterior two pairs of legs in some species appear a little more inflated and have more sole spines than the propodi of the posterior two leg pairs in the same specimen. These inflation and spination differences are much less conspicuous than those of this species.

Inflation and differences in sole spination in *Ammothea* species are opposite to the situation in *Sericosura heteroscela.* In the latter species it is the posterior propodi which are grossly inflated and have different spination from the more slender or "normal" anterior propodi of male specimens.

The only other prevalent character which differs on some legs from others concerns sexual dimorphism. Besides the sex pores which appear on some male legs and not others in most pycnogonid genera, the major difference is that of the male cement gland and the shape of its exterior outlet. Among members of the family Austrodecidae, another mostly Antarctic group, the cement gland exterior cone or tube sometimes appears on the posterior four legs or in rarer instances, on the posterior two legs only and not on any anterior legs. There are some instances of a few species of genera in other families bearing cement glands only on posterior legs, but this is not at all common among any of the pycnogonid groups.

Besides the phenomenon of two different leg shapes in a single specimen, this difference also occurs between the sexes in the genus *Sericosura.* Legs of females, where known, are dimorphic to a greater or lesser degree from those of males in the same species. In the first known species, *S. mitrata,* legs of females have short spines and long setae confined mostly to the ventral surface of the tibiae. In males of the same species, the row of short ventral spines is lacking and any long setae are found only on lateral and dorsal surfaces of the tibiae. These differences are even more marked in *S. cochleifovea* where the male has rows of lateral and dorsal spines little longer than each segment diameter on the femora and tibiae. Females have lateral rows of very long setae on both tibiae and propodi while they are lacking on femora. This situation is reversed in *S. bifurcata* where males have long lateral tibial setae and females apparently have an even greater number of long lateral setae.

There is very little dimorphism of setae or other characters in legs of females of *S. heteroscela* when compared with only the anterior legs of males. The few differences appear mostly in the shorter and less setose female second coxae.

A character showing no sexual dimorphism is that of palp segment numbers. There are now six known species of this genus and two of them, *S. cochleifovea* and *S. bifurcata* have palps of nine segments. The other four, *S. mitrata, S. venticola, S. heteroscela,* and *S. cyrtoma* have palps with seven segments. Many genera, particularly among the Ammotheidae, have members with variable numbers of palp segments and this is therefore not a stable diagnostic character.

All known *Sericosura* species have chelifore scapes of a single segment. Several specimens listed above have what appears to be a wrinkle artifact proximally on the scapes which make them appear as though they have two segments. This is illustrated for the male holotype. Most specimens have scapes which are plainly 1-segmented.

Many of these specimens are lightly to heavily covered with white or brown filamentous bacteria or sulfides which do not appear to inhibit the free movement of their appendages.

Some specimens of this species were observed in situ one meter from a black smoker of the Eiffel Tour site, Lucky Strike hydrothermal area (1630–1685 m), lying on sulfide blocks covered by a light film of hydrothermal sediments. Most of the other specimens came from washings of mytilid samples collected on the walls of active vent structures. These mytilid colonies live near fluid emissions with an average temperature of about 11°C (Van Dover et al. 1996). It should be noted that many of the specimens of *S. heteroscela* were more or less covered with filamentous bacteria. Similar bacterial filaments have been found commonly on pycnogonids collected in the Juan de Fuca and Explorer vent areas (Child 1987:892–901).

Shallow-water pycnogonids usually feed on sponge and hydroid tissues. Sponges such as *Cladorhiza* sp. and hydroids of the genus *Sympectoscyphus* sp. are abundant on active vent structures (among mytilid beds), atop extinct chimneys (Segonzac & Vervoort 1995:151), and could constitute an abundant food source for pycnogonids. These substrata are often covered at their extremities by white filamentous bacteria, probably the same as those observed on the pycnogonids themselves. These colonial organisms may constitute an abundant food source for vent pycnogonids.

Two juvenile specimens came from washings of mytilid samples at the Menez-Gwen area (850 m). These mussels live in dense groups of tens to hundreds of individuals on the slopes of a volcano formed of light grey hydrothermal sediments composed of silica. Translucent fluids are emitted in the vicinity of these colonies at a maximum temperature of 65°C (Y. Fouquet, pers. comm.). In this environment, sessile fauna (except for mytilids) is not visible, but sponges and hydroids can be found in the samples collected. In addition, basalts located less than ten meters away are colonized by gorgonians and scleractinians (*Lophelia pertusa*) which could serve as food for pycnogonids.

Sericosura cyrtoma, new species
Fig. 4

Material examined.—*Hero* 91 cruise, sta. PL 25, East Pacific Rise, Caldera site, 12°48′N, 103°54.6′W, 2563 m, 10 km S of 13°N, in hydrothermal vent area with vestimentiferans, 29 Oct 1991, 1 ♀, holotype, MNHN, Paris.

Description.—Size small, leg span about 17 mm. Trunk compact, lateral processes fairly short, closely spaced at less than half their diameters. Many short broad spines in raised sockets placed around dorsal rim of trunk anterior, dorsodistally on lateral processes and chelifore scapes, dorsally on abdomen and palp second segments. Cephalic segment anterior very broad, ocular tubercle broader than tall, on elevated mound, blind, with conspicuous lateral sensory papillae, and a laterally contracted posterior lobe. Proboscis large, carried ventrally at right angle to trunk, tapering distally from broad base, with distal downcurve at sharp angle. Oral surface small, tip rounded. Abdomen moderately long, carried at ventral oblique angle, armed with four broad dorsolateral spines and several short distal setae.

Chelifores very short, scape slightly less than twice longer than its diameter, armed with row of dorsodistal short spines in sockets. Chelae tiny, globular, fingers reduced to tiny ventral bumps. Palps of seven segments. Second segment with two short dorsal spines and single distal seta. Fourth segment longest, segmentation line between third and fourth segments indistinct, both armed with several dorsal spines and setae longer than segment diameters. Distal three segments short, fifth as long as sixth and seventh combined, sixth shortest, seventh slightly longer and more slender, all three armed with few setae, ventral setae longest.

Oviger second segment almost twice longer than first or third, fourth and fifth longest, subequal, less than four times longer than wide. Sixth short, curved, with two lateral setae. Strigilis with plain spines in for-

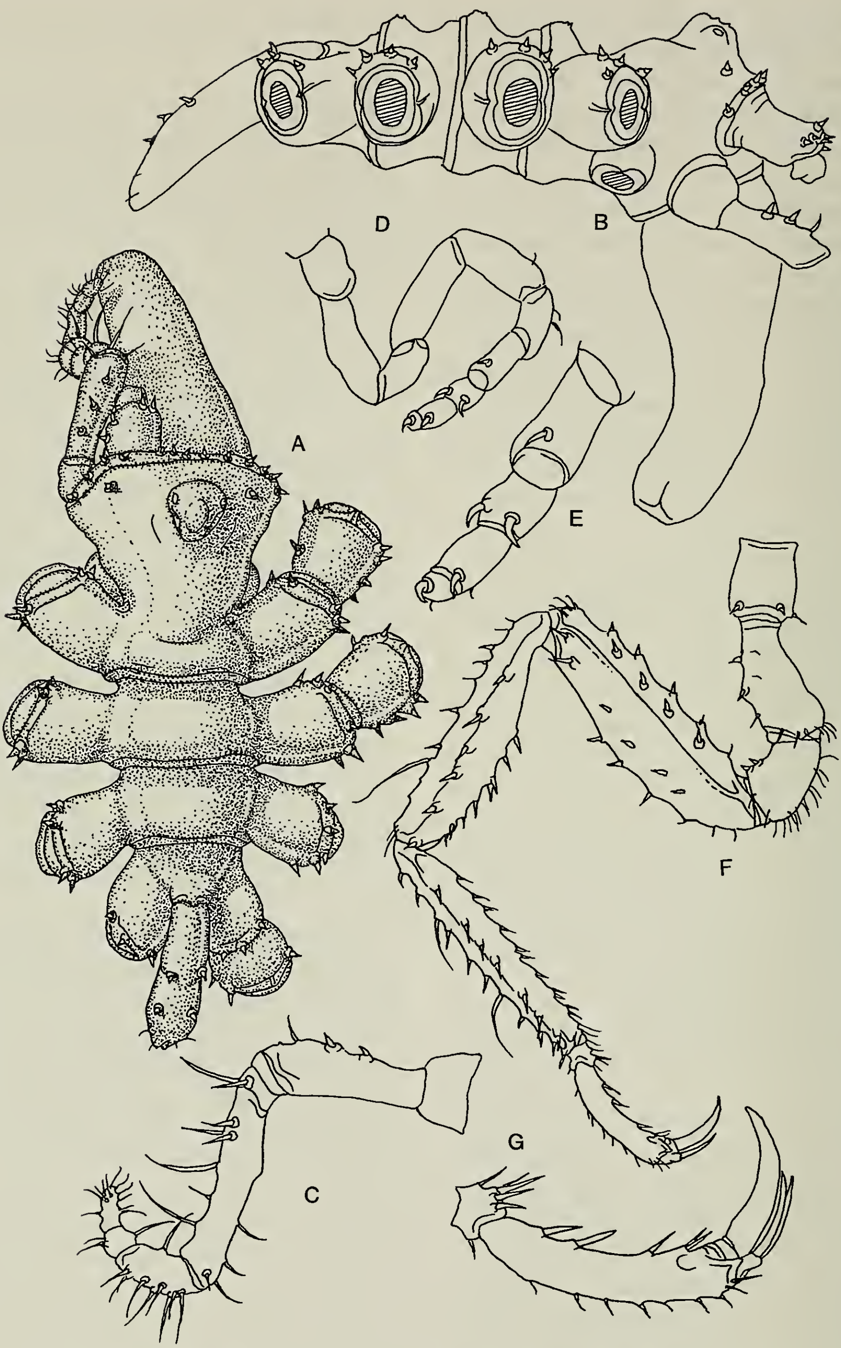

Fig. 4. *Sericosura cyrtoma,* new species, holotype female: A, trunk, dorsal view; B, trunk, lateral view; C, palp; D, oviger; E, oviger distal segments, enlarged; F, third leg; G, third leg distal segments, enlarged.

mula 1:2:1:1, with the terminal segment a tiny bulb.

Legs with many short dorsal, lateral, and ventral spines on sockets in rows. Second and third coxae with field of ventral and ventrodistal setae. Major segments of almost equal length, femora only slightly longer. Second tibiae with row of many short ventral setae. Tarsus very short, with several ventral spines. Propodus long, slender, with two proximal sole spines, and another more distal, a pair of distal setae and several shorter dorsal spines. Claw long, well curved, auxiliaries long, about 0.6 main claw length.

Male characters unknown.

Measurements.—Holotype in mm: trunk length from chelifore insertion to tip 4th lateral processes, 1.91; trunk width across 2nd lateral processes, 1.36; proboscis length, 1.45; abdomen length, 0.92; third leg, coxa 1, 0.43; coxa 2, 0.74; coxa 3, 0.59; femur, 1.65; tibia 1, 1.56; tibia 2, 1.58; tarsus, 0.16; propodus, 0.77; claw, 0.39.

Etymology.—The specific name (Greek: kyrtoma, a curve or hump) refers to the hump-like curve of the proboscis.

Remarks.—There is no other known species in this genus which has such a spiny, cactus-like appearance and a downcurved proboscis. Almost all of the dorsal spines of this specimen are extremely short and broad while the lateral and ventral spines are of a more usual or longer length. There are relatively few setae on this unique specimen except for a ventral field on the second and third coxae and a few on the palp and distal abdomen. Male legs will undoubtedly have different arrangement of spines and setae, consistent with the usual dimorphic leg characters in this genus.

The single specimen of *S. cyrtoma* was found in an active hydrothermal area of the Caldera site, East Pacific Rise, 10 km south of the 13°N hydrothermal area. No pycnogonid has been collected before in this area, despite intensive sampling since 1982. The Caldera site, still undescribed, is not very different from other 13°N sites: with vestimentiferans, living in areas of diffuse venting at temperatures of 6°–7° to 12°C, between inactive chimneys 15 m high atop a sulfur mound 67 m high. Associated fauna is composed of limpets and barnacles on *Riftia* tubes, serpulid polychaetes, galatheid and brachyuran crabs, anemones, fish and shrimp.

Sericosura venticola? Child, 1987

Sericosura venticola Child, 1987:896–899, fig. 2.—Stock, 1991:158–159 [text].

Material examined.—*Naudur* cruise, sta. ND 18–4–8B, Rehu Site, North of Easter Island, SE Pacific Rise, among vestimentiferans, 17°24.8′S, 113°12.1′W, 2578 m, 23 Dec 1993, 1 juvenile.

Distribution.—If this single juvenile specimen is indeed *S. venticola,* then its distribution is greatly extended to the southern hemisphere and to a totally different hydrothermal vent area. The type specimens were taken in the NE Pacific on the Endeavour Segment of the Explorer Ridge, in about 2200 m. If this specimen is *S. venticola,* it would mark the first time a species in this genus has been reported from more than one hydrothermal vent field, separated by several thousand kilometers.

Remarks.—Several characters of this juvenile specimen agree almost exactly with those of *S. venticola,* while several do not. Possibly these differing characters can be attributed to the juvenile state of this specimen or to the lack of a described female for this species. It is extremely difficult to identify a juvenile in this genus of seemingly morphologically uniform species and we assign this specimen to a species with great hesitation.

The chelate specimen appears to be a female, although the oviger is only half formed and there are no sex pores. It has very long setae on major leg segments in keeping with the more or less dimorphic state between sexes in this genus. Male leg setae of *S. venticola* are shorter and placed differently than those of this specimen. The long setae are similar to those on legs of male specimens of *S. bifurcata* Stock, but other characters are very different from that species.

The seven-segmented palps of this juvenile are almost exactly like the palps of *S. venticola,* including two long dorsal setae of the fourth segment. The chelae are rather broad, as are those of *S. venticola,* and the ocular tubercle is the same shape and height, although the laterodistal bumps of the adult ocular tubercle are extended as lateral tubercles twice as long as their diameters in this juvenile. The long downcurved abdomen is virtually alike in both this specimen and the types and juvenile lateral processes are separated by only short intervals and are about the same length as those of the types. The length ratio of proboscis and trunk of this juvenile corresponds to that of the types, with the proboscis carried in the same horizontal aspect. There appear to be sufficient characters in agreement between the types and this juvenile to suggest that they are conspecific. Adults from the same locality are needed to confirm this suggestion.

This juvenile specimen of *S. venticola*? was found in washings of vestimentiferan (probably *Riftia pachyptila* and *Tevnia jerichonana*) samples collected on an active hydrothermal site on the East Pacific Rise north of Easter Island (Geistdoerfer et al. 1994).

Family Callipallenidae Hilton, 1942
Genus *Callipallene* Flynn, 1929
Callipallene producta (Sars, 1888)

Pallene producta Sars, 1888:342; 1891:36–37, pl. III, fig. 2a–d.

Callipallene brevirostris producta.—Stock, 1952:6–7, figs. 9–11 [early literature].

Callipallene producta.—Stock, 1990:227 [recent literature]; 1992:128.—Bamber & Thurston, 1993:849.

Material examined.—*Diva* 1 cruise, sta. DV 13-6, Menez-Gwen site, Mid-Atlantic Ridge, 37°50′N, 031°32′W, 844 m, 21 May 1994, 1 ♂.

Distribution.—This well-known species has been collected from Norway to the Azores, Spain, and the Canary Islands, and in the Mediterranean and Black Sea at several localities. It has a wide depth range of 130–1550 m. This male is well within its known geographic and depth ranges.

Remarks.—This is the first time this species has been found associated with or in the vicinity of known hydrothermal vents. It is probable that many other known species from deeper water eventually will be collected at or near known hydrothermal vents.

Family Colossendeidae Hoek, 1881
Genus *Colossendeis* Jarzynsky, 1870
Colossendeis macerrima Wilson, 1881
Fig. 5

Colossendeis macerrima Wilson, 1881: 246–247, pl. 1, fig. 2, pl. 4, figs. 9–12, pl. 5, fig. 32.—Fry & Hedgpeth, 1969:53 [literature], figs. 7, 8.—Child, 1995:83–84.

Material examined.—*Diva* 2 cruise, Lucky Strike vent area, from inactive chimney next to Isabel site, 37°17.4′N, 032°16.6′W, 1688 m, 1 spec. The specimen was photographed but not collected.

Distribution.—This is a cosmopolitan deep-sea species.

Remarks.—The size and proboscis of the specimen in Fig. 5 leaves almost no doubt that it is this species. For scale, the metal cup in the picture is 18 cm wide. This specimen was filmed for several minutes, moving slowly at the top of an inactive structure. Fauna found elsewhere was almost absent here, except for a white gorgonian.

Acknowledgments

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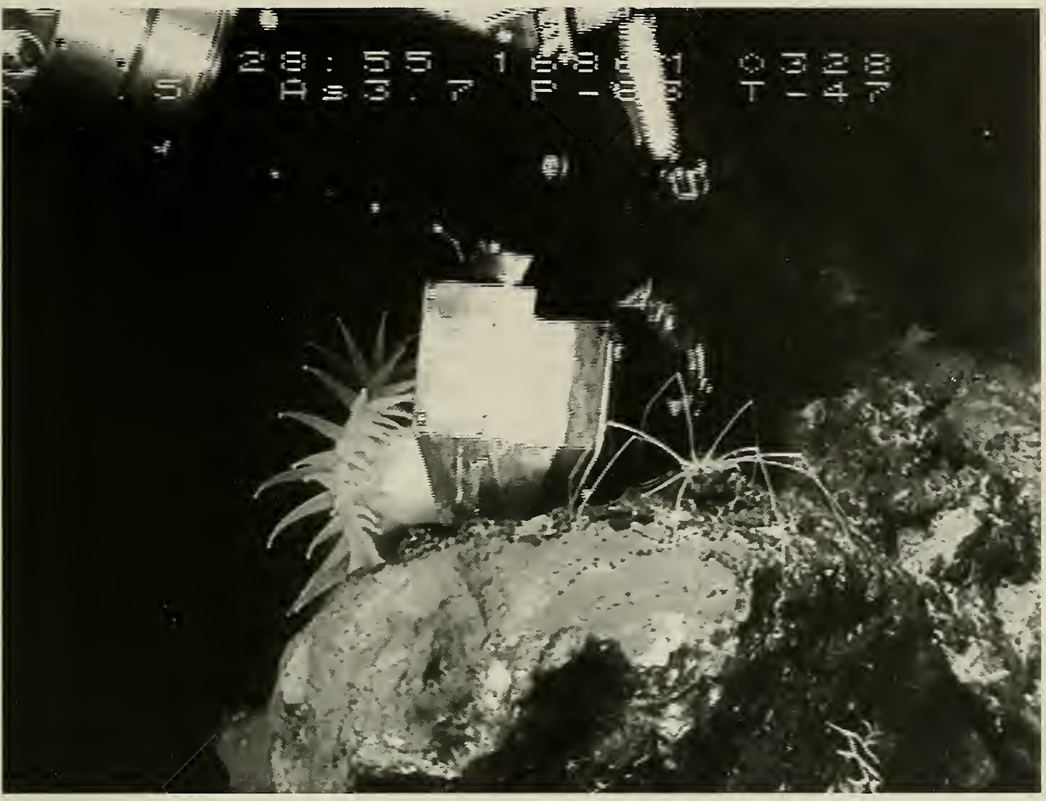

Fig. 5. *Colossendeis macerrima* Wilson. Live specimen in situ. (Width of metal cup = 18 cm.)

crews of both the N/O *Nadir* and the submersible *Nautile,* who participated in the cruises. We thank W. Vervoort (Hydroids) and H. Zibrowius (Scleractinia) for their identifications, P. Briand for his technical aid (specimen sorting and color plate), Mrs. J. Jennings for help with translations, and P. Chevaldonné and T. Comtet for reviewing the manuscript.

The material studied herein originates from French cruises (*Diva 1* and *Diva 2*) organized by IFREMER institution within the framework of the FARA program (French American Ridge Atlantic).

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The Pyconogonida types of William A. Hilton. II. The remaining undescribed species

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Abstract.—The four remaining questionable species named by W. A. Hilton between 1939 and 1942 are described as if they were newly discovered, are illustrated where necessary, and compared with others described by Hilton and other authors of American west coast pycnogonids. The species are: *Achelia simplissima, A. spinoseta, Ammothella setosa,* and *Tanystylum duospinum.* The latter species is found to be the earliest valid name for several synonym species described later. Another little known species, *Achelia harrietae* Marcus, 1940, is illustrated and compared with *A. spinoseta,* a close relation. A complete list of the 66 Hilton species with original names, dates of publication, and current identifications are given.

This is the second paper to investigate the pycnogonids which William A. Hilton described in a preliminary and inadequate form. The first paper (Child 1975) treated a single family, the Phoxichilidiidae. Besides the species discovered to be valid or synonyms by other authors in that paper, this writer later chose to introduce descriptions and illustrations of Hilton's other unknown or inadequately known species when and where they could be placed with others of the same genus or in papers treating pycnogonids of the same locality.

William A. Hilton described 66 pycnogonid species (using 70 names, thus creating a few instant synonyms) mainly collected from California and Alaska, including the Aleutian and other offshore Alaskan Islands. He published these, for the most part, in the Journal of Entomology and Zoology of Pomona College (California), of which he was editor for many years. Most were loaned by the National Museum of Natural History whose collections fortunately now contain 57 of these types or type series while nine are deposited in the B. P. Bishop Museum, Honolulu, Hawaii.

It has been difficult at times to introduce some of Hilton's species for clarification in publications based on localities other than California and Alaska, and thus it has been found necessary to place these last few descriptions and illustrations in their own report. All of these species remain valid. All species named by Hilton, including the four listed herein, have now been redescribed or reduced to synonyms by this writer and other authors, most notably Hedgpeth in his several eastern Pacific rim reports (Table 1). It was found beneficial to illustrate a little known species of *Achelia*; *A. harrietae* Marcus, 1940 (described as *A. discoidea* Exline, 1936, preoccupied). This is done both because the original illustrations are inadequate and the report is generally unavailable to today's specialists. The species has not been collected or illustrated since the type was described. It is also illustrated herein because it must be compared with the closely related species, *A. spinoseta* Hilton, 1939, described and illustrated herein. The types of Exline's species (undamaged holotype and 23 paratypes, USNM 71500 and 71501), from Puget Sound, Washington, are also deposited in the National Museum of Natural History collections.

Table 1.—List of Pycnogonid species named by William A. Hilton.

Hilton's species name	Present designation
Ammotheidae:	
Ammothea chelata, 1939a	*Achelia chelata* (Hilton)
A. elongata, 1942g	*Achelia borealis* (Schimkewitsch)
A. grossifemora, 1942g	*Tanystylum grossifemora* (Hilton)
A. megova, 1942g	*Achelia megova* (Hilton)
A. ovosetosa, 1942g	*Achelia ovosetosa* (Hilton)
A. simplissima, 1939a	*Achelia simplissima* (Hilton)
A. spinoseta, 1939a	*Achelia spinoseta* (Hilton)
Ammothella biunguiculata var. *fusca,* 1942d	*Ammothella biunguiculata* (Dohrn)
A. heterosetosa, 1942b	Name Valid
A. pacifica, 1942d	Name Valid
A. setosa, 1942g	Name Valid
Ascorhynchus laterospinus, 1942g	Name Valid
Eurycyde longisetosa, 1942b	Name Valid
E. spinosa, 1916	Name Valid
Lecythorhynchus ovatus, 1942d	*Ammothea hilgendorfi* (Böhm)
Leionymphon dorsiplicatum, 1942g	*Ammothea dorsiplicata* (Hilton)
Nymphopsis duodorsospinosa, 1942b	Name Valid
Tanystylum californicum, 1939a	Name Valid
T. duospinum, 1939a	Name Valid
T. nudum, 1939a	Nomen Dubium, specimen lost
T. oculospinosum, 1942e	*T. duospinum* Hilton
T. panamum, 1942e	*T. intermedium* Cole
Phoxichilidiidae:	
Anoplodactylus compactus, 1939a	Name Valid
A. intermedius, 1942d	*A. batangensis* (Helfer)
A. nodosus, 1939a	Name Valid
A. oculospinus, 1942f	Name Valid
A. pacificus, 1942f	Name Valid
A. projectus, 1942d	*A. californiensis* Hall
A. robustus, 1939a	*A. californiensis* Hall
A. unospinus, 1942f	*Phoxichilidium* sp. juv.
Halosoma compactum, 1942f	*Anoplodactylus compactus* (Hilton)
Phoxichilidium micropalpidum, 1942f	Name Valid
P. parvum, 1939a	Name preoccupied
P. quadradentatum, 1942f	Name Valid
P. truncatum, 1942d	*Anoplodactylus pycnosoma* (Helfer)
Pigrogromitus robustus, 1942c	*Pycnosomia strongylocentroti* Losina-Losinsky
Colossendeidae:	
Colossendeis chitinosa, 1943a	*Hedgpethia chitinosa* (Hilton)
C. microsetosa, 1943a	Name Valid
C. spinifera, 1943a	*C. colossea* Wilson
C. tenera, 1943a	Name Valid
Endeididae:	
Endeis compacta, 1943b	*Anoplodactylus viridintestinalis* Cole
E. nodosa, 1942d	Name Valid
Phoxichilus compactus, 1939a	(see *Endeis compacta*)
Nymphonidae:	
Chaetonymphon duospinum, 1942a	*Nymphon duospinum* (Hilton)
C. quadrispinum, 1942a	*Nymphon duospinum* (Hilton)
Nymphon basispinosum, 1942a	Name Valid
N. elongatum, 1942a	Name Valid
N. microcollis, 1942a	*N. brevitarse* (Krøyer)

Table 1.—Continued.

Hilton's species name	Present designation
N. microsetosum, 1942a	Name Valid
N. molum, 1942a	Name Valid
N. nigroanathum, 1942a	*N. grossipes* (Krøyer)
N. noctum, 1942a	*N. profundum* Hilton
N. oculospinum, 1942a	*N. grossipes* (Krøyer)
N. profundum, 1942a	Name Valid
N. variatum, 1942a	*N. pixellae* Scott
Callipallenidae:	
Callipallene ovigerosetosa, 1942c	(see *Oropallene o.*)
Clotenopsa prima, 1942d	*Pigrogromitus timsanus* Calman
Cordylochele microspines, 1942c	*Pseudopallene circularis* (Goodsir)
C. setospines, 1942c	*P. circularis* (Goodsir)
Decachela discata, 1939a	Name Valid
Oropallene heterodenta, 1942c	*Anoropallene palpida* (Hilton)
O. (*Pallene*) *ovigerosetosus,* 1942d	Callipallenid?
O. palpida, 1942c	*Anoropallene palpida* (Hilton)
Pallenopsis oculotuberculosis, 1942c	Name Valid
P. pacifica, 1942c	Name Valid
P. profundis, 1942c	Name Valid
P. truncatum, 1942d	?*Anoplodactylus pycnosoma* (Helfer)
Pseudopallene setosa, 1942c	*P. circularis* (Goodsir)
P. spinosa, 1942c	*P. circularis* (Goodsir)

Methods.—For uniformity of references and to avoid repetition, the letter suffixes next to the dates of Hilton's publications correspond to the same letter suffixes of his complete list of publications in Child's (1975) first paper. The literature citations in that paper will only be repeated in this report where they apply. Other papers treating the species discussed and published later by other authors are included. The type catalog numbers are those of the system used by the U.S. National Museum (USNM) and are retained for convenience.

Family Ammotheidae Dohrn, 1881

Genus *Achelia* Hodge, 1864

Achelia simplissima (Hilton)

Fig. 1

Ammothea simplissima Hilton, 1939a:31–32.—Hedgpeth, 1941:256 [key].

Ammothea simplisicma [sic] Hilton, 1942g: 94.

Achelia simplissima.—Hedgpeth, 1951: 106, 108; 1964:208 [key], fig. 94e.

Material examined.—Dillon Beach, Marin County, California, on bryozoans, coll. O. Hartman, 20 Dec 1934, USNM 81523 (1 ♀ syntype, 1 ♂ juvenile syntype).

Distribution.—This elusive species is only known from the adult and chelate juvenile syntypes from Dillon Beach, just north of San Francisco. No depth was given, but it was probably shallow or littoral.

Description.—(Female.) Species very small, trunk ovoid, unsegmented, with few short spines on anterior rim of cephalic segment. Lateral processes contiguous, without large distal tubercles, with lateral row of short dorsodistal spines, anterior spine of each segment on low inconspicuous tubercle. Ocular tubercle low (squashed down on holotype), without apical cone, eyes small, prominent. Abdomen carried almost horizontally, extending just beyond rim of first coxae of fourth leg pair, armed with three short dorsodistal spines. Proboscis moderately inflated (slightly squashed in holotype) little shorter than trunk, oral surface flat.

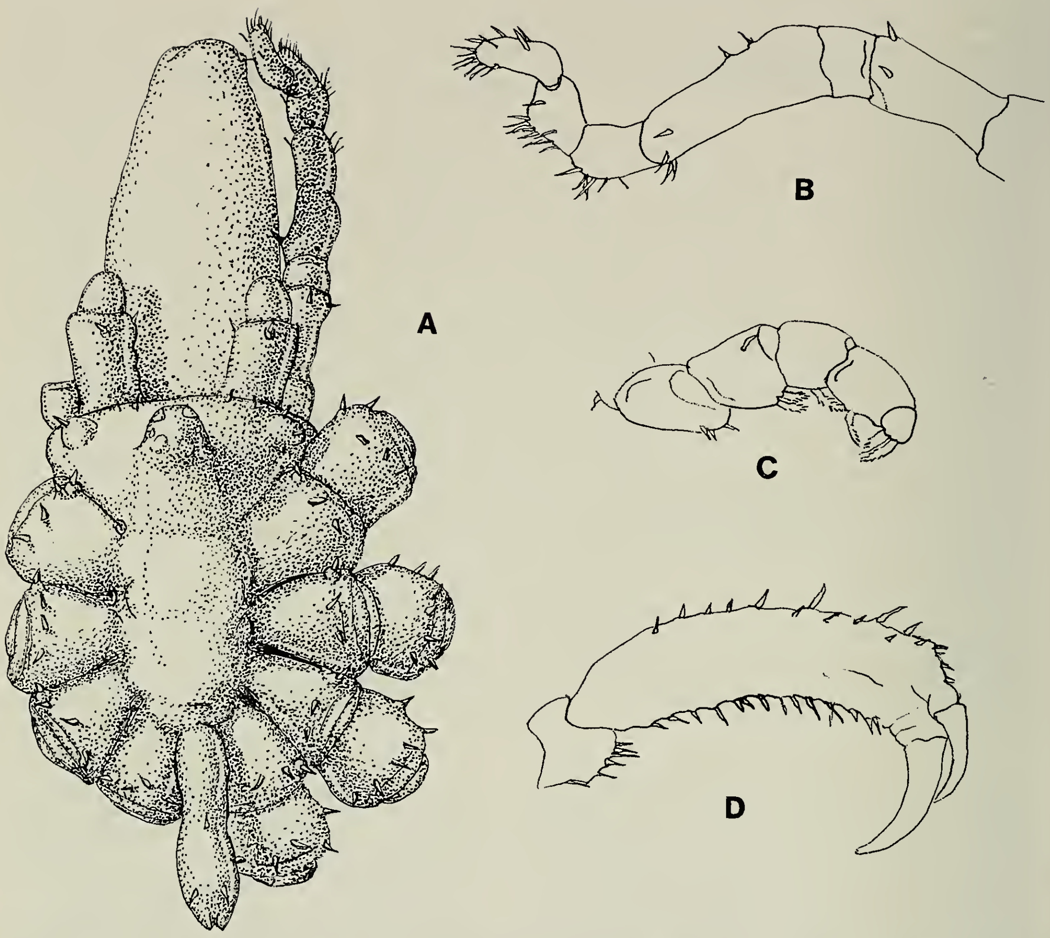

Fig. 1. *Achelia simplissima* (Hilton), holotype female: A, trunk, dorsal view; B, palp; C, oviger terminal segments, enlarged; D, distal leg segments, enlarged.

Chelifore scapes broad cylinders, short, only twice as long as their diameters, with one short dorsodistal spine. Chelae rounded bumps with distal cleft marking residual finger separation, without spines. Palps seven-segmented, third very short, not half as long as wide, fourth longest, with tuft of four or five short ventrodistal spines. Distal three segments with fields of ventral spines; fifth a bent cylinder, sixth with triangular ventral tubercle, seventh long, curved, suggesting two coalesced segments. Oviger segments short, fifth little longer than fourth, strigilis segments little longer than wide, each armed with two short denticulate spines, spines with six or seven lateral lobes.

Legs robust, femora inflated, without dorsodistal tubercles, second tibiae the longest segments, all segments armed with randomly placed short spines. First coxae without tubercles, with row of spines matching those of lateral processes. Tarsus without broad ventral spine, propodus with three slightly larger heel spines, many smaller sole spines, and slightly narrow, well curved main claw. Auxiliaries narrow, about half main claw length.

Male characters unknown.

Measurements.–Female syntype in mm:

Trunk length (chelifore insertion to tip 4th lateral processes), 0.98; trunk width (across 2nd lateral processes), 0.92; proboscis length, 0.93; abdomen length, 0.41; third leg, tarsus, 0.15; propodus, 0.61; main claw, 0.23.

Remarks.—The two specimens are in good condition but the ocular tubercle of the adult female has been flattened under cover glass, and the proboscis is slightly flattened.

This species is similar to *Achelia ovosetosa* (Hilton, 1942g) (see Child 1995, for description and figures), which has short trunk and appendage spines in the same places as this species, but the former species has many more spines than *A. simplissima.* The chelifores of *A. ovosetosa* are as broad but are shorter and the chelae are larger and longer in this species. The major difference between these two species is in the distal palps which have four bulbous segments and many longer setae in *A. ovosetosa.* There are only three distal segments (third and fourth coalesced?) with fewer spines and the terminal segment is a narrow curved cylinder in *A. simplissima.* The size of *A. ovosetosa* is approximately twice as large as *A. simplissima,* although size alone is not diagnostic. There are also other minor differences in oviger segment length and strigilis spination in the types of the two species, both of which are female.

Achelia spinoseta (Hilton)
Fig. 2

Ammothea spinoseta Hilton, 1939a:31; 1942g:95.—Hedgpeth, 1941:256 [key].
Achelia spinoseta.—Hedgpeth, 1951:106; 1964:208, fig. 94d.

Material examined.—Moss Beach, S of San Francisco, California, coll. W. Lewis, 8 Jul 1923, USNM 79427 (1 ♂ holotype).

Distribution.—This species has only been known from the unique holotype. No collecting depth was given, but it probably was taken in a shallow or littoral depth.

Description.—Size tiny, trunk unsegmented, with single seta at dorsolateral corners of cephalic segment. Lateral processes almost contiguous, some with tiny openings between, armed with pair of small dorsolateral tubercles, the anterior ones with single short spine, the posterior tubercles with two, sometimes three short spines. Ocular tubercle a low cone (squashed flat in the type), eyes small, very inconspicuous. Abdomen carried almost horizontally, cylindrical, length extending to just short of distal rim on fourth coxae pair, armed with four short distal spines. Proboscis well inflated (squashed in type specimen), base very narrow, with narrow flat oral surface.

Chelifore scapes moderately broad, tapering distally, armed with small dorsodistal tubercle having three short spines. Chelae ovoid, half as long as scapes, armed with few very short lateral spines, with ventral cleft separating finger stubs. Palp eight-segmented, increasingly spinose distally, fifth, sixth, and seventh segments with conspicuous ventral lobes, terminal segment long, slender. Oviger second segment broader than distal segments, third as long as fourth, little longer than fifth, all three armed with short curved lateral spines, two rows on fifth segment. Sixth with few lateral spines, seventh with low lateral bulge having several longer spines. Strigilis distal three segments attached laterally to seventh, each armed with short ectal spine and short denticulate spines, one on eighth and ninth segments, two on tenth. Denticulate spines with seven-eight rounded lateral lobes.

Legs with conspicuous, randomly placed, long and short spines, none longer than segment diameters. First coxae with dorsolateral tubercles similar to those of lateral processes, armed with anterolateral and posterolateral row of short spines on tiny low tubercles. Second coxae with moderately long spines, coxae of posterior four legs with long ventrodistal tubercle as long as segment diameter, armed with few short spines. Third coxae shortest, armed with moderately long spines. Femur the longest segment, with few short spines and dorso-

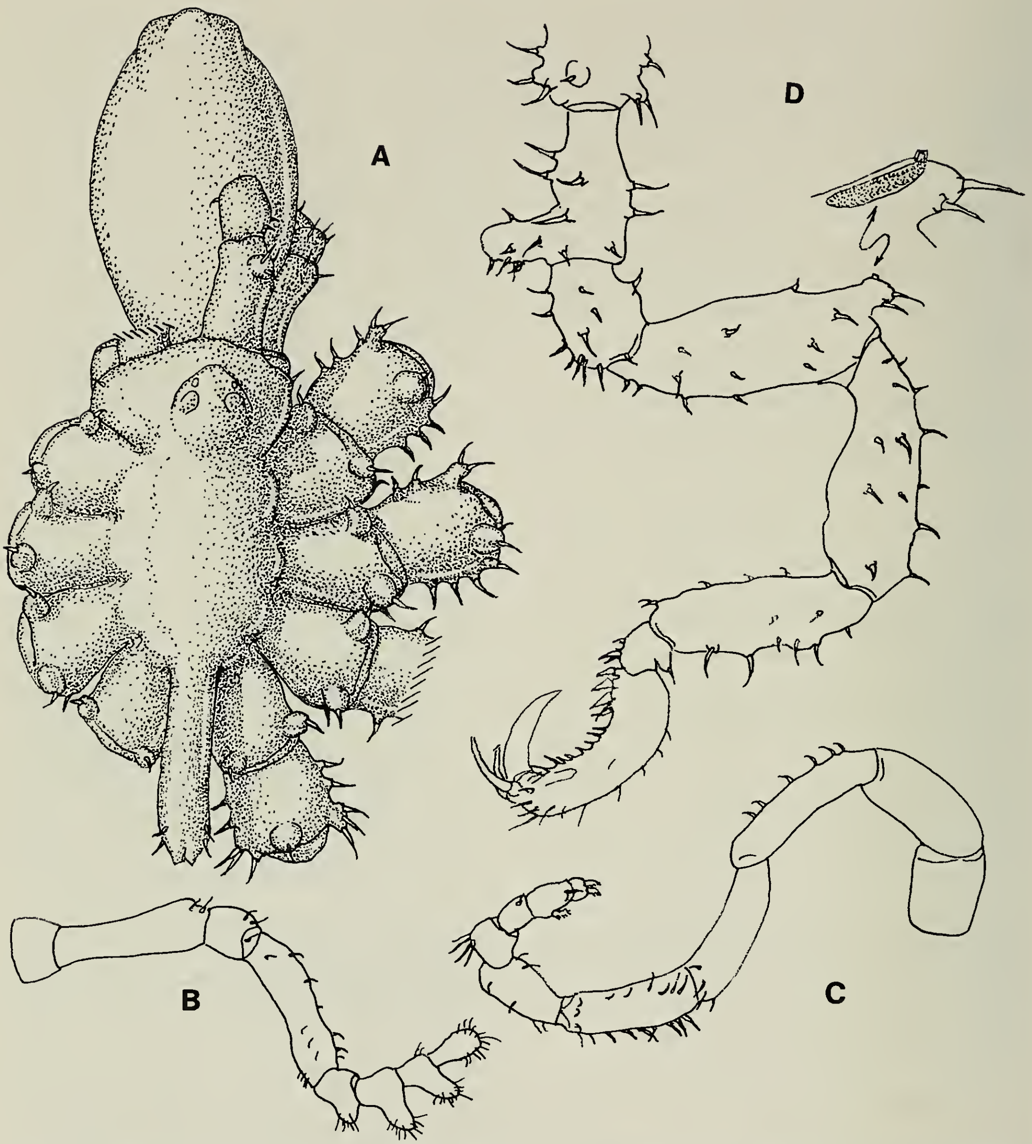

Fig. 2. *Achelia spinoseta* (Hilton), holotype male: A, trunk, dorsal view; B, third leg, with enlargement of cement gland and tube; C, palp; D, oviger.

distal tubercle bearing tiny short cement gland tube and two spines. Tibiae with few lateral and dorsal spines. Tarsus short, without prominent heel spine. Propodus well curved, with four larger heel spines, eight-nine smaller sole spines, and long slightly curved claw with auxiliaries approximately half main claw length.

Female characters unknown.

Measurements.—Holotype male in mm: Trunk length (chelifore insertion to tip 4th lateral processes), 1.19; trunk width (across 2nd lateral processes), 1.16; proboscis length (approximate), 0.98; abdomen length, 0.53; third leg, coxa 1, 0.28; coxa 2, 0.34; coxa 3, 0.3; femur, 0.77; tibia 1, 0.71; tibia 2, 0.67; tarsus, 0.15; propodus, 0.57; main claw, 0.3.

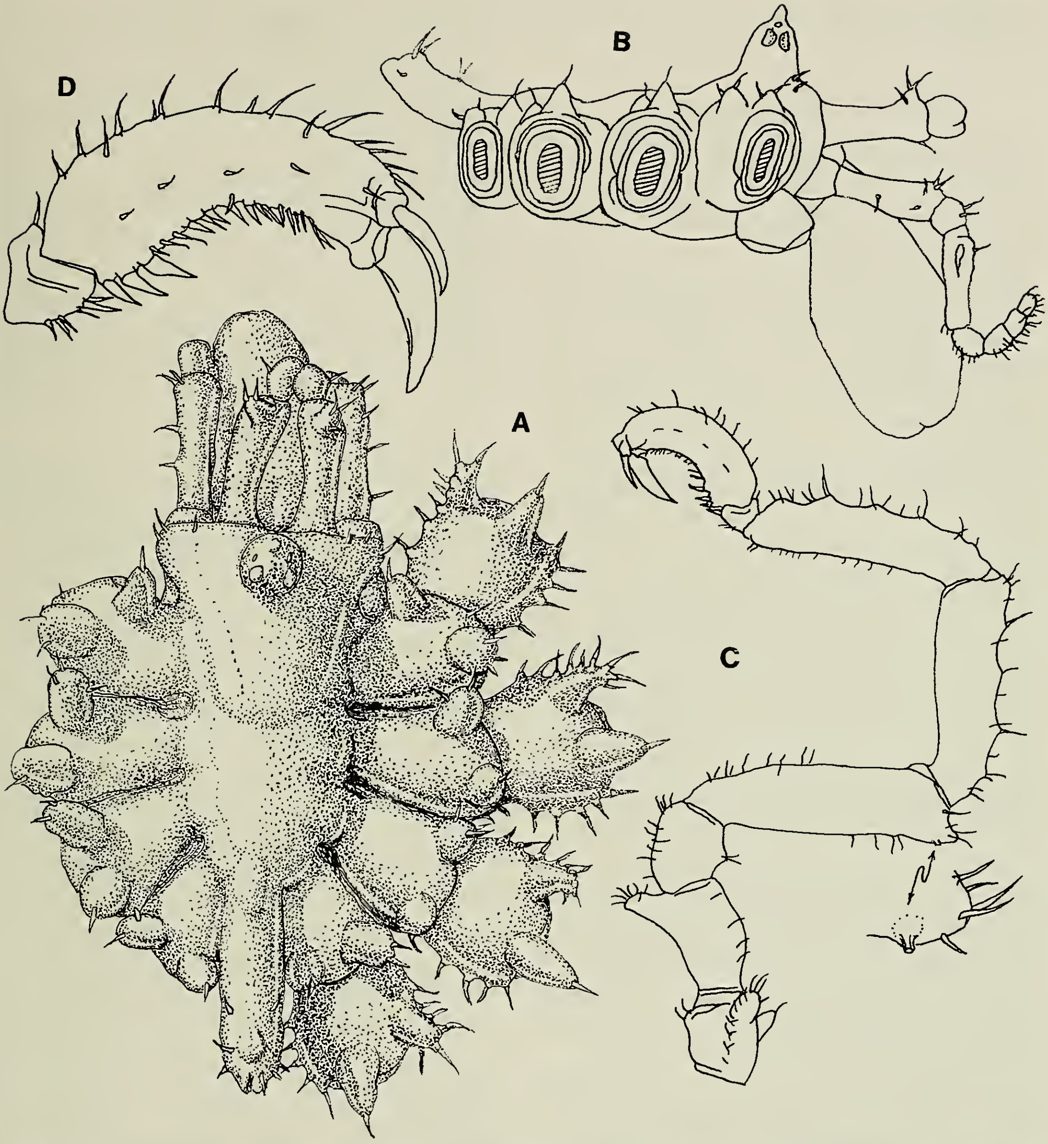

Fig. 3. *Achelia harrietae* Marcus, paratype male: A, trunk, dorsal view; B, trunk, lateral view; C, third leg, with enlargement of cement gland tube; D, distal leg segments, enlarged.

Remarks.—The whole specimen is slightly flattened with the ocular tubercle receiving most damage. One oviger is missing and a palp and leg are separated.

The specimen is closely related to *A. harrietae* Marcus, 1940 (Fig. 3 herein) which is very similar in most characters. Hilton's species differs from that of Marcus (Exline) in having ventrally serrate distal palp segments, and a shorter and wider proboscis. It has several segments which are shorter, including the scapes, and an ocular tubercle which is also placed more posterior on the cephalic segment. The second oviger segment is shorter, along with shorter major leg segments and second coxae ventral tubercles. The major difference, again, is in the distal palp segmentation with serrate lobes in Hilton's species. Most other differences are less evident.

Ammothella setosa Hilton

Ammothella setosa Hilton, 1942g:97.—Hedgpeth, 1964:206 [key], fig. 94i.
Ammothella killix Dojiri, Cadien & Phillips, 1991:31–41, figs. 1–5.

Material examined.—San Nicolas Island, off East Point, Channel Islands, California, coll. U.S. Fisheries Steamer *Albatross,* 532 m, sta. 4421, 12 Apr 1904 (1 ♀ holotype, USNM 79434, 1 ♂ paratype, USNM 124015).

Non-type specimens: Same station as type (10 ♂, 15 ♀, 2 juveniles, 10 larvae specimens, USNM 77074). Same station as type (2 ♀, USNM 128037).

Distribution.–This species has a very restricted known distribution; off San Nicolas Island in 366–532 m. That it was first described in 1942 and more specimens were not recorded until 1991 (as *A. killix*) suggests that very little collecting is done at these intermediate depths below 100 m.

Remarks.—The female type specimen is in good condition with several disjointed legs and a broken anterior trunk tubercle. The non-type specimens were deposited by Hilton sometime before he sent the type specimens for deposit, and are in excellent condition. They probably can not be classified as part of the type-lot.

The illustrations of male and female trunks and appendages in the Dojiri, Cadien, and Phillips report are among the finest to be found in any paper on pycnogonid systematics since the time when monographs were elaborately illustrated by professional artists in the last century. They will serve well to display all the mysteries of this species which Hilton never illustrated.

Tanystylum duospinum Hilton

Tanystylum duospinum Hilton, 1939a:33; 1942e:69.–Hedgpeth, 1941:255 [key]; 1964:209 [key], fig. 96b.
Tanystylum oculospinosum Hilton, 1942g: 70.–Child, 1979:34; 1992:23–24.—Stock, 1994:38 [complete literature].
Tanystylum tubirostre Stock, 1954:117–120, figs. 24, 25.
Tanystylum tubirostrum.—Stock, 1975: 984.–Child, 1979:34–35; 1982:363.
Tanystylum mexicanum Child, 1979:32–34, fig. 11.

Material examined.—"Central California Coast" in literature, but label in bottle has Pacific Grove [Monterey Bay], California (1 juvenile holotype, USNM 81531).

Distribution.—This species has had a spotty distribution, under its various names, around the Pacific rim and elsewhere. It is known from central California, Mexico, Ecuador, Peru, the Galapagos, and also in Australia, Papua New Guinea, Kenya, Indonesia, and the West Indies. It is a dweller of the shallows, from the intertidal to 37 m, and with little doubt it is circumtropical.

Remarks.—Hilton's *T. duospinum* has small differences in morphology from his type specimen of *T. oculospinosum.* The principal one is that the former species is described from a juvenile with only two heel spines, while adult specimens from the type locality have three heel spines. A number of specimens which were determined to be *T. duospinum* over the years by various specialists and deposited in the USNM collections all have three heel spines. Other differences between adults of the two species: the ocular tubercle of *T. duospinum* has an apical cone while the other species does not, and the oviger denticulate spines of *T. duospinum* have finely serrate edges over most of their length while those of his other species appear to have only distal serrations. There are several small differences in the legs of male specimens. In *T. duospinum,* the first coxae of the anterior pair of legs has three distal tubercles while the first coxae pair of *T. oculospinosum* lack the posterior tubercle. The dorsodistal bulge or tubercle carrying the cement gland tube is larger and longer in *T. duospinum,* and it has slightly shorter auxiliary claws than those of *T. oculospinosum.* In light of known interspecific variation in some members of this genus, the above small differences do not permit the two species to stand apart. The two agree in all other diagnostic characters. It is unfortunate that this often named species must resort to a misnomer for its earliest or senior epithet. Many of Hilton's names were simple but unimaginative and sometimes even in error as in this instance.

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Copepod taxonomy: Discovery vs. recognition

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Abstract.—A table of copepod orders, families, and type genera, with authors and dates, revealed a general marked delay between the discovery of a genus and the establishment of higher taxa based on that genus. The average time from genus definition to order definition was 51 yr. For families, this delay was 31 yr, with a range of 0 to 159 yr. Excluding the 54 families defined simultaneously with the discovery of their type genus, the average delay was 42 yr. The future trajectory of accumulating family definitions is discussed. The present dynamics of copepod taxonomy may require additional decades before a falling off of new orders and families can be predicted.

A recently published copepod classification (Bowman & Abele 1982), in contrast to many such summaries, indicated authors and dates for taxa down to family. Since that publication, other authors have made additions or alterations to this classification (Fosshagen & Iliffe 1985, 1989; Ho 1990, 1991; Kim 1991, Grygier 1994). A revised classification of the current 10 copepod orders and 205 families is given in Table 1; changes from the table of Bowman & Abele are indicated. It became of interest to plot the establishment of the listed families by decade (Fig. 1), as a representation of the historical awareness of copepods as a large, distinct group of Crustacea. What is apparent is a steady increase in defined families over 160 yr, with at least four periods of exceptionally rapid progress. These periods can be attributed mostly to James Dwight Dana (1840s and 1850s), to Wilhelm Giesbrecht (1890s), to Georg Ossian Sars (1900s and 1910s), and to several investigators since 1950. Besides an obvious expression of personal energy, the association of those periods with individuals reflects in part an ability to sample in or obtain material from a wide variety of new habitats. There is also a necessary time-lag, since in any era there had to be a reasonable background of described species against which the higher taxa could be discerned. [Note that an investigator could have defined nearly any and all of these higher taxa from literature, without once looking at a specimen—fortunately, this was not the case.]

A second relationship (Fig. 1) shows the establishment of the highest taxa within Copepoda, namely the eight orders into which the subclass was divided, as given by Bowman & Abele (1982), and two orders added in the subsequent decade (see Ho 1990). Again, this indicated a steady increase over the same long time. But was the establishment of these 10 orders, and their contained families as well, indicative of newly discovered fundamental copepod types, or were these higher taxa based on delayed recognition? Answering this question first for the copepod orders, it was seen that the genera upon which all 10 principal groups are based had been defined between 1776 and 1977, with 8 by 1891 and with 7 by 1865. The range of time between discovery of the genus and the recognition that it represented an entirely new major copepod division was 0 yr, for Siphonostomatoida, to 88 yr, for Mormonilloida. The average time from discovery of the genus to the definition of the order for which that genus is the type was 51 yr. That the earliest order, Cyclopoida, was defined in 1835 does not

Table 1.—Copepod classification to family, including type genera of families (modifications to Bowman & Abele (1982) indicated by *). The original date of a preoccupied and replaced genus name is indicated by PN.

*Subclass Copepoda Milne Edwards, 1830

- Order Calanoida Sars, 1903
  - Acartiidae Sars, 1903
    - *Acartia* Dana, 1846
  - Aetideidae Giesbrecht, 1892
    - *Aetideus* Brady, 1883
  - Arietellidae Sars, 1902
    - *Arietellus* Giesbrecht, 1892
  - Augaptilidae Sars, 1905
    - *Augaptilus* Giesbrecht, 1889
  - Bathypontiidae Brodsky, 1950
    - *Bathypontia* Sars, 1905
  - *Boholiniidae Fosshagen & Iliffe, 1989
    - *Boholina* Fosshagen, 1989
  - Calanidae Dana, 1849
    - *Calanus* Leach, 1816
  - Calocalanidae Bernard, 1958
    - *Calocalanus* Giesbrecht, 1888
  - Candaciidae Giesbrecht, 1892
    - *Candacia* Dana, 1846
  - Centropagidae Giesbrecht, 1892
    - *Centropages* Krøyer, 1849
  - Clausocalanidae Giesbrecht, 1892
    - *Clausocalanus* Giesbrecht, 1888
  - Diaixidae Sars, 1902
    - *Diaixis* Sars, 1902
  - Diaptomidae Baird, 1850
    - *Diaptomus* Westwood, 1836
  - Discoidae Gordejeva, 1975
    - *Disco* Grice & Hulsemann, 1965
  - Epacteriscidae Fosshagen, 1973
    - *Epacteriscus* Fosshagen, 1973
  - Eucalanidae Giesbrecht, 1892
    - *Eucalanus* Dana, 1852
  - Euchaetidae Giesbrecht, 1892
    - *Euchaeta* Philippi, 1843
  - Heterorhabdidae Sars, 1902
    - *Heterorhabdus* Giesbrecht, 1898 (PN 1863)
  - Lucicutiidae Sars, 1902
    - *Lucicutia* Giesbrecht, 1898 (PN 1863)
  - Mecynoceridae Andronov, 1973
    - *Mecynocera* I. C. Thompson, 1888
  - Megacalanidae Sewell, 1947
    - *Megacalanus* Wolfenden, 1904
  - Mesaiokeratidae Matthews, 1961
    - *Mesaiokeras* Matthews, 1961
  - Metridiidae Sars, 1902
    - *Metridia* Boeck, 1865
  - Paracalanidae Giesbrecht, 1892
    - *Paracalanus* Boeck, 1865
  - Parapontellidae Giesbrecht, 1892
    - *Parapontella* Brady, 1878
  - Phaennidae Sars, 1902
    - *Phaenna* Claus, 1863
  - Phyllopodidae Brodsky, 1950
    - *Phyllopus* Brady, 1883
  - Pontellidae Dana, 1853
    - *Pontella* Dana, 1846 (PN 1828)
  - Pseudocyclopidae Giesbrecht, 1893
    - *Pseudocyclops* Brady, 1872
  - Pseudocyclopiidae Sars, 1902
    - *Pseudocyclopia* T. Scott, 1892
  - Pseudodiaptomidae Sars, 1902
    - *Pseudodiaptomus* Herrick, 1884
  - Ridgewayiidae M. S. Wilson, 1958
    - *Ridgewayia* I. C. Thompson & A. Scott, 1903
  - Ryocalanidae Andronov, 1974
    - *Ryocalanus* Tanaka, 1956
  - Scolecithricidae Giesbrecht, 1892
    - *Scolecithrix* Brady, 1883
  - Spinocalanidae Vervoort, 1951
    - *Spinocalanus* Giesbrecht, 1888
  - Stephidae Sars, 1902
    - *Stephos* T. Scott, 1892
  - Sulcanidae Nicholls, 1945
    - *Sulcanus* Nicholls, 1945
  - Temoridae Giesbrecht, 1892
    - *Temora* Baird, 1850
  - Tharybidae Sars, 1902
    - *Tharybis* Sars, 1902
  - Tortanidae Sars, 1902
    - *Tortanus* Giesbrecht, 1898 (PN 1883)
- Order Harpacticoida Sars, 1903
  - Adenopleurellidae Huys, 1990
    - *Adenopleurella* Huys, 1990
  - Aegisthidae Giesbrecht, 1892
    - *Aegisthus* Giesbrecht, 1891
  - Ambunguipedidae Huys, 1990
    - *Ambunguipes* Huys, 1990
  - Ameiridae Monard, 1927
    - *Ameira* Boeck, 1865
  - Ancorabolidae Sars, 1909
    - *Ancorabolus* Norman, 1903
  - Balaenophilidae Sars, 1910
    - *Balaenophilus* P. O. Aurivillius, 1879
  - Cancrincolidae Fiers, 1990
    - *Cancrincola* C. B. Wilson, 1913
  - Canthocamptidae Sars, 1906
    - *Canthocamptus* Westwood, 1836
  - Canuellidae Lang, 1948
    - *Canuella* T. & A. Scott, 1893
  - Cerviniidae Sars, 1903
    - *Cervinia* Brady, 1878
  - Chappuisiidae Chappuis, 1940
    - *Chappuisius* Kiefer, 1938
  - Cletodidae T. Scott, 1904
    - *Cletodes* Brady, 1872

Table 1.—Continued.

*Subclass Copepoda Milne Edwards, 1830
Cristacoxidae Huys, 1990
Cristacoxa Huys, 1990
Cylindropsyllidae Sars, 1909
Cylindropsyllus Brady, 1880
Darcythompsoniidae Lang, 1936
Darcythompsonia T. Scott, 1906
Diosaccidae Sars, 1906
Diosaccus Boeck, 1872
Ectinosomatidae Sars, 1903
Ectinosoma Boeck, 1865
Hamondiidae Huys, 1990
Hamondia Huys, 1990
Harpacticidae Dana, 1846
Harpacticus Milne Edwards, 1840
Laophontidae T. Scott, 1904
Laophonte Philippi, 1840
Latremidae Bozic, 1969
Latremus Bozic, 1969
Longipediidae Sars, 1903
Longipedia Claus, 1863
Louriniidae Monard, 1927
Lourinia C. B. Wilson, 1924 (PN 1866)
Metidae Sars, 1910
Metis Philippi, 1843
Miraciidae Dana, 1846
Miracia Dana, 1846
Neobradyidae Olofsson, 1917
Neobradya T. Scott, 1892
Paramesochridae Lang, 1948
Paramesochra T. Scott, 1892
Parastenheliidae Lang, 1936
Parastenhelia I. C. Thompson & A. Scott, 1903
Parastenocaridae Chappuis, 1933
Parastenocaris Kessler, 1913
Peltidiidae Sars, 1904
Peltidium Philippi, 1839
Phyllognathopodidae Gurney, 1932
Phyllognathopus Mrazek, 1893
Porcellidiidae Sars, 1904
Porcellidium Claus, 1860 (PN 1840)
Pseudopeltidiidae Poppe, 1891
Clytemnestra Dana, 1848
Tachidiidae Sars, 1909
Tachidius Lilljeborg, 1853
Tegastidae Sars, 1904
Tegastes Norman, 1903
Tetragonicepsidae Lang, 1944
Tetragoniceps Brady, 1880
Thalestridae Sars, 1905
Thalestris Claus, 1863
Tisbidae Stebbing, 1910
Tisbe Lilljeborg. 1853
Order Cyclopoida Burmeister, 1835
Archinotodelphyidae Lang, 1949
Archinotodelphys Lang, 1949

Table 1.—Continued.

*Subclass Copepoda Milne Edwards, 1830
Ascidicolidae Thorell, 1859
Ascidicola Thorell, 1859
Botryllophillidae Sars, 1921
Botryllophilus Hesse, 1864
Buproridae Thorell, 1859
Buprorus Thorell, 1859
Cyclopidae Dana, 1853
Cyclops Muller, 1776
Cyclopinidae Sars, 1913
Cyclopina Claus, 1863
Doropygidae Brady, 1878
Doropygus Thorell, 1859
Enterocolidae Sars, 1921
Enterocola van Beneden, 1860
*Enteropsidae C. W. S. Aurivillius, 1885
Enteropsis C. W. S. Aurivillius, 1885
*Lernaeidae C. B. Wilson, 1917
Lernaea Linnaeus, 1758
*Mantridae Leigh-Sharpe, 1934
Mantra Leigh-Sharpe, 1934
Notodelphyidae Dana, 1853
Notodelphys Allman, 1847
Oithonidae Dana, 1853
Oithona Baird, 1843
Ozmanidae Ho & Thatcher, 1989
Ozmana Ho & Thatcher, 1989
*Phyllodicolidae Delamare-Deboutteville & Laubier, 1960
Phyllodicola Delamare-Deboutteville & Laubier, 1960
*Schizoproctidae C. W. S. Aurivillius, 1885
Schizoproctus C. W. S. Aurivillius, 1885
Speleoithonidae da Rocha & Iliffe, 1991
Speleoithona da Rocha & Iliffe, 1991
Order Poecilostomatoida Thorell, 1859
*Amazonicopeidae Thatcher, 1986
Amazonicopeus Thatcher, 1986
Anchimolgidae Humes & Boxshall, 1996
Anchimolgus Humes & Stock, 1972
Anomoclausiidae Gotto, 1964
Anomoclausia Gotto, 1964
Anomopsyllidae Sars, 1921
Anomopsyllus Sars, 1921
*Antheacheridae M. Sars, 1870
Antheacheres M. Sars, 1857
*Anthessiidae Humes, 1986
Anthessius Della Valle, 1880
*Bomolochidae Claus, 1875
Bomolochus von Nordmann, 1832
Catiniidae Bocquet & Stock, 1957
Catinia Bocquet & Stock, 1957
Chondracanthidae Milne Edwards, 1840
Chondracanthus Delaroche, 1811
Clausidiidae Embleton, 1901
Clausidium Kossmann, 1874

Table 1.—Continued.

*Subclass Copepoda Milne Edwards, 1830
Clausiidae Giesbrecht, 1895
Clausia Claparede, 1863
Corallovexiidae Stock, 1975
Corallovexia Stock, 1975
Corycaeidae Dana, 1852
Corycaeus Dana, 1845
Cucumaricolidae Bouligand & Delamare-Deboutteville, 1959
Cucumaricola Peterson, 1958
Echiurophilidae Delamare-Deboutteville & Nunes-Ruivo, 1955
Echiurophilus Delamare-Deboutteville & Nunes-Ruivo, 1955
*Entobiidae Ho, 1984
Entobius Dogiel, 1908
*Erebonasteridae Humes, 1987
Erebonaster Humes, 1987
*Ergasilidae Burmeister, 1835
Ergasilus von Nordmann, 1832
Eunicicolidae Sars, 1918
Eunicicola Kurz, 1877
Gastrodelphyidae List, 1889
Gastrodelphys Graeffe, 1883
*Herpyllobiidae Hansen, 1892
Herpyllobius Steenstrup & Lutken, 1861
Intramolgidae Marchenkov & Boxshall, 1995
Intramolgus Marchenkov & Boxshall, 1995
Kelleriidae Humes & Boxshall, 1996
Kelleria Gurney, 1927
Lichomolgidae Kossmann, 1877
Lichomolgus Thorell, 1859
Macrochirontidae Humes & Boxshall, 1996
Macrochiron Brady, 1872
*Mesoglicolidae de Zulueta, 1911
Mesoglicola Quidor, 1906
Myicolidae Yamaguti, 1936
Myicola Wright, 1885
Mytilicolidae Bocquet & Stock, 1957
Mytilicola Steuer, 1902
Nereicolidae Claus, 1875
Nereicola Keferstein, 1863
Nucellicolidae Lamb, Boxshall, Mill, & Grahame, 1996
Nucellicola Lamb, Boxshall, Mill, & Grahame, 1996
Octopicolidae Humes & Boxshall, 1996
Octopicola Humes, 1957
Oncaeidae Giesbrecht, 1892
Oncaea Philippi, 1843
*Paralubbockiidae Boxshall & Huys, 1990
Paralubbockia Boxshall, 1977
Pharodidae Illg, 1948
Pharodes C. B. Wilson, 1935
*Philichthyidae Vogt, 1877
Philichthys Steenstrup, 1862
Philoblennidae Izawa, 1976
Philoblenna Izawa, 1976
Pseudanthessiidae Humes & Stock, 1972
Pseudanthessius Claus, 1889
*Rhynchomolgidae Humes & Stock, 1972
Rhynchomolgus Humes & Ho, 1967
Sabelliphilidae Gurney, 1927
Sabelliphilus M. Sars, 1862
Sapphirinidae Thorell, 1859
Sapphirina J. V. Thompson, 1829
Serpulidicolidae Stock, 1979
Serpulidicola Southward, 1964
Shiinoidae Cressey, 1975
Shiinoa Kabata, 1968
*Spiophanicolidae Ho, 1984
Spiophanicola Ho, 1984
Splanchnotrophidae Norman & T. Scott, 1906
Splanchnotrophus Hancock & Norman, 1863
Synapticolidae Humes & Boxshall, 1996
Synapticola Voigt, 1892
Synaptiphilidae Bocquet & Stock, 1957
Synaptiphilus Canu & Cuenot, 1892
Taeniacanthidae C. B. Wilson, 1911
Taeniacanthus Sumpf, 1871
*Tegobomolochidae Avdeev, 1978
Tegobomolochus Izawa, 1976
Telsidae Ho, 1967
Telson Pearse, 1952
Thamnomolgidae Humes & Boxshall, 1996
Thamnomolgus Humes, 1969
Tuccidae Vervoort, 1962
Tucca Krøyer, 1837
Urocopiidae Humes & Stock, 1972
Urocopia Sars, 1917
Vahiniidae Humes, 1967
Vahinius Humes, 1967
*Vaigamidae Thatcher & Robertson, 1984
Vaigamus Thatcher & Robertson, 1984
Xarifiidae Humes, 1960
Xarifia Humes, 1960
Order Siphonostomatoida Thorell, 1859
Artotrogidae Brady, 1880
Artotrogus Boeck, 1859
Ascomyzontidae Thorell, 1859
Ascomyzon Thorell, 1859
Asterocheridae Giesbrecht, 1899
Asterocheres Boeck, 1859
Brychiopontiidae Humes, 1974
Brychiopontius Humes, 1974
Caligidae Burmeister, 1835
Caligus Muller, 1785
*Calverocheridae Stock, 1968
Calverocheres C. B. Wilson, 1932 (PN 1902)
Cancerillidae Giesbrecht, 1897
Cancerilla Dalyell, 1851

Table 1.—Continued.

*Subclass Copepoda Milne Edwards, 1830
Catlaphilidae Tripathi, 1960
Catlaphila Tripathi, 1960
Cecropidae Dana, 1852
Cecrops Leach, 1816
Choniostomatidae Hansen, 1887
Choniostoma Hansen, 1887
Chordeumiidae Boxshall, 1988
Chordeumium Stephensen, 1918
Coralliomyzontidae Humes & Stock, 1991
Coralliomyzon Humes & Stock, 1991
*Dichelesthiidae Milne Edwards, 1840
Dichelesthium Hermann, 1804
Dinopontiidae Murnane, 1967
Dinopontius Stock, 1960
Dirivultidae Humes & Dojiri, 1980
Dirivultus Humes & Dojiri, 1980
Dissonidae Yamaguti, 1963
Dissonus C. B. Wilson, 1906
Dyspontiidae Giesbrecht, 1895
Dyspontius Thorell, 1859
Ecbathyriontidae Humes, 1987
Ecbathyrion Humes, 1987
Entomolepidae Brady, 1899
Entomolepis Brady, 1899
*Eudactylinidae C. B. Wilson, 1932
Eudactylina van Beneden, 1853
Euryphoridae C. B. Wilson, 1905
Euryphorus Milne Edwards, 1840
Hatschekiidae Kabata, 1979
Hatschekia Poche, 1902
Hyponeoidae Heegaard, 1962
Hyponeo Heegaard, 1962
Kroyeriidae Kabata, 1979
Kroyeria van Beneden, 1853
*Lamippidae Joliet, 1882
Lamippe Bruzelius, 1858
Lernaeoceridae Gurney, 1933
Lernaeocera de Blainville, 1822
*Lernaeopodidae Milne Edwards, 1840
Lernaeopoda de Blainville, 1822
Lernanthropidae Kabata, 1979
Lernanthropus de Blainville, 1822
Megapontiidae Heptner, 1968
Megapontius Hulsemann, 1965
Micropontiidae Gooding, 1957
Micropontius Gooding, 1957
Myzopontiidae Sars, 1915
Myzopontius Giesbrecht, 1895
Nanaspididae Humes & Cressey, 1959
Nanaspis Humes & Cressey, 1959
Naobranchiidae Yamaguti, 1939
Naobranchia Hesse, 1863
Nicothoidae Dana, 1852
Nicothoe Audouin & Milne Edwards, 1826
Pandaridae Milne Edwards, 1840
Pandarus Leach, 1816
Pennellidae Burmeister, 1835
Pennella Oken, 1816
Pontoeciellidae Giesbrecht, 1895
Pontoeciella Giesbrecht, 1895
Pseudocycnidae C. B. Wilson, 1922
Pseudocycnus Heller, 1865
Rataniidae Giesbrecht, 1897
Ratania Giesbrecht, 1892
Saccopsidae Lutzen, 1964
Saccopsis Levinsen, 1878
*Sphyriidae C. B. Wilson, 1919
Sphyrion Cuvier, 1830
Spongiocnizontidae Stock & Kleeton, 1964
Spongiocnizon Stock & Kleeton, 1964
Stellicomitidae Humes & Cressey, 1958
Stellicomes Humes & Cressey, 1958
Tanypleuridae Kabata, 1969
Tanypleurus Steenstrup & Lutken, 1861
*Trebiidae C. B. Wilson, 1905
Trebius Krøyer, 1838
Ventriculinidae Leigh-Sharpe, 1934
Ventriculina Bassett-Smith, 1903
Xenocoelomatidae Bresciani & Lutzen, 1966
Xenocoeloma Caullery & Mesnil, 1915
Order Monstrilloida Sars, 1903
*Monstrillidae Dana, 1849
Monstrilla Dana, 1849
*Order Misophrioida Gurney, 1927
Misophriidae Brady, 1878
Misophria Boeck, 1865
Order Mormonilloida Boxshall, 1979
Mormonillidae Giesbrecht, 1892
Mormonilla Giesbrecht, 1891
*Order Platycopioida Fosshagen, 1985
Platycopiidae Sars, 1911
Platycopia Sars, 1911
*Order Gelyelloida Huys, 1988
Gelyellidae Rouch & Lescher-Moutoue, 1977
Gelyella Rouch & Lescher-Moutoue, 1977
Order uncertain
Chitonophilidae Avdeev & Sirenko, 1991
Chitonophilus Avdeev & Sirenko, 1991
Sponginticolidae Topsent, 1928
Sponginticola Topsent, 1928
Staurosomatidae de Zulueta, 1911
Staurosoma Will, 1844

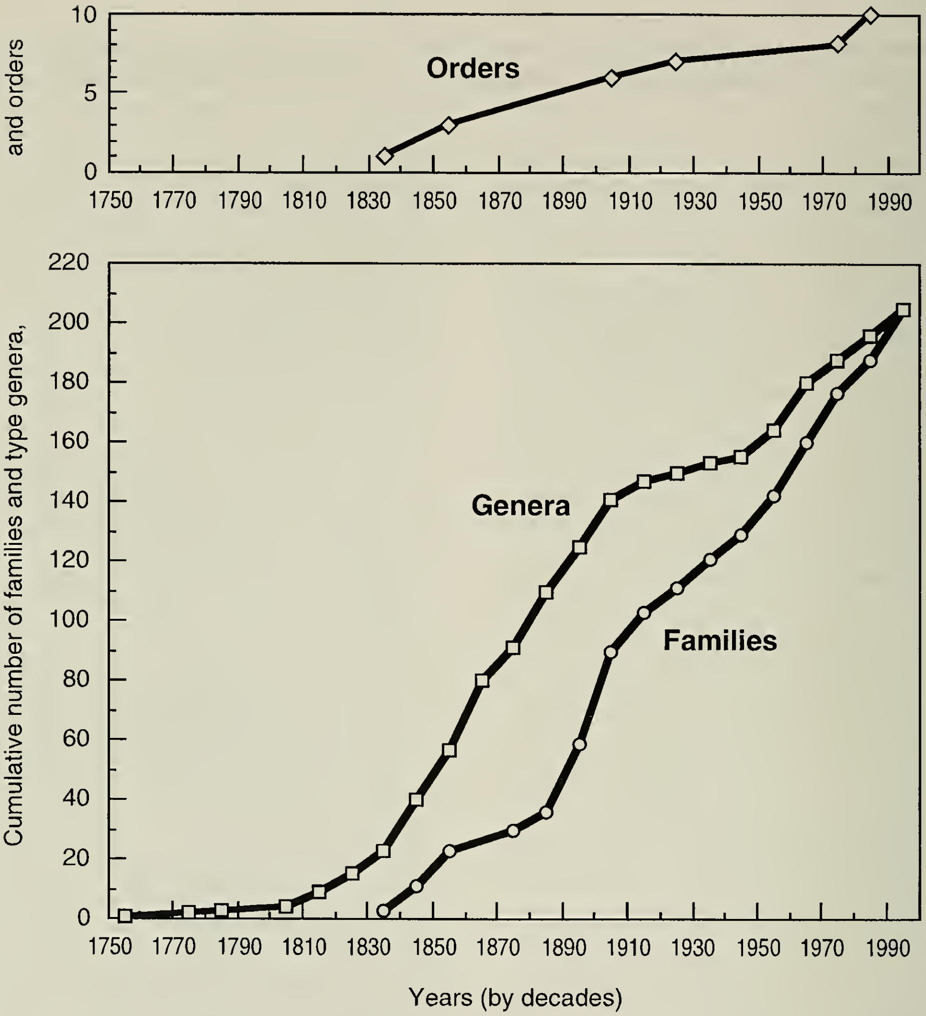

Fig. 1. Cumulative number of defined families, type genera, and orders of copepods, by decade, from 1750 to 1996.

mean that there were no other order-level taxa at that time, but that the other analogous groups have fallen out of favor in the meantime.

This prompted a similar approach toward the families: were they indicative of newly discovered family-level Copepoda, or were they mostly the result of deliberative comparison of accumulating genus descriptions? This was not so easily answered; a foray into the literature spread across the whole of Copepoda to determine the type-genus (and date) for each family was not trivial. This is also a dynamic process, and undoubtedly alterations and additions are now occurring. In fact, seven families were described in 1996 after the first draft was completed. As with Bowman & Abele, I do not provide references for the indicated authors; this would be beyond the intention of the survey. Some type genera are dated from the time a new name was proposed to replace a preoccupied name; in these cases I have used the older date for the calculations, since the discovery was based on the earlier date; these extended dates are indicated in Table 1.

A third relationship (Fig. 1) shows the time-dependency of the descriptions of what became type-genera for families. The indication, when comparing the family and type-genus curves, is that copepodologists are in general a conservative company. Over the preceding 160 yr, 54 families (26%) were proposed at the time that the type genus was described. (These "instant" families arose between 1846 and 1996, with the median year of 1963; that is, the phenomenon is skewed to recent years, as one might expect given the accumulated background of defined families.) Another way to look at this is that most of the fundamental (family) copepod types were discovered long before they were recognized as such. Overall, the average delay time was 31 yr, with a range of 0 to 159 yr. Excluding the families that were defined at the time the type genus was described, the average delay time for family definition was 42 yr. If the type species, rather than the type genus, is considered, the dates would be set back even farther in some cases, although probably not significantly so.

Note that 10 genera would define the present 10 orders, just as the 205 type genera basically define the 205 families. All the many other genera are superfluous, except, of course, that they define the *limits* of higher taxa already defined in their essentials.

Can we use the curves to make predictions? The type-genus curve cannot be predictive, mainly because it does not exist until families are defined; a predictive genus curve would have to include the many more genera besides type genera. The genus curve should not be compared within decades to the family curve; the only comparison should be horizontal, reflecting the time lags. Since families must await the discovery of their type genera, there will always, in general, be a lag time. Recently discovered genera that become type genera force the two curves to converge, since there is obviously not much time available for a newly discovered genus to have become the type of a new family. Future association of the two curves depends on whether families are made from recently described genera (the curves will remain together) or from older genera (the curves will again separate). The availability of large numbers of well-defined families potentially makes it easier to discern new families with the discovery of new genera or with reconsideration of older genera. Clearly, a trend to be avoided would be the creation of a new family from each genus, thereby defeating the notion of a classification hierarchy.

There is no trend suggesting that families might not be defined at the previous rate, or that we are running out of new families. Of course, as new habitats are explored, such as caves and deep-ocean thermal vents, new genera representing new families would be expected. Given the present dynamics of copepod taxonomy, predictions may require a few more decades of observation.

Even without the discovery of absolutely new types, taxa above genera will be added as more details, especially of developmental biology, are added to the framework in place and more comparisons are made. Copepod taxonomy has long been vexed by many imperfectly described species, and a re-working of these will add some surprises. Also, there are some copepod families that cannot now be placed into the defined orders; there are also many genera that are not yet assigned to families. These may be raw material for additional higher taxa, or the discovery of intermediate species may link them to established groups. There is a wealth of material to contemplate, with future intensive rearranging. However, eventually there will be no more orders and no more families to discover.

For those who are depressed by this prospect, and fear coming idleness, there is an infinitude of related research to be done. I offer the insight of Herman Melville (1851): "Dissect him how I may, then, I but go skin deep; I know him not, and never will."—Moby Dick, Chapter 86.

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The freshwater crab fauna (Crustacea: Decapoda: Brachyura) of the Philippines. IV. On a collection of Parathelphusidae from Bohol

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Abstract.—Five species of freshwater crabs of the genus *Sundathelphusa* are recognised from the island of Bohol in the Philippines: *S. cavernicola* (Takeda, 1983), and four new species, *S. boex, S. sottoae, S. urichi* and *S. vedeniki.* Specimens from Bohol previously referred to *S. philippina* (von Martens, 1868) belong to *S. boex,* and those identified as *S. cavernicola* belong to two separate species.

The freshwater crab fauna of the Philippines is one of exceptional diversity, although this is not apparent from the number of described species. In recent years, Ng & Takeda (1992a, 1992b, 1993a, 1993b) have been involved in a systematic revision of this fauna based on extensive collections made by staff of the National Science Museum (Tokyo) and the National Museum of the Philippines (Manila). The revision of the two largest genera, *Sundathelphusa* Bott, 1969, and *Archipelothelphusa* Bott, 1969, is now in progress.

In February 1995, the Slovene Caving Association launched two caving expeditions to Asia: to Guizhou, China (Trontelj 1996, Ng & Trontelj 1996), and the Philippines (Sket 1995). Altogether, the expedition team investigated about 30 caves in Pleistocene to Miocene aged limestone. The Philippine island of Bohol in particular, harbours one of the largest continuous karst areas in the Philippine archipelago (Balasz 1973), and because of this, exploration efforts were centered there. Studies of the collections made show that Bohol has a rich freshwater crab fauna.

Few cavernicolous crabs are known from the Philippines. Takeda (1983) described a new troglobitic species, *Archipelothelphusa cavernicola,* from caves in Bohol, and Ng (1991) reported *Archipelothelphusa longipes* Balss, 1937, from Bautakay Cave in Luzon. A total of four species of freshwater crabs of the family Parathelphusidae were collected by the present expedition. All are undescribed. Of these, three are apparently troglobitic species while one epigeal species makes occasional forays into caves.

Only two true freshwater species have been reported from Bohol thus far, *Sundathelphusa philippina* (von Martens, 1868) and *Archipelothelphusa cavernicola* Takeda, 1983 (Bott 1970, Takeda 1983). Previous collections, however, are rather poor, so the discovery of new taxa is not unexpected.

In view of the good series of specimens available from Bohol, the homogeneity nature of the fauna (all the species seem to be more closely related to each other than to others in the Philippines) and the cavernicolous habits of the species, it was felt that it would be useful to document this fauna in a single paper.

The generic system used by Bott (1969, 1970) for the Southeast Asian fauna is problematic. *Sundathelphusa* Bott, 1969, and *Archipelothelphusa* Bott, 1969, are so close that there seems to be no good reason for separating them. As both *Sundathelphusa* and *Archipelothelphusa* were described in the same paper (Bott, 1969), *Sundathelphusa* Bott, 1969, is herein regarded as having seniority over *Archipelothelphusa* Bott, 1969. In any case, the name *Sundathelphusa* Bott, 1969, appears before *Archipelothelphusa* Bott, 1969, in Bott's (1969) paper.

The abbreviations G1 and G2 are used for the male first and second pleopods respectively. All measurements are indicated as carapace width x carapace length. The terminology used follows that by Ng (1988). Specimens are deposited in the National Museum of the Philippines, Manila (NMCR); National Science Museum, Tokyo (NSMT); Department of Biology, University of Ljubljana (ULB); and Zoological Reference Collection, School of Biology, National University of Singapore (ZRC).

Systematic Account

Family Parathelphusidae Alcock, 1910

Genus *Sundathelphusa* Bott, 1969

Sundathelphusa boex, new species

Figs. 1A, 2a–f, 4a–f

? *Telphusa leschenaulti.*—Bürger, 1894:2 (part) (not *Thelpheusa leschenaudii* H. Milne Edwards, 1834, misspelling by Bürger, 1894).

Material examined.—Holotype male (37.4 × 30.9 mm) (NMCR), small stream near Sierra Bulliones, about 9°42′N, 124°20′E, about 5 km northwest of Jagna, Bohol, leg. H. Morioka, 22 Jul 1985. Paratype male (34.2 × 27.8 mm), paratype female (almost mature) (26.8 × 22.4 mm) (ZRC 1996.1550–1551), Castigio Cave, Batuan, Bohol, leg. B. Sket, Feb 1995. Paratype male (41.0 × 33.0 mm) (ZRC 1996.1549), Batuan, Bohol, leg. B. Sket, Feb 1995. 1 male (NMCR), 1 male (ULB), 1 male (NMCR), brook, Pahangong Talon, Ginguyuran, Bohol, leg. B. Sket, Feb 1995. 1 male (34.6 × 28.8 mm) (NMCR), spring in Batuan, Bohol, leg. B. Sket, Feb 1995. 1 juvenile (NMCR), Capiro Spring, Batuan, Bohol, leg. B. Sket, Feb 1995. 1 young male (10.2 by 8.7 mm) (ULB), Carmulaon, lower part, Cugon, Jagna, Bohol, leg. B. Sket, Feb 1995.

Description.—Dorsal surface of carapace gently convex; anterolateral regions rugose; posterolateral regions covered with oblique striae; cervical grooves deep; epigastric cristae low, rugose, not confluent with low postorbital cristae; postorbital cristae interrupted medially by cervical groove, not reaching epibranchial tooth. Frontal median triangle well defined, with dorsal and lateral margins cristate; dorsal ridge not fused with lateral margins. Anterolateral margin distinctly convex, smooth; epibranchial tooth low to very low, separated from external orbital angle by small notch; posterolateral margins gently converging towards posterior carapace margin. Ocular peduncle and cornea well developed; eye occupying almost entire orbit. Carpus of chelipeds with surface smooth; inner margin with 1 large sublamelliform tooth and 1 smaller tooth. Ambulatory legs relatively short; meri of third and fourth legs about 2.7 times longer than broad; dactylus of third and fourth legs subequal or shorter than propodus. Male abdomen with slender segment 6, about 1.1 times longer than broad. G1 slender, gently curved outwards; terminal segment slender, conical, about 0.4 times length of subterminal segment. G2 about 1.0 times length of G1; distal segment well developed, about 0.5 times length of basal segment.

Discussion.—Bürger (1894) reported a large 50 × 41 mm female from Bohol as *Telphusa leschenaulti,* but his specimen is most likely *S. boex* instead. *Telpheusa leschenaudii* H. Milne Edwards, 1834 (type locality Pondicherry, India) (spelling of genus name erroneous) is now regarded as a junior synonym of *Oziothelphusa senex* (Fabricius, 1798) (see Bott 1970:100). The specific epithet of *T. leschenaudii* is often spelled "leschenaulti" (changed by H. Milne Edwards, 1853) but under current rules (ICZN 1985), the original spelling must be preserved.

Sundathelphusa philippina (von Martens, 1868) somewhat resembles *S. boex,* but *S.*

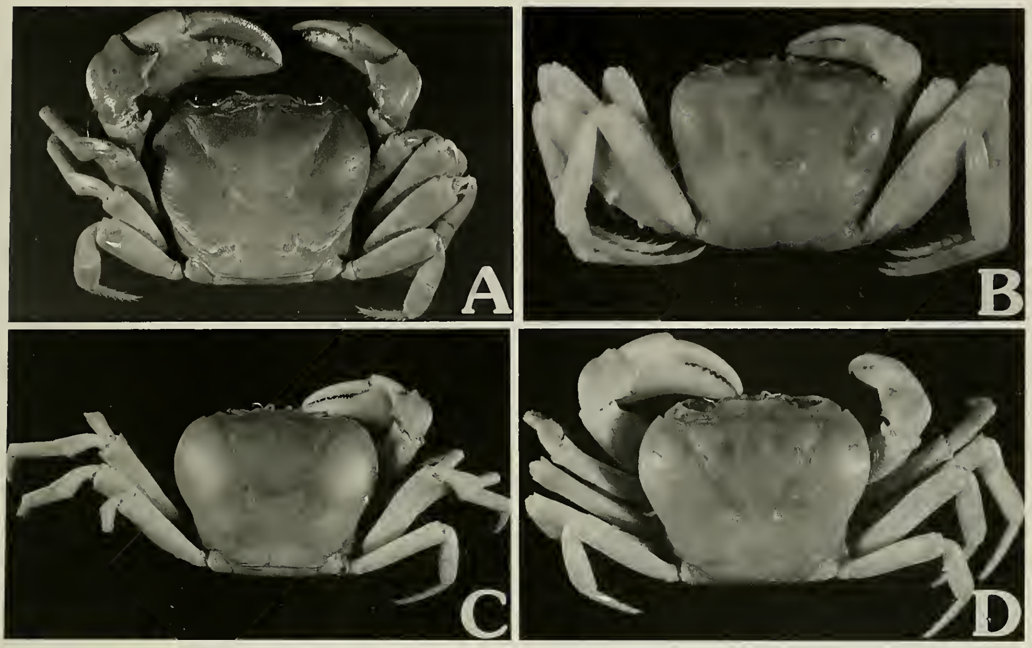

Fig. 1. Dorsal views of new *Sundathelphusa* species. A, *S. boex,* holotype male (37.4 × 30.9 mm) (NMCR); B, *S. sottoae,* holotype male (17.3 × 13.4 mm) (NSMT-Cr 8938); C, *S. urichi,* holotype male (36.6 × 27.9 mm) (NMCR); D, *S. vedeniki,* holotype male (28.2 by 22.3 mm) (NMCR).

philippina differs markedly in having a more inflated and proportionately broader carapace, as well as the differently structured anterolateral margin and G1. The first author has examined the types of *Sundathelphusa philippina* in the Berlin Museum. *Sundathelphusa philippina* is known for certain only from the islands of Leyte, Cebu and Samar (PKLN, pers. obs.).

Sundathelphusa boex was found in surface waters as well as in caves. Both caves where the crabs were found are rich in organic nutrients. Castigio Cave is inside a mogote ("chocolate hill") and has a very high amount of plant debris. Carmulaon Cave is a vertical cave receiving waters from nearby rice fields. All specimens are usually pigmented. The eyestalks of adults are subequally thick both distally and proximally, while in juveniles the distal part is proportionately broader.

Etymology.—The species name is derived from the acronym B.O.E.X. (Bohol Outdoor Explorers Club), whose members acted as the Philippine component of the expedition. The name is used here as a noun in apposition.

Sundathelphusa cavernicola
(Takeda, 1983)
Fig. 4g

Archipelothelphusa cavernicola Takeda, 1983:169 (part).

Material examined.—Holotype female (25.7 × 21.0 mm) (NSMT-Cr 8937), muddy bottom on subterranean stream, 20–30 cm deep, about 300 m from entrance to east branch of Quinapon-an Cave, Antequera, 09°49′38″N, 123°54′10″E, Bohol, leg. S. I. Ueno, 4 Mar 1983.

Description.—Dorsal surface of carapace gently convex; anterolateral regions gently rugose; posterolateral regions covered with oblique striae; cervical grooves distinct but relatively shallow; epigastric cristae low, rugose, not confluent with low postorbital cristae; postorbital cristae interrupted medially by cervical groove, not reaching epibranchial tooth. Frontal median triangle poorly defined; lateral margins cristate, dorsal margin not cristate or meeting lateral margins. Anterolateral margin distinctly convex, smooth; epibranchial tooth distinct, separated from external orbital angle by distinct notch; posterolateral margins gently converging towards posterior carapace margin. Ocular peduncle reduced, cornea strongly reduced; eye occupying about half of orbit. Surface of chelipedal carpus rugose; inner margin with one large sublamelliform tooth and one denticle. Ambulatory legs relatively long; meri of third and fourth legs about 5.2 and 3.8 times longer than broad respectively; dactylus of third and fourth legs distinctly longer than propodus. Male abdomen, G1 and G2 not known.

Discussion.—This species is here transferred to *Sundathelphusa* in line with our proposed synonymy of *Archipelothelphusa* and *Sundathelphusa.* Takeda (1983) described this species from one large female and one small male from different caves in Bohol. The holotype female possesses strongly reduced eyes, the cornea being highly degenerated. The paratype male, however, possessed a larger cornea and more developed eyes. Takeda (pers. comm.) has also expressed doubts as to the conspecificity of the two specimens. The localities where the two types were collected (Quinapon-an and Ughob Caves) are on different parts of the island.

The good series of specimens from the Batuan area (where Ughob Cave is located) confirms the suspicion that the specimens which have been previously referred to "*Archipelothelphusa cavernicola*" (fide Takeda, 1983) actually belong to two distinct species, easily separated by the degree of degeneration of the eyes and cornea, as well as proportions of the third ambulatory merus. One species, *S. cavernicola,* is represented only by a single female specimen (the holotype) whilst the others (including the paratype male of *A. cavernicola*) is referred to *S. sottoae,* new species (see *Discussion* for *S. sottoae*). Unfortunately, no males of *S. cavernicola* are known.

Sundathelphusa sottoae,
new species

Figs. 1B, 2g–k, 4h–l

Archipelothelphusa cavernicola Takeda, 1983:169 (part).

Material examined.—Holotype male (17.3 × 13.4 mm) (NSMT-Cr 8938), in shallow subterranean water, about 50 m from entrance to Ughob Cave, about 2 km southwest of Batuan, 09°46′45″N, 124° 07′54″E, Bohol, leg. S. I. Ueno, 28 Feb 1983. Paratype female (26.0 × 21.0 mm) (ZRC 1996.1553), Bonugan, Batuan, Bohol, leg. B. Sket, Feb 1995. Paratype female (28.0 × 25.0 mm) (NMCR), upper part of cave, Bonugan Cave, Batuan, Bohol, leg. B. Sket, Feb 1995. 1 male (14.8 × 12.5 mm) (ULB), Kalumpan, Behind-the-Clouds, Batuan, Bohol, leg. B. Sket, Feb 1995. 1 male (17.4 × 13.8 mm) (ZRC 1996.1548), open well, Batuan, Bohol, leg. B. Sket, Feb 1995.

Description.—Dorsal surface of carapace gently convex; anterolateral regions gently rugose; posterolateral regions covered with oblique striae; cervical grooves distinct but relatively shallow; epigastric cristae low, rugose, barely confluent with low postorbital cristae; postorbital cristae interrupted medially by cervical groove, not reaching epibranchial tooth. Frontal median triangle poorly defined; lateral margins cristate, dorsal margin not cristate and not meeting lateral margins. Anterolateral margin distinctly convex, smooth; epibranchial tooth distinct, separated from external orbital angle by distinct notch; posterolateral margins gently converging towards posterior carapace margin. Ocular peduncle and cornea reduced; eye occupying about ⅔ of orbit. Surface of chelipedal carpus rugose; inner margin with 1 large sublamelliform tooth and one denticle. Ambulatory legs relatively long; meri of third and fourth legs 3.4–3.5 and 3.4–3.6 times longer than broad respectively; dactylus of third and fourth legs distinctly longer than propodus. Male abdomen with segment 6 about 1.1 times longer than broad. G1 slender, gently curved outwards; terminal segment slender, distal part especially slim, about 0.3 times length of subterminal segment. G2 about 1.1 times length of G1; distal segment well developed, about 0.5 times length of basal segment.

Discussion.—Sundathelphusa sottoae, new species, is very similar to *S. cavernicola,* both species sharing a high carapace in which the anterolateral margins are gently convex, lateral regions have distinct striae, reduced eyes, as well as elongate ambulatory dactyli. They differ, however, markedly in the condition of the eyes, which in *S. cavernicola* are far more reduced than those in *S. sottoae.* Also distinct are the proportions of the ambulatory legs, with the meri of *S. cavernicola* relatively longer, especially that of the third ambulatory leg (length/width ratio = 5.2 and 3.4–3.5 respectively).

In his description of *S. cavernicola,* Takeda (1983: 172) stated that the paratype male of *S. cavernicola* agrees "... with the holotype female in the general formation of the carapace, chelipeds and ambulatory legs, but the cornea is not as strongly reduced and the eyestalk is slightly movable and occupies about two-thirds the longer axis of the orbit. ..." Our specimens from the Batuan area, where the paratype male of *S. cavernicola* was collected, has allowed us to ascertain that Takeda's paratype male actually represents *S. sottoae,* and is here chosen as the holotype for this new species.

Two of the larger females from Bonugan Cave (ZRC, NMCR) agree very well with the holotype male for *S. sottoae* and confirms the usefulness of the diagnostic characters used to separate this species from *S. cavernicola.* The identities of the two smaller males (14.8 × 12.5 mm, ULB, and 17.4 × 13.8 mm, ZRC) from Kalumpan and Batuan respectively are more difficult to determine. In general carapace and leg morphology, the Kalumpan and Batuan specimens agree best with the holotype male of *S. sottoae.* They nevertheless differ in having the eye occupying more of the orbit (0.74–0.75 vs. 0.63–0.66), the cornea is proportionately larger (relative to the whole eye) (0.35–0.37 vs. 0.25–0.31), the tooth on the inner angle of the chelipedal carpus proportionately shorter, the length of the last ambulatory dactylus being about 7.1 times longer than the maximum width (excluding spines) (vs. about 10 times), and the median part of the subterminal segment of the G1 being more slender, with the tip of the terminal segment gently but distinctly upturned (vs. straight). These differences suggest the possibility that these specimens represent two species. However, until larger specimens from Batuan and Kalumpan are collected, this cannot be ascertained.

Sundathelphusa sottoae was found in a number of rather diverse habitats, all in the Batuan region in the center of Bohol. Pigmented specimens originate from a surface spring pool. The specimen (male, 17.4 × 13.8 mm, ZRC) from a garden well in the middle of Batuan is pale, while those from within caves (Ughob, Bonugan and Kalumpan: NSMT-Cr 8938, ZRC, NMCR, ULB) are poorly pigmented. Bonugan Cave is one of a chain of caves along the same brook. The substrate of this stream is only moderately enriched with organic matter and the surface fauna (including Anura) is present only near the entrances. In Kalumpan, the crab was found among stones in an illuminated siphon pool which had no direct connection with any surface stream.

Etymology.—The species is named after Prof. Dr. Filipina Sotto of the Marine Biology section at the University of San Carlos, Cebu City, whose help with logistics contributed substantially to the successful expedition.

Sundathelphusa urichi, new species

Figs. 1C, 3a–f, 4m–p

Material examined.—Holotype male (36.6 × 27.9 mm) (NMCR), Quilas Cave, Nueva Vida Norte, Batuan, Bohol, leg. B. Sket, Feb 1995. Paratype male, paratype female (ULB), 2 paratype males (28.0 × 20.0 mm [crushed], 21.6 × 15.5 mm), paratype female (32.6 × 25.0 mm) (ZRC 1996. 1554–1556), same data as holotype. 1 juvenile (NMCR), Quilas Cave, Nueva Vida Norte, Batuan, Bohol, leg. B. Sket, Feb 1995.

Description.—Dorsal surface of carapace strongly convex; anterolateral regions smooth; posterolateral regions with very low oblique striae; cervical grooves deep; epigastric cristae very low, rugose, not confluent with very low postorbital cristae; postorbital cristae interrupted medially by cervical groove, not reaching epibranchial tooth. Frontal median triangle poorly defined; lateral margins cristate, dorsal margin not cristate or meeting lateral margins. Anterolateral margin strongly convex, smooth; epibranchial tooth very low, separated from external orbital angle by faint but distinct notch; posterolateral margins strongly converging towards posterior carapace margin. Ocular peduncle and cornea slightly reduced; eye occupying about 3/4 of orbit. Surface of chelipedal carpus smooth; inner margin with 1 large sublamelliform tooth and 1 denticle. Ambulatory legs relatively long; meri of third and fourth legs about 3.7 and 3.5 times longer than broad respectively; dactylus of third leg subequal to length of propodus; dactylus of fourth leg longer than propodus. Male abdomen with slender segment 6, medially constricted, about 1.2 times longer than broad. G1 slender, gently curved outwards; terminal segment slender, conical, about 0.4 times length of subterminal segment. G2 about 1.2 times length of G1; distal segment well developed, about 0.4 times length of basal segment.

Discussion.—Sundathelphusa urichi, new species, differs markedly from *S. sottoae,* new species (which occurs in the same area) in having distinctly proportionately shorter and more falcate ambulatory dactyli (straighter in *S. sottoae*), a distinctly more swollen carapace and more convex anterolateral margins. In physiognomy, *S. urichi* is closer to *S. vedeniki,* but the carapace of *S. urichi* is distinctly more swollen than *S. vedeniki.*

Sundathelphusa urichi was found only in Quilas Cave, which is in the central plateau east of Batuan. The cave is part of a long chain of chambers with large pools. They do not seem to be connected directly to any permanent surface stream but rather, are fed diffusely or by periodical inputs from the surface. However, the presence of pigmented catfish (Clariidae: *Clarias* sp.) in the cave suggests that a hidden connection to surface waters might exist. The rich organic matter present, mostly detritus from the surface, supports a rich population of shrimps (Decapoda: Atyidae), with amphipods (*Eriopisa* sp.) being less numerous. Many specimens of this amphibious crab were observed.

Etymology.—The present species honours Dr. Peter Urich, a "caver" and sociogeographer, now at the Waikato University, New Zealand. An expert on Boholano society and nature, he efficiently took care of the expedition group.

Sundathelphusa vedeniki,
new species

Figs. 1D, 3g–l, 4q, r

Material examined.—Holotype male (28.2 × 22.3 mm) (NMCR), Boho sa Bikahan, Bikahan, Antequera, Bohol, leg. B. Sket, Feb 1995. Paratype male (33.9 × 26.5 mm) (ZRC 1996.1552), same data as holotype.

Description.—Dorsal surface of carapace distinctly convex; anterolateral regions rugose; posterolateral regions with distinct oblique striae; cervical grooves deep; epigastric cristae low, rugose, not confluent with low postorbital cristae; postorbital cristae interrupted medially by cervical groove, not reaching epibranchial tooth. Frontal median triangle not well defined; lateral margins cristate, dorsal margin weakly cristate and not meeting lateral margins. Anterolateral margin distinctly convex, smooth; epibranchial tooth well developed to low, separated from external orbital angle by distinct notch; posterolateral margins strongly converging towards posterior carapace margin. Ocular peduncle and cornea slightly reduced; eye occupying about ¾ of orbit. Surface of chelipedal carpus smooth; inner margin with 1 large sublamelliform tooth and 1 denticle. Ambulatory legs relatively short; meri of third and fourth legs about 3.2 and 3.0 times longer than broad respectively; dactylus of third and fourth legs subequal to length of propodus. Male abdomen with rectangular segment 6, about 1.1 times longer than broad. G1 slender, gently curved outwards; terminal segment slender, conical, distal part particularly slim, about 0.4 times length of subterminal segment. G2 about 1.0 times length of G1; distal segment well developed, about 0.5 times length of basal segment.

Discussion.—The relatively short ambulatory legs of *S. vedeniki,* new species, allies it with *S. boex,* new species. The leg proportions of *S. vedeniki,* however, are still greater than those of *S. boex.* The G1s of *S. vedeniki* are relatively stouter and the terminal segment straighter than those of *S. boex.* The posterolateral margins of *S. vedeniki* converge towards the posterior carapace margin more strongly than those of *S. boex,* giving it a less squarish appearance. In addition, the carapace of *S. vedeniki* is distinctly more inflated than that of *S. boex.*

Sundathelphusa vedeniki was found in a cave (Boho sa Bikahan) northwest of Antequera which is subjected to periodic resurgence of waters. At the end of the rainy season, the water in the cave is stagnant. There is a large amount of organic debris-like tree branches and leaves in the pools, as well as numerous mollusc shells. Live surface-dwelling gastropods are numerous, particularly a large species of *Brotia.* Also common is a normally pigmented catfish (Clariidae: *Clarias* sp.).

Etymology.—The second author takes pleasure in naming the present species after Mr. Tone Vedenik, the "moving spirit" of the Caving Club "Crni galeb" in Prebold, Slovenia, and its expeditions abroad.

Discussion

The caves where crabs had been collected are mostly of modest dimensions. Some contain sinking streams, while others are primary springs of purely hypogean brooks. The water temperature on average, was between 22.5°C (at 400 m above sea level, below high mountains) and 27–28°C (at sea level). The pH was generally 7.5–8.0. The food resources in the investigated caves are very diverse. While some of them are evidently nutrient-poor, others contain large amounts of plant debris. These are also the ones inhabited by a rich trogloxene fauna. The most frequently observed animals in these caves are pigmented or troglomorphic shrimps of the family Atyidae (*Caridina* spp.) while Palaemonidae (*Macrobrachium* sp.) are generally rare and never troglomorphic. The relatively large number of crabs as well as large mollucs (including *Brotia* sp. and *Corbicula* sp.) found in the Bohol caves is interesting. It contrasts somewhat with dinaric sinking rivers which are usually richer in insect larvae (Sket 1970, 1979).

With regards to the cavernicolous species discussed here, there are some interesting morphological and ecological trends. *Sundathelphusa cavernicola* is clearly a completely troglobiomorphic species, with very reduced pigmentation and eyes (Fig. 4g). *Sundathelphusa sottoae* on the other hand, is a less troglobiomorphic species, with more well developed eyes (Fig. 4h-l) and less obvious loss of pigmentation. *Sundathelphusa urichi* has also been found in one cave only, and while its body is poorly pigmented, the eyes are only slightly reduced (Fig. 4m, p). *Sundathelphusa vedeniki* has been found in nutrient rich caves only but it is probably mainly an epigean species,

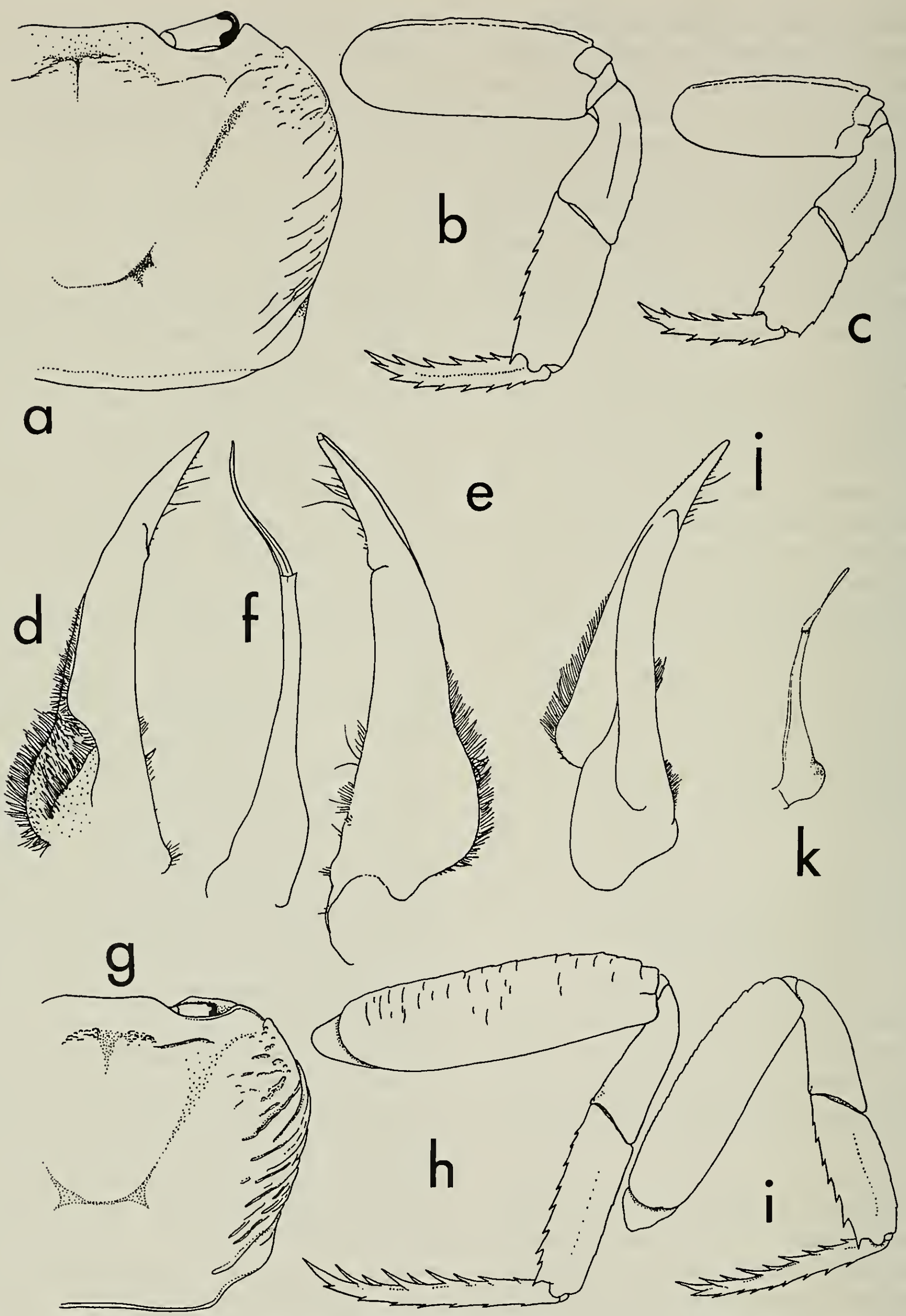

Fig. 2. a–f, *Sundathelphusa boex,* new species, holotype male (37.4 × 30.9 mm) (NMCR); g, *S. sottoae,* new species, paratype female (26.0 × 21.0 mm) (ZRC 1996.1553); h–k, *S. sottoae,* new species, h–k, holotype male (17.3 × 13.4 mm) (NSMT-Cr 8938). a, carapace; b, right third ambulatory leg; c, right fourth ambulatory leg; d, ventral view of left G1; e, dorsal view of left G1; f, left G2; g, carapace; h, right third ambulatory leg; i, right fourth ambulatory leg; j, ventral view of left G1; k, left G2 (after Takeda, 1983) (different scale from j).

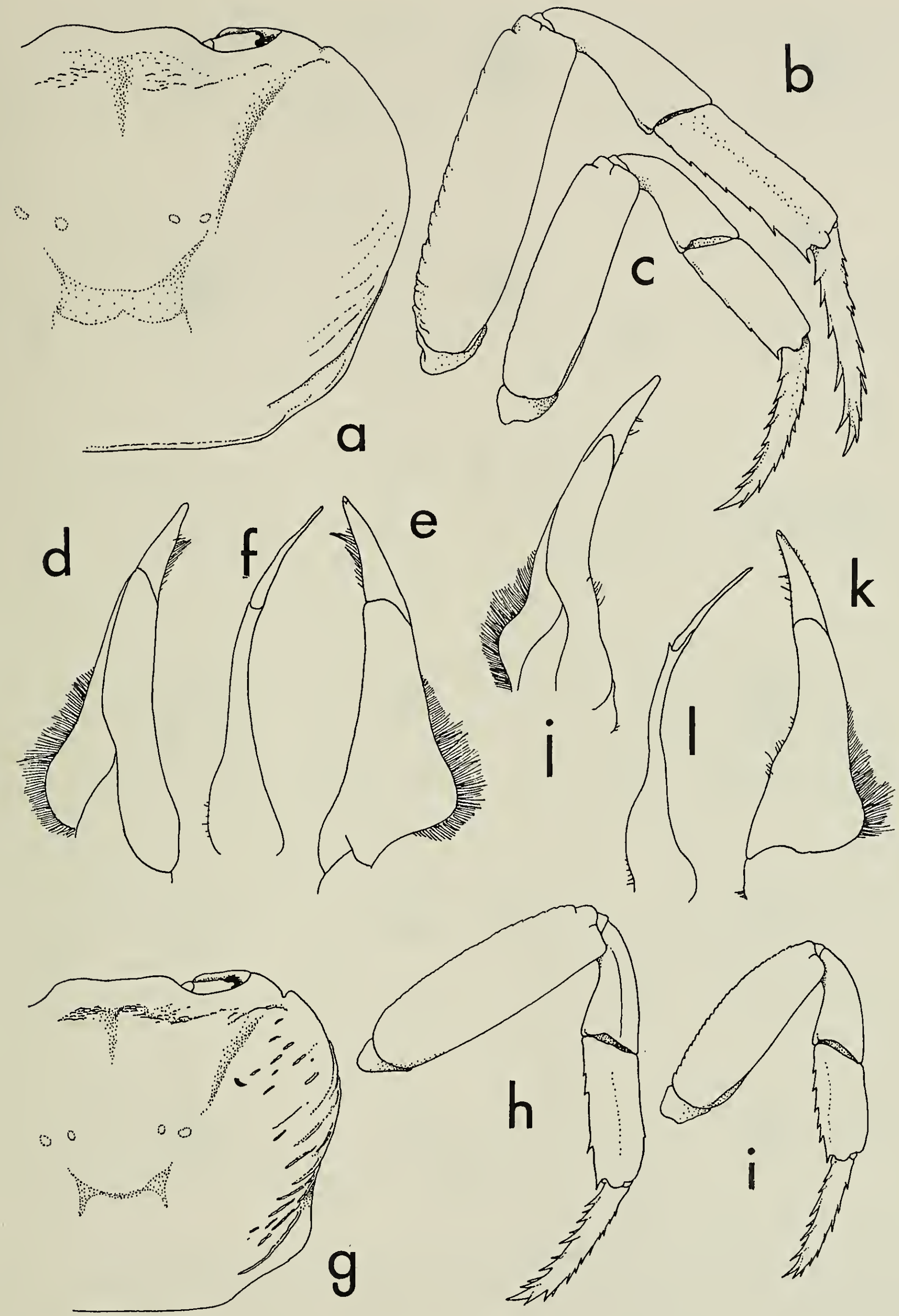

Fig. 3. a–f, *Sundathelphusa urichi*, new species, holotype male (36.6 × 27.9 mm) (NMCR); g–l, *S. vedeniki*, new species, holotype male (28.2 × 22.3 mm) (NMCR). a, carapace; b, right third ambulatory leg; c, right fourth ambulatory leg; d, ventral view of left G1; e, dorsal view of left G1; f, left G2; g, carapace; h, right third ambulatory leg; i, right fourth ambulatory leg; j, ventral view of left G1; k, dorsal view of left G1; l, left G2.

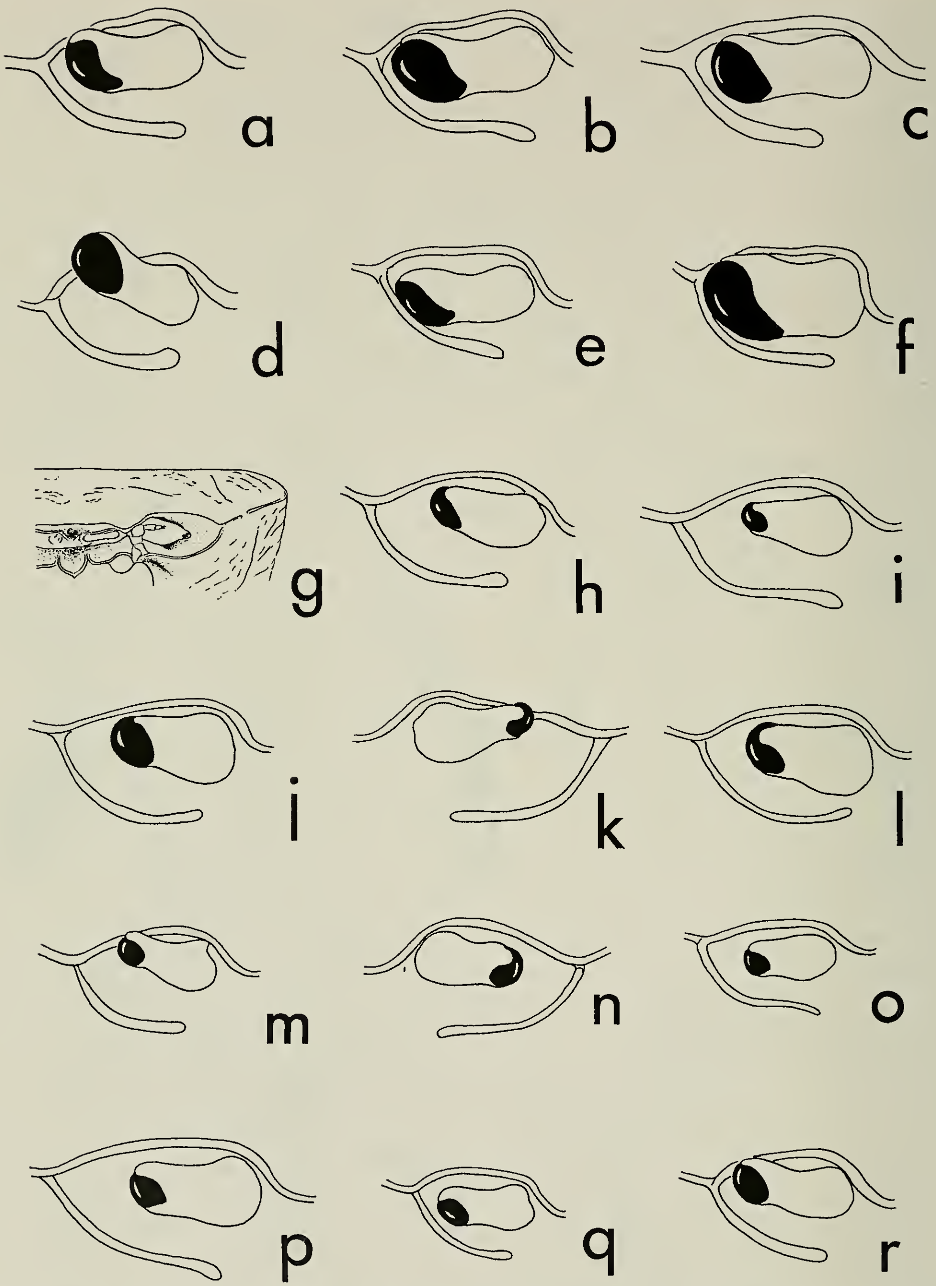

Fig. 4. Orbits and eyes of *Sundathelphusa* species from Bohol. a–f, *S. boex*: a, holotype male (37.4 × 30.9 mm, Sierra Bulliones, NMCR); b, male (24.0 × 20.1 mm, Pahangong Talon, ULB); c, paratype male (41.0 × 33.0 mm, Batuan, ZRC 1996.1549); d, paratype male (34.2 × 27.8 mm, Castigio Cave, ZRC 1996.1550); e, male (34.6 × 28.8 mm, Batuan, NMCR); f, male (10.2 × 8.7 mm, Carmulaon, ULB). g, *S. cavernicola*: holotype female (25.7 by 21.0 mm, Quinapon-an Cave, NSMT-Cr 8937) (after Takeda, 1983: Fig. 2). h–l, *S. sottoae*: h, holotype male (17.3 × 13.4 mm, Ughob Cave, NSMT-Cr 8938); i, paratype female (26.0 × 21.0 mm, Bonugan Cave, ZRC 1996.1553); j, male (17.4 × 13.8 mm, Batuan, ZRC 1996.1548); k, paratype female (28.0 × 25.0 mm, Bonugan Cave, NMCR); l, male (14.8 × 12.5 mm, Kalumpan, ULB); m–p, *S. urichi* (Quilas Cave): m, holotype male (36.6 × 27.9 mm, NMCR); n, paratype male (16.5 × 20.5 mm, ULB); o, paratype male (21.6 × 15.5 mm, ZRC 1996.1555); p, paratype female (32.6 × 25.0 mm, ZRC 1996.1556). q, r, *S. vedeniki* (Boho sa Bikahan): q, holotype male (28.2 × 22.3 mm, NMCR); r, paratype male (33.9 × 26.5 mm, ZRC 1996.1552).

with well developed pigmentation and eyes (Fig. 4g, r) as well as relatively short legs. *Sundathelphusa boex,* with normal eyes (Fig. 4a–f) and short legs, occurs in nutrient rich caves, but is also common in epigean waters.

With regards to their distributions, *S. boex* is probably a widely distributed species in central and southeastern parts of Bohol, being found in open areas as well as occasionally in caves. The other species seem to have more restricted distributions. In the Antequera area in southern Bohol, two very different species are present, *S. cavernicola* and *S. vedeniki,* the former being troglomorphic. In the central Batuan area, two possibly troglobitic species, *S. urichi* and *S. sottoae* are present. It is important, however, to note that it is possible that with more specimens, what is now regarded as one variable species, i.e., *S. sottoae,* may actually contain two species which differ, among other characters, in their degree of troglobiomorphism. The presence of several cavernicolous species in one cave system is not surprising (see Holthuis 1979, Ng 1989). It is, however, difficult to ascertain if any species, whether slightly troglobiomorphic or not, is a true troglobite or just an occasional cave inhabitant, especially since epigean habitats were not sampled adequately during this study.

It is also of interest to note that another cavernicolous crab of the varunine genus *Orcovita* Ng & Tomascik, 1994 (Grapsidae), has recently been reported from anchialine habitats in Bohol. *Orcovita fictilia* Ng, Guinot & Iliffe, 1996, is known only from Hinagdanan Cave, Panglao, which is southwest of Bohol.

Acknowledgments

The second author thanks all the members of the expedition for their support during the investigations. The expedition was supported by the Ministry of Science and Technology of the Republic of Slovenia, Open Society Fund for Slovenia as well as by other sponsors, which have been gratefully acknowledged in the general expedition report. The first author thanks Dr M. Takeda (NSMT) for loan of specimens as well as the useful discussions on the identity of *S. cavernicola.*

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On the status of *Pachycheles laevidactylus* Ortmann, 1892 (Crustacea: Decapoda: Porcellanidae)

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Abstract.—*Pachycheles laevidactylus* Ortmann, 1892, previously considered a synonym of the eastern Pacific *P. grossimanus* (Guérin-Méneville, 1835), has been found to be a distinct species. Examination of type and non-type specimens of *P. laevidactylus, P. grossimanus,* and the western Atlantic *P. haigae* Rodrigues da Costa, 1960 also demonstrated that *P. haigae* is a junior synonym of *P. laevidactylus.*

Guérin-Méneville (1835) briefly described the porcelain crab *Porcellana grossimana* from specimens collected in Chile; later he provided a more complete description and an illustration, and restricted the type locality to Valparaiso (Guérin-Méneville 1838). Stimpson (1858) designated *P. grossimana* as the type species for his new genus *Pachycheles.* Subsequent records indicate that *P. grossimanus* is broadly distributed along the temperate eastern Pacific coast of South America (Rathbun 1910, Haig 1955, 1960).

In his survey of the decapod crustacean collections of the Strasbourg Museum, Ortmann (1892) described *P. laevidactylus* from Brazil. Ortmann (1897) subsequently decided that this locality data was unreliable, and synonymized *P. laevidactylus* with the eastern Pacific *P. grossimanus.* He based this decision on his examination of specimens of *P. grossimanus* during a visit to the Academy of Natural Sciences in Philadelphia (ANSP). Ortmann (1897) did not provide catalog numbers for the three specimens of *P. grossimanus* he examined at the ANSP. However, during a recent visit to the ANSP collections, we could find only three specimens labelled as *P. grossimanus.* The low catalog numbers of these specimens indicate that they have been at the ANSP since at least the 1880's (G. Rosenberg, pers. comm.) and thus are probably the same specimens studied by Ortmann. Our examination of these specimens indicates that Ortmann was correct in his assessment that they are conspecific with *P. laevidactylus.*

Unfortunately, two of the ANSP specimens also lack locality data, and the third (ANSP 4168), from the U.S. Exploring Expedition, is only labelled "Pacific Ocean." This vague labelling may be considered suspect given the extent to which specimens from this expedition were separated from their labels (Dana 1852:2). Both the types of *P. laevidactylus* and the ANSP specimens differ in several respects from the type specimen of *P grossimanus.* Furthermore, they appear to be identical to *P. haigae* Rodrigues da Costa, 1960. We thus conclude that *P. laevidactylus* is not conspecific with *P. grossimanus* but is identical to *P. haigae,* and that therefore *P. haigae* is a junior subjective synonym of *P. laevidactylus.*

In this paper we provide diagnoses and illustrations for *P. grossimanus* and *P. laevidactylus,* and a full description of *P. laevidactylus* (see Haig 1960 for a full description of *P. grossimanus*). Material from this study came from the collections of the Academy of Natural Sciences at Philadelphia, American Museum of Natural History

(AMNH), Muséum national d'Histoire naturelle (MNHN), Musée Zoologique de l'Université Louis Pasteur et de la Ville de Strasbourg (MZS), Museu de Zoologia Universidade de São Paulo (MZUSP), Swedish Museum of Natural History (SMNH), and Natural Museum of Natural History (USNM). Carapace length (CL) is provided as an indicator of specimen size. Illustrations were created using an improved version of the approach used by Harvey (1992): specimen images were first captured on a Macintosh™ computer with a digital camera connected to a Wild M8 dissecting microscope, then prepared for publication using the programs Adobe Photoshop™ and Adobe Illustrator™.

Pachycheles grossimanus (Guérin-Méneville, 1835)

Fig. 1

Porcellana grossimana Guérin-Méneville, 1835:116; 1838:8; plate VII 26, fig. 3.

Pachycheles grossimanus: Stimpson, 1858: 228.—Haig, 1960:167–169, plate 35, fig. 1 (in part), and references therein.—Antezana et al., 1965:25–26.—Viviani, 1968:51; fig. 10, 14k. (See remarks.)

Holotype.—Chile: 1 specimen, presumably male (CL 7.8 mm), "Chili", MNHN-Ga 3954. (See remarks.)

Additional material examined.—Chile: 1 ovigerous female (CL 17.00 mm), Montemar, near Valparaiso, 32°57′24″S, 71° 33′25″W, littoral, 16 Oct 1948, Lund University Chile Expedition sta. no. M123, SMNH 15319; 1 male (CL 4.23 mm), 1 female (CL 2.38 mm), 1 juvenile (CL 1.87 mm), Tocopilla, 22°05′S, 70°13′W, littoral, 5 Jan 1949, Lund University Chile Expedition sta. no. M158, SMNH 15315; 1 female (CL 6.67 mm), 4 juveniles (CL 2.16–2.88 mm), Cavancha, S of Iquique, 20°14′07″S, 70°10′05″W, littoral, 5 Jul 1949, Lund University Chile Expedition sta. no. M135, SMNH 15316; 5 males (CL 5.60–14.58 mm), 3 females (CL 5.65–6.61 mm), 8 juveniles (CL 2.68–5.36 mm), Bahía San Vicente, 36°43′36″S, 73°08′10″W, littoral, 9 Jun 1949, Lund University Chile Expedition sta. no. M121, SMNH 15317; 1 male (CL 21.00 mm), 1 female (CL 12.89 mm), Canal Chacao, 41°46′30″S, 73°45′ 45″W, 40 m, 4 May 1949, Lund University Chile Expedition sta. no. M94, SMNH 15318; 3 males (CL 5.78–7.71 mm), 6 females (CL 6.63–9.28 mm), 40 juveniles (CL 1.96–3.93 mm), Peninsula Coquimbo 29°55′56″S, 71°21′08″W, littoral, 24 Jun 1949, Lund University Chile Expedition sta. no. M127, SMNH 15320; 1 male (CL 17.00 mm), numerous juveniles (CL 1.96–4.17 mm), Puerto Mejillones del Sur, 23°06′30″S, 70°28′00″W, 0–0.5 m, 30 Jun 1949, Lund University Chile Expedition sta. no. M129, SMNH 15321.

Peru: 1 female (CL 5.83 mm), Chincha, N. island, from seaweed, 18 Jun 1907, coll. R. E. Cocker, USNM 40477; 1 male (CL 18.41 mm), Callao, MNHN-Pg 5321.

Diagnosis.—Carapace with lateral margins parallel. Front rounded in dorsal view; dorsal surface with tuft of setae. Lateral walls of carapace consisting of 1 large anterior piece, 1 large posterior piece, and several small posterior fragments. Basal segment of antennule armed with up to 3 tubercles on medial anterior margin, and few flattened granules on anterolateral dorsal surface. Carpus and manus of chelipeds with rounded, indistinct posterior margins and large, densely packed granules forming irregular rows near posterior margin. Carpus with anterior crest granular to serrate, divided by notch into broad proximal tooth and acute subdistal tooth. Manus with large granular tubercle near base of pollex. Walking legs densely setose. Telson 7-plated, sometimes incompletely so. Second pleopods present in males.

Distribution.—Callao, Peru to Canal Chacao, Chile; primarily intertidal; exceptionally to 40 m (Haig 1960).

Remarks.—Guérin-Méneville (1835, 1838) did not specify where his specimens were deposited, but Prof. Jacques Forest

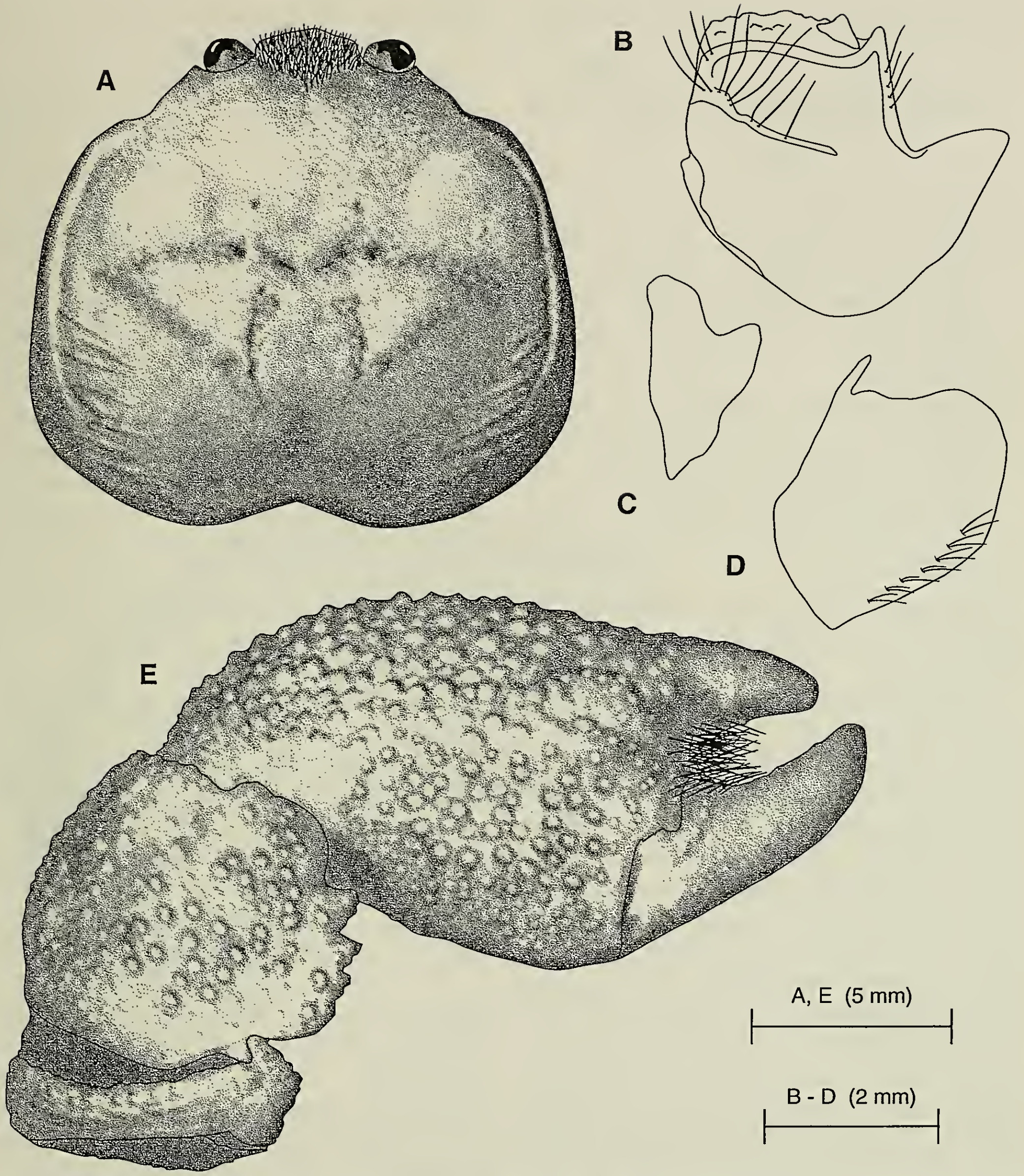

Fig. 1. *Pachycheles grossimanus* (Guérin-Méneville, 1835); male, USNM 98288. A, carapace; B, basal segment of right antennule, ventral view; C, merus of right outer maxilliped, ventral view; D, ischium of right outer maxilliped, ventral view; E, major cheliped.

and Dr. Nguyen Ngoc-Ho (in litt.) of the MNHN concur that the single dry specimen was part of Guérin-Méneville's collection and is most likely the holotype. We could not determine the sex of the holotype with certainty because the specimen is glued to a wooden base.

Pachycheles grossimanus co-occurs with *P. crinimanus* Haig, 1960 in Peru (see Haig 1960 for distinguishing characteristics of these species), but otherwise appears to be the only *Pachycheles* in its range. Haig (1960) recorded ANSP 4168 as *P. grossimanus,* as did Ortmann (1897), but this specimen is in fact referable to *P. laevidactylus* (see below).

Pachycheles laevidactylus Ortmann, 1892
Fig. 2

Pachycheles laevidactylus Ortmann, 1892: 266. plate 12, fig. 1.

Pachycheles grossimanus: Ortmann, 1897: 292.—Haig, 1955:43–44 (in part); 1960: 167, plate 35, fig. 1 (in part). (See remarks.) [Not *P. grossimanus* (Guérin-Méneville).]

Pachycheles haigae Rodrigues da Costa, 1960:21, figs. 1–4.—Boschi, 1963:31, figs. 1, 3; 1979:137; 1981: 735.—Boschi et al., 1967:6; 1992:56.—Bremec & Cazzaniga, 1984, fig. 2.—da Silva et al., 1989, figs. 2, 11.

Syntypes.—1 male (CL 9.04 mm), 1 female (CL 8.43 mm), no collection data, MZS 380.

Additional material examined.—Brazil: 2 males (CL 4.85–7.93 mm), 1 female (damaged), Gragoatá, Rio de Janeiro, coll. H. R. Costa, Aug 1959, MZUSP 10593; 3 males (CL 5.40–6.25 mm), 1 ovigerous female (CL 5.67 mm), Abrolhos, Bahia, coll. H. R. Costa, 3 Feb 1957, MZUSP 10594; 3 males (3.96–8.26 mm), 2 ovigerous females (6.04–10.40 mm), Isla de São Francisco, Santa Catarina, coll. F. H. A. Costa, 31 Jul 1989, MZUSP 9984; 6 males (CL 2.74–10.96 mm), 6 females (CL 2.50–8.67 mm), 3 juveniles (CL 1.67–1.73 mm), Paronopria Beach, São Vicente, shore, coll. C. V. Micheletti, 4 Oct 1994, AMNH 17451; 2 males (CL 9.40–10.72 mm), Rio De Janeiro, MCZ 11848; 1 female (CL 5.12 mm), Vitória, coll. Hartt and Copeland, Thayer Expedition, MCZ 11849; 10 males (CL 4.23–9.52 mm), 8 ovigerous females (CL 4.29–7.35 mm), Ilhas De Sante Anna, coll. Hartt, MCZ 11850; 1 male (CL 8.67 mm), received in 1865 from Smithsonian Institution, U.S. Exploring Expedition, MCZ 1395.

Uruguay: 3 males (CL 9.40–11.33 mm), 3 females (CL 9.88–13.01 mm), Isla De Lobos, 8 Jul 1953, on the coast after storm, coll. Leoncio Sanabria, USNM 99851.

"Pacific Ocean" (but see remarks): 1 male (CL 10.46 mm), U.S. Exploring Expedition, ANSP 4168.

No locality data: 2 females (CL 8.81–10.67 mm), ANSP 740.

Diagnosis.—Front triangular in dorsal view; dorsal surface with tuft of setae. Lateral margins of carapace consisting of 1 large anterior piece, 1 large posterior piece, and usually several small posterior fragments. Basal segment of antennule armed with 3 to 5 strong spines on medial anterior margin, and 2 to 4 spines on the anterolateral dorsal surface. Carpus and manus of chelipeds with posterior submarginal furrow, scattered long setae, and small, evenly spaced granules. Carpus with anterior crest divided by notch into broad proximal tooth and acute subdistal tooth; dorsal surface with 3 lateral longitudinal ridges, each topped with row of enlarged granules. Manus with large, elongate, granular tubercle near base of pollex. Walking legs with setose margins. Telson 5-plated. Second pleopods present in males.

Description.—Carapace (Fig. 2A) about as broad as long in males, slightly broader than long in females; posterolateral margins convex; dorsolateral ridges pronounced; dorsal surface with posterolateral regions plicate; posterior margin curving inward medially; dorsal surface nearly naked except for tuft of short plumose setae on frontal region. Front triangular in dorsal view, trilobate in frontal view; median lobe projecting farther than lateral lobes; with median groove dorsally. Outer orbital angle produced into an acute tooth, inner orbital angle slightly pronounced. Orbits deep, and broad; eyes large. Lateral margins of carapace (Fig. 2B) consisting of 1 large anterior piece, 1 large posterior piece, and usually several small posterior fragments.

Basal segment of antennule (Fig. 2C) armed with 3 to 5 spines (the type male has 2 spines on the right basal antennular segment, 3 on the left) on medial anterior mar-

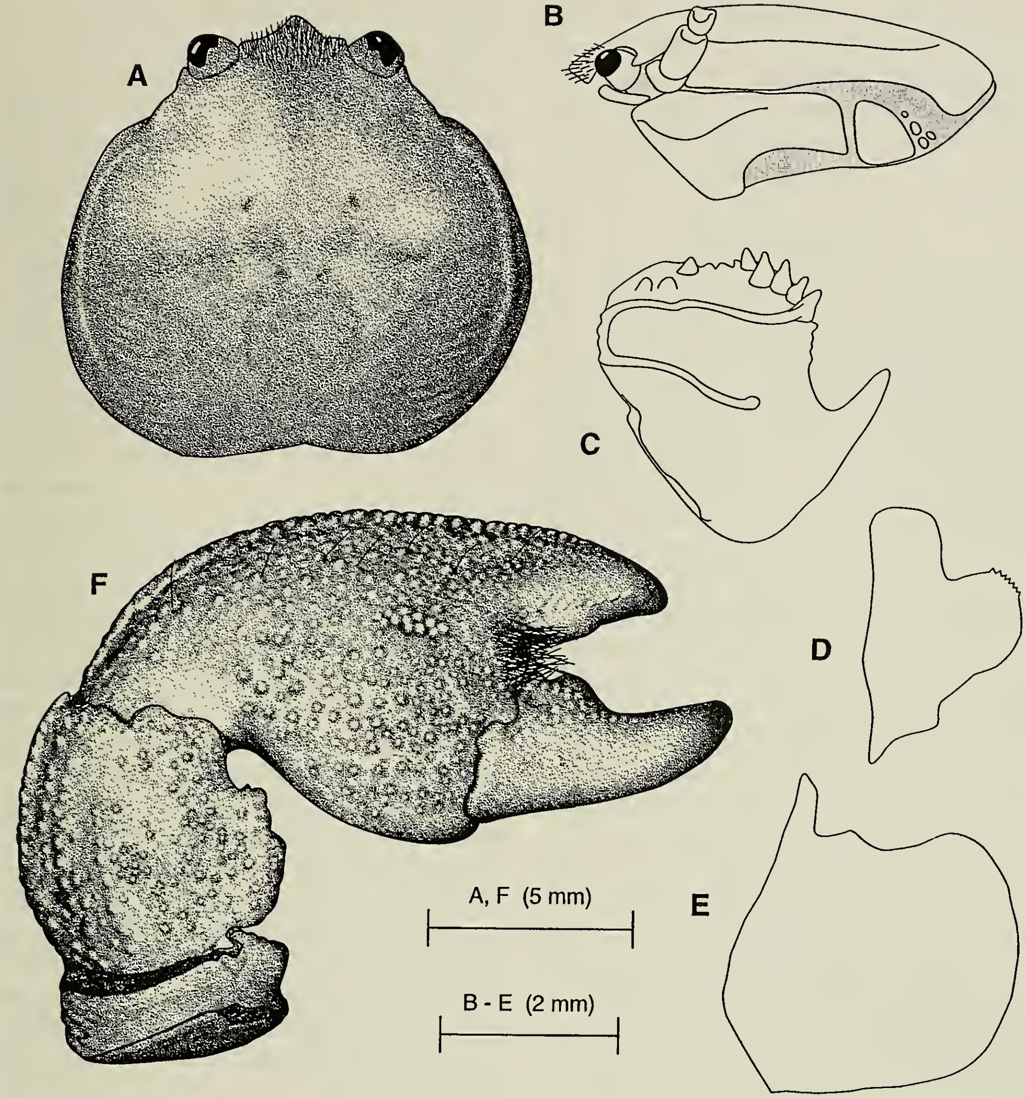

Fig. 2. *Pachycheles laevidactylus* Ortmann, 1892; male, USNM 99851. A, carapace; B, left side wall of carapace; C, basal segment of right antennule, ventral view; D, merus of right outer maxilliped, ventral view; E, ischium of right outer maxilliped, ventral view; F, major cheliped.

gin (visible from dorsal view); with 2 to 4 spines on anterolateral dorsal surface; dorsal surface with 2 transverse granular lines. Second segment of antenna with distal tubercule on anterior margin; third segment granular, sometimes more pronounced near distal and proximal margins. Flagella with minute setae.

Third maxillipeds with moderately deep, trilobate sternite; median lobe of sternite equalling or slightly exceeding lateral lobes; ischium (Fig. 2E) with medioproximal angle only slightly obtuse, almost right-angled; merus (Fig. 2D) with pronounced medial lobe, subquadrate in shape, and usually dentate anteriorly.

Chelipeds unequal in size (major: Fig. 2F). Merus with granular tooth on anterior margin, projecting about as far as carpus teeth; ventral margin of merus distinct, ventrodistal angle usually with 2 small granules. Carpus and manus with weak submarginal furrow on posterior margins, and scattered long plumose setae towards posterior margins; with very short, often vestigial, plumose setae arising in groups from distal side of larger granules. Carpus with crest on anterior margin, divided by notch into broad proximal tooth and somewhat acute subdistal tooth; dorsal surface covered with small granules, more pronounced near posterior margin; surface with 3 longitudinal ridges, each topped with row of enlarged granules; 1 ridge is medial, 2 close together between medial ridge and lateral margin; dorsal surface with few long plumose setae. Manus covered with small granules; large, elongate, granular tubercle near base of pollex; fingers with smaller, flattened granules on minor chela, nearly smooth on major chela. Major manus nearly lacking pubescence dorsally; ventral surface of manus with tuft of setae at base of fingers; pollex pubescent, with single medial tubercule on cutting edge; dactyl pubescent on distal half, cutting edge with basal tubercule; fingers gaping, crossing at tips. Minor cheliped with at most trace of setation on dorsal surface, outer margin with long bristles; fingers meeting entire length of cutting edge, crossing at tips.

Walking legs with scattered setae on anterior margins of merus, carpus, and propodus. Anterior margin of carpus with 1 small tubercle and 2 granules distally. Propodus with 4 moveable spines ventrally: 2 distal, 1 subdistal, and 1 medial; dactyl with 3 corneous spines along ventral margin.

Abdomen smooth; telson with five plates in males and females. Second pleopods present in males.

Distribution.—Pernambuco, Brazil to Monte Hermoso, Argentina (39°00′S, 61°16″W); intertidal to 12 m.

Remarks.—Although Ortmann (1982) cited Brazil as the type locality in his description of *P. laevidactylus,* he later (Ortmann 1897) noted that the specimens lacked acquisition data, and thus could not safely conclude where they came from. Unfortunately, locality data is also lacking for two of the three ANSP specimens that led Ortmann to synonomize *P. laevidactylus* with *P. grossimanus,* and the locality of the third specimen (i.e., "Pacific Ocean") is vague and open to question.

The syntype specimens of *P. laevidactylus* differ from *P. grossimanus* in numerous respects (because the holotype of *P. grossimanus* is dry, fragile, and glued to a frame, most of the following comparisons are based on non-type specimens of *P. grossimanus* that we established to be conspecific with the holotype). In *P. grossimanus,* the front of the carapace has a rounded anterior margin (Fig. 1A); the lateral margins of the carapace are parallel (Fig. 1A); the basal segment of the antennule has three or fewer tubercles on the distal margin and at most a few flattened granules on the anterolateral surface (Fig. 1B); in the outer maxillipeds, the medial lobe of the merus is obliquely subtriangular (Fig. 1C), and the medioproximal angle of the ischium is broadly obtuse (Fig. 1D); the chelipeds (Fig. 1E) lack submarginal furrows, and are more densely covered with larger granules; the margin of the anterior crest of the carpus of the chelae is granular to serrate; the walking legs are densely setose; and the telson is seven-plated, although the anterior plates are sometimes partially fused.

We could not examine type specimens of the western Atlantic *P. haigae* for this study. The holotype was deposited at the Instituto Oceanográfico, which apparently no longer exists (G. de Melo, pers. comm.), and the location of the holotype is unknown. Several paratypes are deposited at the Museu Nacional, which was unfortunately closed due to a strike during this study. However, we were able to examine several specimens of *P. haigae* from the type locality and two other localities (Abrolhos and Isla de São Francisco), where paratypes were collected, including part of Rodrigues da Costa's collections, which were donated to the MZUSP after his death.

Whereas *P. laevidactylus* is easily distinguished from *P. grossimanus,* we can find no differences between *P. laevidactylus* and *P. haigae,* and must conclude that *P. haigae* is a junior subjective synonym of *P. laevidactylus.* Thus, whether or not Ortmann's type material came from Brazil, *P. laevidactylus* is currently known only from the western Atlantic.

The tuft of setae on the front of the carapace distinguishes *P. laevidactylus* from all other species in the western Atlantic except *P. chubutensis* Boschi, 1963 and *P. monilifer* Dana, 1852. In *P. chubutensis* the front is rounded, and the lateral walls of the carapace consist of a very large anterior piece and only a single small posterior fragment. In *P. monilifer,* the basal segment of the antennule lacks obvious spination, and males lack pleopods.

Cheliped morphology can also easily distinguish *P. laevidactylus* from other western Atlantic species of *Pachycheles.* Unlike *P. laevidactylus,* several species (*P. ackleianus* A. Milne-Edwards, 1880; *P. monilifer*; *P. rugimanus* A. Milne-Edwards, 1880; and *P. susanae* Gore & Abele, 1973) have heavily sculptured chelipeds; *P. pilosus* (H. Milne-Edwards, 1837) has spiny, setose chelae, whereas the chelae of *P. riisei* (Stimpson, 1858) are smooth and shiny. In *P. greeleyi* (Rathbun, 1900), *P. serratus* (Benedict, 1901), *P. chacei* Haig, 1955, and *P. cristobalensis* Gore, 1970, the chelae lack submarginal furrows, the enlarged tubercle at the base of the pollex, and the tuft of setae between the fingers; they also are more evenly covered with granules than those of *P. laevidactylus,* and the anterior crest of the chelae carpus consists of small granular teeth in these species. The chelae of *P. chubutensis* are similar to those of *P. laevidactylus,* but the granules are smaller and more evenly spaced, the tubercle at the base of the pollex is absent, and the teeth of the anterior carpal crest are irregular and serrate. Furthermore, in *P. chubutensis* the dorsal surface of the carpus and manus is usually covered with short dense setae, but this varies considerably and we have seen virtually naked individuals.

Acknowledgments

For access to the types of *P. laevidactylus,* we thank Elisabeth Lang of the MSZ. We also thank Raymond B. Manning and Rafael Lemaitre (USNM), Lennart Sandberg (SMNH), Gustavo A. S. de Melo (MZUSP), Gary Rosenberg (ANSP), and Nguyen Ngoc-Ho and Jacques Forest (MNHN), for providing specimens and suggestions, and Carla Valéria Micheletti, at the Universidade Estadual Paulista, for providing freshly collected specimens of *P. laevidactylus.* Thanks also to Lara Tolchin, who assisted with the illustrations. This work was supported by a NSF Research Experience for Undergraduates fellowship (E. M. De Santo), which was extended by the AMNH.

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The first species of *Prionalpheus* from the eastern Pacific, and new records of caridean shrimp (Crustacea: Decapoda: Caridea) from the western coast of Mexico

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Abstract.—Four species of shallow water caridean shrimp new to the Mexican fauna are reported. The specimens were collected along the coast of the state of Nayarit and at Isla Isabel, Mexico. *Prionalpheus nayaritae,* new species, represents the first occurrence of this rare genus in the eastern Pacific. The new species can be recognized by the presence of asymmetrical mandibles, a characteristic of *Prionalpheus.* Three other new records extend the previous known distributions from Panama (*Alpheus firmus*), Colombia (*Synalpheus bannerorum*), and Hawaii and Clipperton Island (*Processa hawaiensis*), to continental Mexico. Morphological differences with specimens used in previous descriptions or reports are provided.

The shallow water caridean shrimp fauna from the Pacific coast of Mexico and their distribution have been studied by Ríos & Carvacho (1983a, 1983b), Wicksten (1983, 1984), Ríos (1989, 1992), Hendrickx (1992), and Wicksten & Hendrickx (1992). Although these studies have focused primarily on the Gulf of California, the overall distribution of the species has been summarized. According to these authors 119 species of caridean shrimp have been reported to occur along the Pacific coast of Mexico, belonging to 11 families and 51 genera (Wicksten & Hendrickx 1992).

In this study we present the description of a new species, *Prionalpheus nayaritae,* the first species of the genus to be found in the eastern Pacific. *Prionalpheus* was erected by Banner & Banner (1960) to accommodate specimens of Alpheidae in which the mouth parts were entirely unlike those of any other genus of the family. It is a rare genus known only from 21 specimens belonging to six species, of which five are from the Indo-Pacific and one from the Caribbean (Banner & Banner 1982, Bruce 1986, Martínez & Carvacho 1991). In addition, new records of three species previously unknown from Mexico are presented. Two records are for species of the family Alpheidae, which is the most diverse in the Mexican Pacific (42% of the caridean species), and one belonging to the family Processidae. These findings expand considerably our knowledge of the distribution of the four taxa, and suggest that in the future additional species known from Central and South America, and oceanic islands in the tropical eastern Pacific, will likely be discovered on the western coast of Mexico.

The material has come from five sampling trips carried out along the coast of Nayarit, Mexico, between March 1992 and November 1993, including samples from Isla Isabel, 23 km off the coast (Fig. 1). Samples of dead coral were collected at depths ranging from 1 to 5 m. The coral blocks were broken and all crustacean cryptofauna preserved in 70% alcohol. The material treated is deposited in the Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de

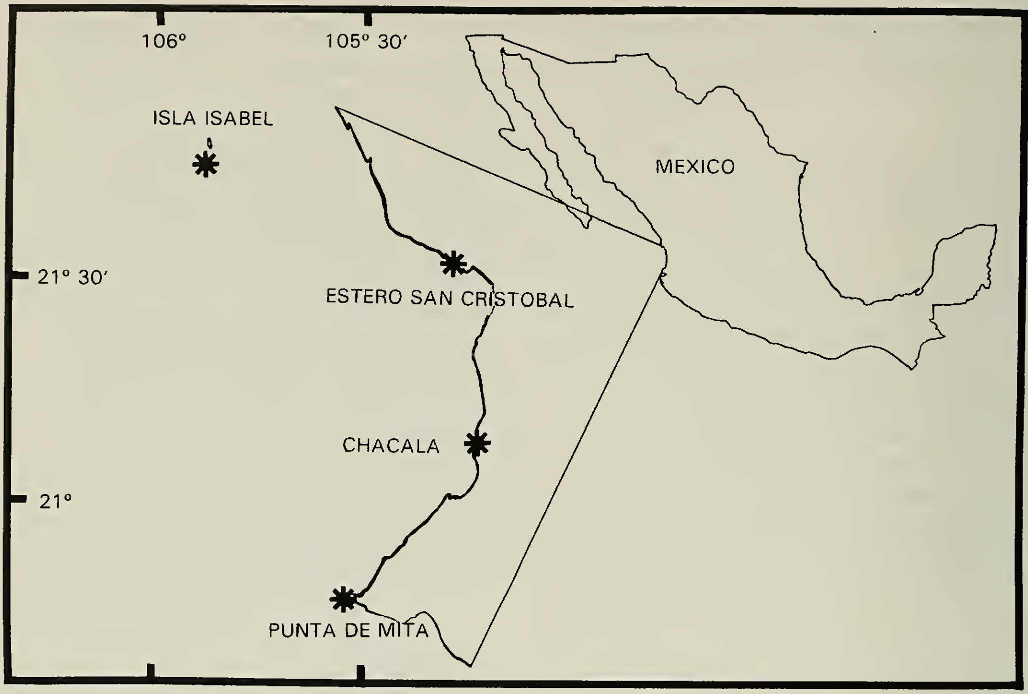

Fig. 1. Collection sites (asterisks) along the State of Nayarit, Pacific coast of Mexico.

México (CNCR), and was collected by M. E. Camacho and J. L. Villalobos. The abbreviations "cl" and "tl" indicate carapace length and total length (including rostrum), respectively.

Family Alpheidae Rafinesque, 1815
Alpheus firmus Kim & Abele, 1988
Fig. 2

Material examined.—4 ♂, cl 11.0, 10.0, 9.0, 9.0 mm, tl 32.7, 27.2, 25.6, 27.3 mm; 1 ♀, cl 6.5 mm, tl 18.0 mm; 4 ♀ ovigerous, cl 17.0, 10.0, 10.0, 9.0 mm, tl 34.5, 29.7, 29.0, 25.0 mm; 23 May 1993; Estero San Cristóbal, Bahía de Matanchén, Nayarit, 21°31′N, 105°14′W; CNCR 12759.

Remarks.—The only existing records of *Alpheus firmus* are those of the original description, based on material collected in Panama (Kim & Abele 1988), from Miraflores Locks (holotype, a male, cl 9.2 mm) and Punta Paitilla. This is a shallow water species that has been collected intertidally (0–1 m) under rocks. Our records are from a similar habitat in a rocky substrate in tidal pools. In live specimens, the body color is translucent, with the internal surface of both palms of chelipeds blue-green, and tip of movable finger of major chela red. Morphological differences between the type material and the organisms reported here consist in: 1) the absence in the latter of a lateral spine on the basicerite, a feature previously observed by Kim & Abele (1988) that is probably size related, and 2) a long ultimate segment of the third maxilliped (twice as long as the penultimate instead of slightly longer, as in the type material) (Fig. 2b). This new record and second for the species, extends its distribution by more than 9° of latitude.

Synalpheus bannerorum Abele, 1975
Fig. 3

Material examined.—5 ♂, cl 4.8, 3.0, 3.5, 3.0, 2.7 mm, tl 8.0, 5.1, 6.7, 5.8, 4.5 mm; 5 ♀ ovigerous, cl 3.7, 3.5, 3.5, 3.2, 3.0 mm, tl 7.2, 6.7, 6.5, 6.3, 5.5 mm; 29

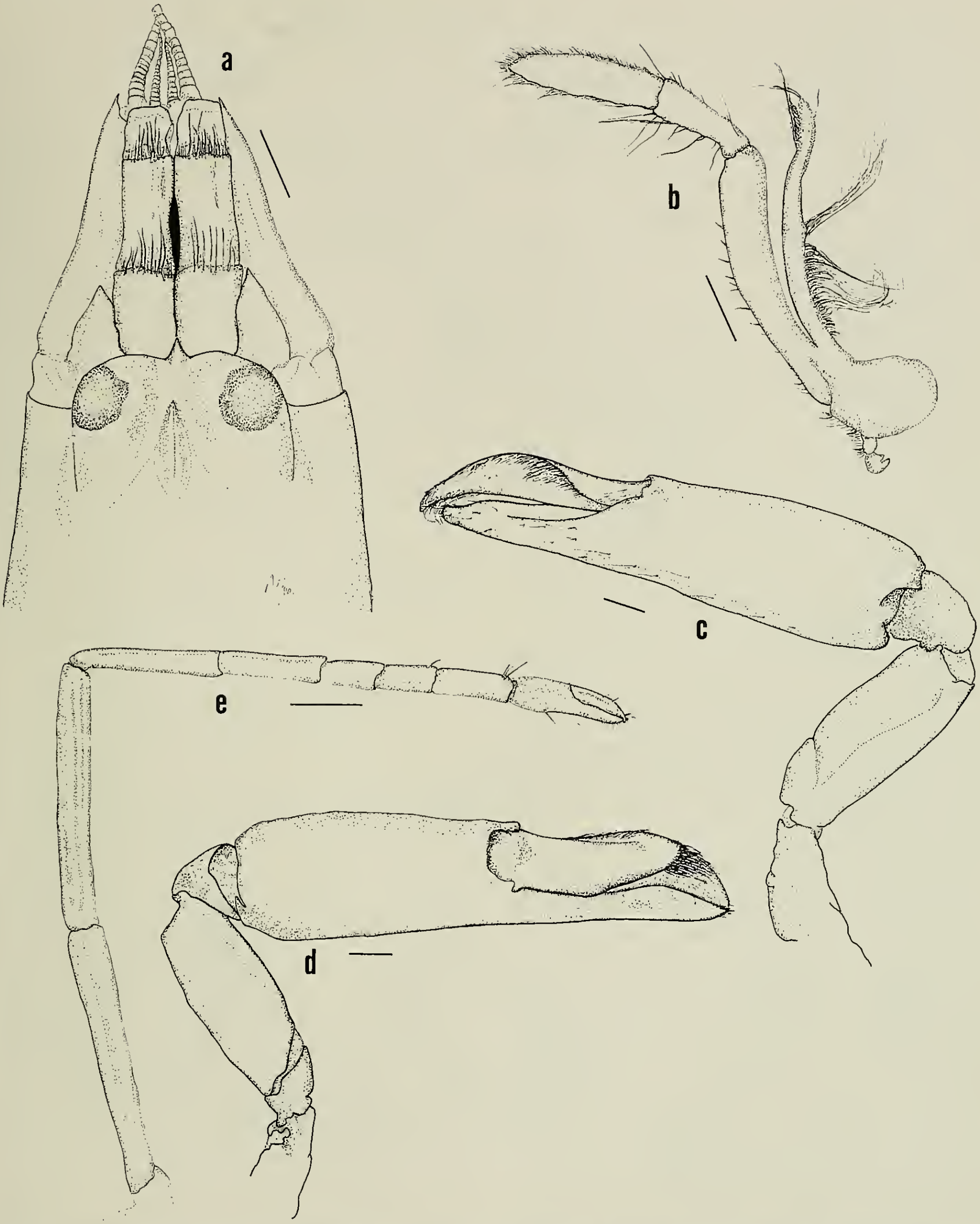

Fig. 2. *Alpheus firmus* Kim & Abele, 1988: a, anterior portion of carapace and cephalic appendages; b, third maxilliped; c, minor chela of male, internal view; d, minor chela of male, external view; e, second pereopod. Scale bars = 1 mm.

Mar 1992; Bahía Chacala, Nayarit, 20°10′N, 105°13′W; CNCR 11910. 1 ♀ ovigerous, cl 3.7 mm, tl 8.7 mm; same locality; 21 May 1993, CNCR 12746. 1 ♂, cl 3.0 mm, tl 6.6 mm; 1 ♀ ovigerous, cl 4.0 mm, tl 9.2 mm; 23 May 1993; Estero San Cristóbal, Bahía de Matanchén, Nayarit, 21°31′N, 105°14′W; CNCR 12754. 1 ♂, cl

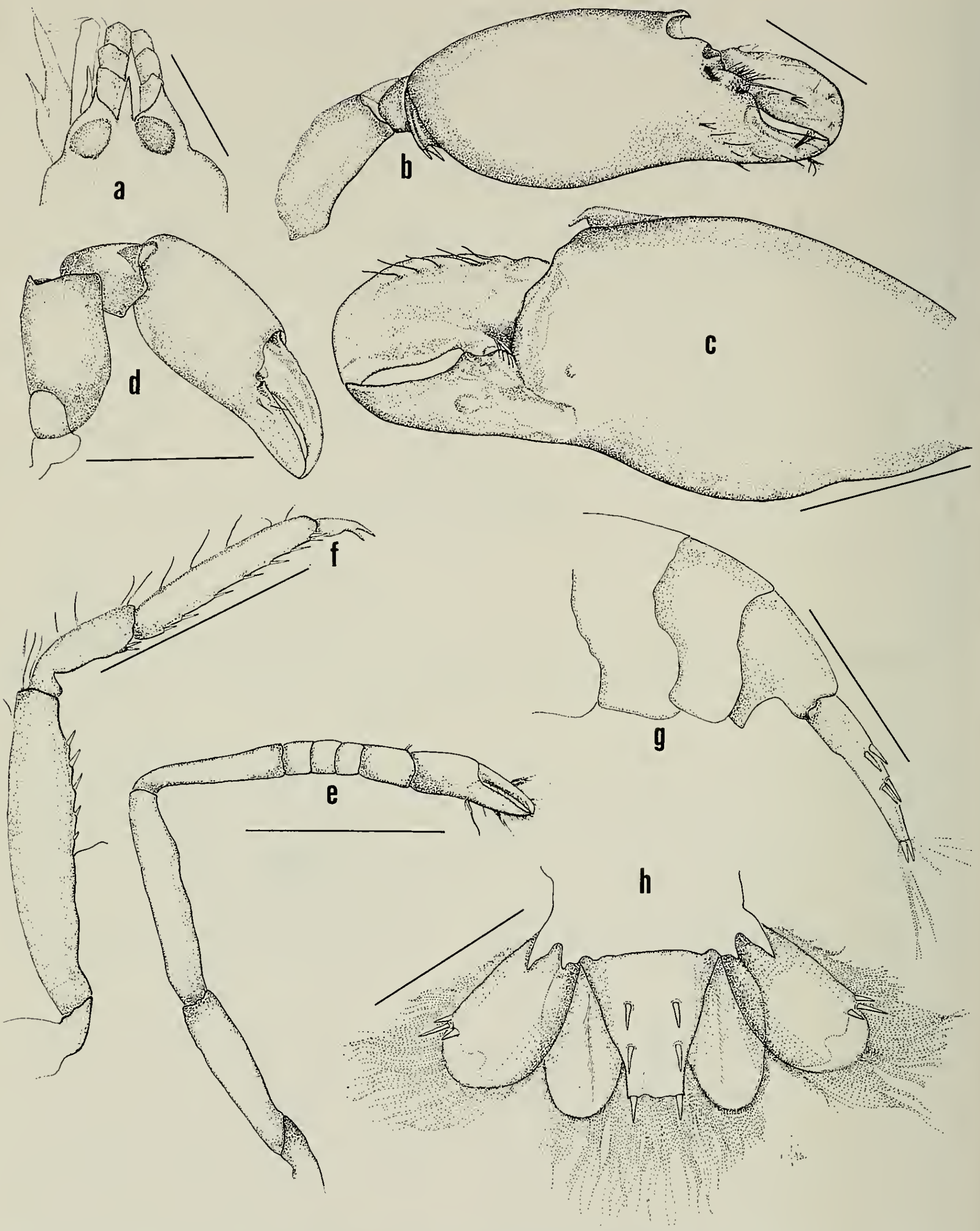

Fig. 3. *Synalpheus bannerorum* Abele, 1975: a, anterior portion of carapace, dorsal view; b, internal view of major chela; c, external view of major chela; d, external view of minor chela; e, second pereopod; f, third pereopod; g, lateral view of last three abdominal segments and telson; h, dorsal view of telson and uropods. Scale bars = 1 mm.

3.3 mm, tl 5.5 mm; 1 ♀ ovigerous, cl 4.0 mm, tl 6.5 mm; 2 Feb 1993; Punta de Mita, Nayarit, 20°46′N, 105°31′W; CNCR 12678.

Remarks.—*Synalpheus bannerorum* was described from Isla Malpelo, Colombia, inhabiting coral at a depth of 10 m. Compared to the original description, the morphological differences encountered here were: 1) the rostrum reaches the distal margin of the basal antennular segment (Fig. 3a), 2) in the second pair of pereopods, the first carpal segment is 5.5 times as long as the second (Fig. 3e), and 3) the fifth abdominal segment is half the length of the sixth and of equal length as the telson (Fig. 3g). Abele (1975) postulated that this species might be endemic to Isla Malpelo, and until now no other occurrences had been reported. This species seems to be abundant along the rocky portion of the coast of Nayarit (Camacho 1996).

Prionalpheus nayaritae, new species

Fig. 4

Holotype.—1 ♀ ovigerous, cl 2.2 mm, tl 5.0 mm; 1 Nov 1993; Punta de Mita, Nayarit, 20°46′N, 105°31′W; CNCR 12983.

Description.—Rostrum short, triangular, ending in acute tip with small single seta; dorsal carina low, reaching anterior half of first antennular segment (Fig. 4b). Margins contiguous to rostrum concave, not covering eyes completely dorsally or laterally (Fig. 4c). Orbital hood unarmed. Corneae oval shaped. Anterolateral margin of carapace slightly produced, descending first from eyes, then convex and produced forming blunt pterygostomial angle (Fig. 4a). Posterior margin of carapace with well marked cardiac notch (Fig. 4a). First abdominal segment with pleura straight. Second segment with large nearly circular pleura, maximum length of pleura 1.6 times that of first segment. Third segment with pleura rounded, extending posteriorly and covering part of fourth segment. Fourth and fifth segments subrectangular. Sixth segment almost as long as deep, posteroventral angle with triangular movable plate. Telson 1.4 times longer than broad, bearing 2 pairs of dorsal spines (first pair medial, second pair closer to first pair than to posterior margin); posterior margin of telson with 2 pairs of long spines, inner pair shortest (Fig. 4i).

First antennular segment irregular in shape, longer than broad, and longer than second and third segments. Carina on ventral side of first antennular segment reaching distal margin of segment, with acute tip. Stylocerite 3.6 times longer than broad, reaching distal margin of second antennular segment. Scaphocerite 2.4 times longer than broad, laminar portion reaching distal margin of second antennular segment, lateral spine reaching beyond third antennular segment. Carpocerite 3.4 times longer than broad, reaching beyond antennular peduncle.

Mandibles asymmetrical, incisor process well developed, without palp or molar process; protruding considerably so as to be clearly seen in lateral view. Left mandible with 5 finger-like teeth decreasing in size proximally (Fig. 4d). Teeth oriented approximately in same direction; distal tooth longest, with rounded end, middle 3 teeth with tips becoming more acute proximally, proximal tooth broken. Right mandible elongated, becoming narrower distally; incisor process ending in 4 teeth, 2 middle ones the shortest (Fig. 4e). First maxilla broken, upper lacinia missing; lower lacinia 4.7 times longer than broad, armed distally with more than 10 spines; palp simple and cylindrical, with long apical setae. Second maxilla missing. First maxilliped broken, distal part of inner lobe missing. External lobe of first maxilliped broad, outer margin straight, inner margin rounded, armed with 7 spines. Second maxilliped with ischium bilobed longitudinally and fused with merus. Internal margin of merus with strong spines. Carpus broader than long, articulated along proximal margin of merus, with spines on inner margin. Exopod of second maxilliped tubular, not segmented, distally with 2 long setae. Third maxilliped missing.

First pair of pereopods missing. Second

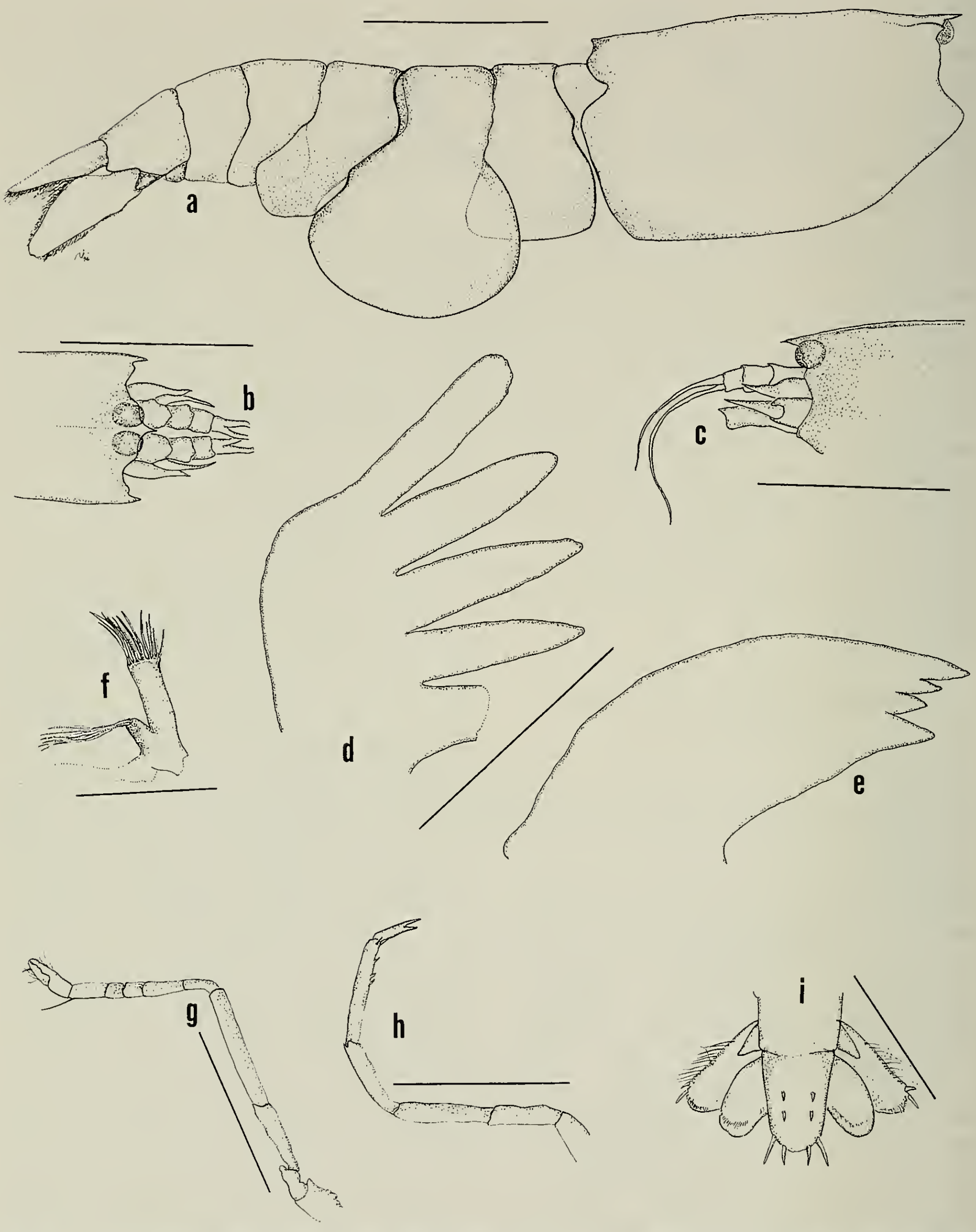

Fig. 4. *Prionalpheus nayaritae* new species, female holotype: a, lateral view of carapace and abdomen (appendages omitted); b, anterior portion of carapace, dorsal view; c, anterior portion of carapace, lateral view; d, left mandible; e, right mandible; f, first maxilla (incomplete); g, second pereopod; h, fifth pereopod; i, telson and uropods. Scale bars = 1 mm (a–c, f–i), 0.5 mm (d, e).

pereopod short and slender, basis with small rounded protuberance on distal posterior margin, carpus with 5 segments (ratio: 7.8, 10, 5, 3.8, 9), chela longer than broad with scattered setae; cutting edges of fingers simple (Fig. 4g). Fifth pereopod slender; ischium 4 times longer than deep; merus simple 4.7 times longer than deep; carpus with notch on superior distal margin; propodus the longest segment, armed with 3 spines on inferior margin and 2 on distal portion; dactyl biunguiculate, with superior hook longer and stronger than inferior one (Fig. 4h).

Uropods as long as telson; exopod with outer margin straight, setose, with 2 distal spines on external angle; endopod oval-shaped, with short setae on internal and distal margins (Fig. 4i).

Etymology.—The specific name of this species is derived from "Nayarit", the state where the holotype was collected.

Remarks.—The genus *Prionalpheus* was erected for *P. triarticulatus* Banner & Banner, 1960, based on a single specimen from Fiji, and differs from the closely related *Alpheopsis* Coutière, 1897, in the extremely modified mouthparts, specially the mandibles. Five other species had previously been assigned to *Prionalpheus: P. brachytomeus* Banner & Banner, 1971 (two specimens; Fiji and Tahiti); *P. sulu* Banner & Banner, 1971 (13 specimens; Philippines); *P. fissipes* (coutière, 1908), (one specimen; Seychelles); *P. mortoni* Bruce, 1986 (two specimens; Tolo Channel, Hong Kong); and *P. gomezi* Martinez & Carvacho, 1991 (one specimen; Cuba). Banner & Banner (1982), reported two additional specimens of *P. triarticulatus* from Lizard Island, Australia, collected at a depth of 20 m from "solid reef rock." With the single specimen reported here, the total number of known specimens belonging to *Prionalpheus* is 22. Although remarkably rare, the presence of *Prionalpheus* on the western coast of America, in the Caribbean, and the Indo-Pacific, suggests a pantropical distribution of the genus.

The single specimen, an ovigerous female, reported here from Punta de Mita, Nayarit, Mexico, differs from other known species in the area in the form of the mandibles, maxillulae, and maxillipeds, the spinulation pattern of the uropods, and the degree of exposure of the cornea of the eyes.

Family Processidae Ortmann, 1896

Processa hawaiensis Dana, 1852

Fig. 5

Material examined.–2 ♀ ovigerous, cl 4.5, 4.8 mm, tl 11.5, 15.0 mm; 31 Jan 1993; Punta de Mita, Nayarit, 20°46′N, 105°31′W; CNCR 12655. 2 ♂, cl 3.5, 3.8 mm, tl 7.5, 9.0 mm; 1 Feb 1993; Punta de Mita, Nayarit, 20°46′N, 105°31′W; CNCR 12671. 2 ♂, cl 2.5, 2.7 mm, tl 7.0, 8.0 mm; 9 Feb 1993; Playa Pescadores, Isla Isabel, Nayarit, 21°50′N, 105°54′W; CNCR 12707. 2 ♂, cl 2.5, 3.7 mm, tl 7.2, 8.5 mm; 8 Nov 1993; Playa Las Monas, Isla Isabel, Nayarit, 21°50′N, 105°54′W; CNCR 12843.

Remarks.—There are only two published records of *Processa hawaiensis,* one from Hawaii (Dana 1852), and another from Clipperton Island (Chace 1962). Morphologically, *P. hawaiensis* differs from the other four species of *Processa* known from the western coast of Mexico (*P. aequimana* Paulson, 1875, *P. peruviana* Wicksten, 1983, *P. hemphilli* Manning & Chace, 1971, *P. pipinae* Wicksten & Mendez, 1985), in that the exopod of the third maxilliped is rudimentary and in the number of segments of the carpus and merus of the second pair of pereopods. Our material differs in minor details from the description presented by Edmondson (1930). In our specimens, the merus of the chelate first pair of pereopods is longer (2.2. to 2.6 times the length of carpus) (Fig. 5e, f), and the propodus of the fourth pair of pereopods is more than three times as long as the dactylus.

Discussion

The new records presented provide significant new information on the potential for dispersal of the species, and the zoogeography of the tropical eastern Pacific.

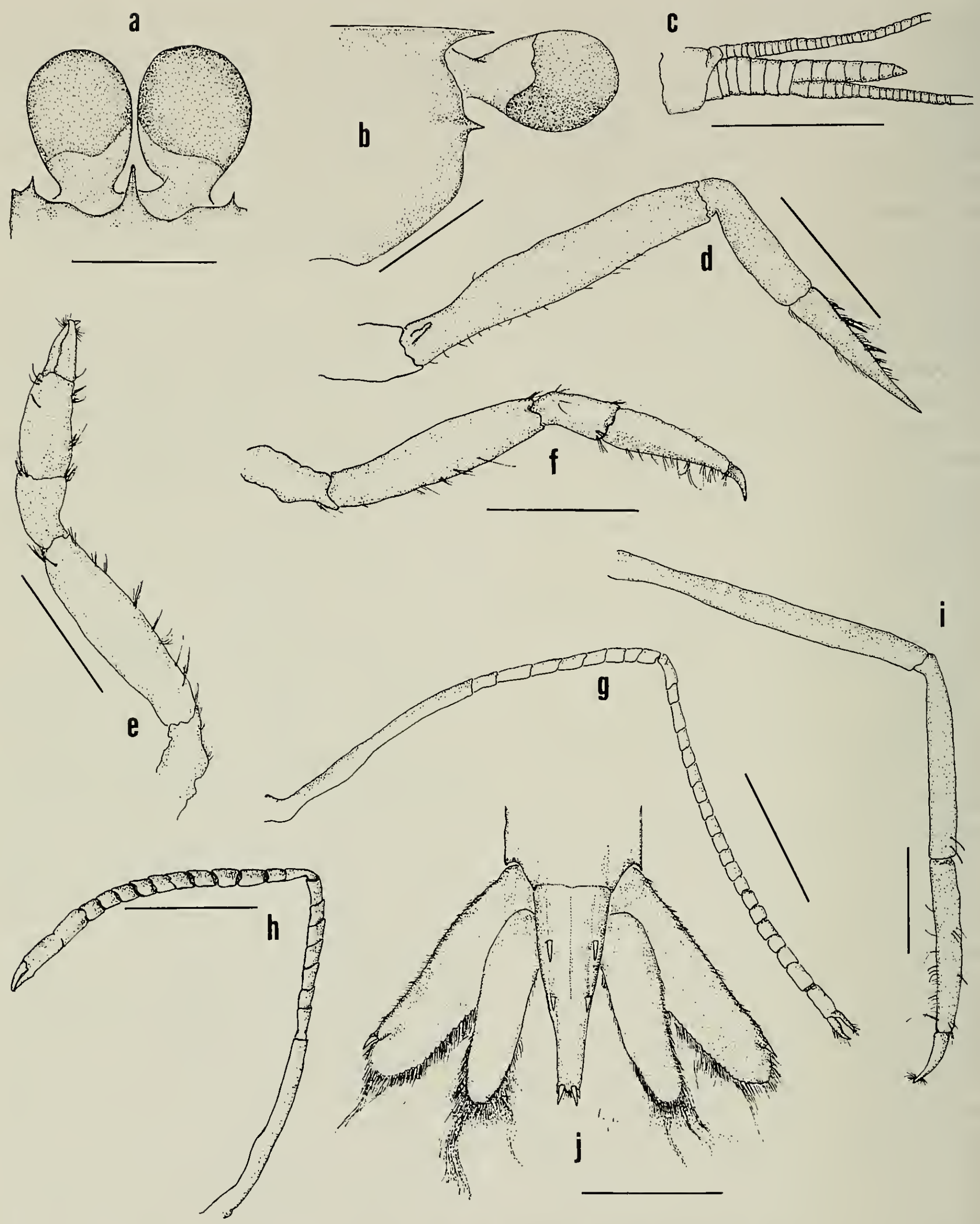

Fig. 5. *Processa hawaiensis* Dana, 1852: a, rostrum and eyes, dorsal view; b, anterior portion of carapace, lateral view; c, antennule; d, third maxilliped; e, first right pereopod; f, first left pereopod; g, second right pereopod; h, second left pereopod; i, third pereopod; j, telson and uropods. Scale bars = 1 mm.

Two of the species treated above, *Alpheus firmus* and *Synalpheus bannerorum,* were previously considered endemic to Central and South America (Abele 1975, Holthuis 1980, Kim & Abele 1988). Although minor morphological differences were observed between our material and the original descriptions (probably as result of the small samples used in the original descriptions), it is clear that the areas of distribution of these species range in the thousands of kilometers. The distribution of *Processa hawaiensis* has now been increased considerably, from Hawaii to the western coast of Mexico, including Clipperton Island (Edmondson 1930). The information presented adds to the evidence used in the elucidation of the boundaries of the Panamanian and Mexican zoogeographic provinces of the tropical eastern Pacific (Briggs 1974). The finding in Mexico of two species, *Alpheus firmus* and *Synalpheus bannerorum,* previously known from Central and South America, weakens the concept of a Mexican Province (Briggs 1974); however, the southern portion of the Pacific coast of Mexico has been poorly studied.

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Cinetorhynchus manningi, a new shrimp (Crustacea: Decapoda: Caridea: Rhynchocinetidae) from the western Atlantic

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Abstract.—A new rhynchocinetid shrimp, *Cinetorhynchus manningi*, is described and illustrated based on two ovigerous female specimens from the western Atlantic Ocean. The new species is readily distinguished from the other seven congeners by the absence of arthrobranchs on the second and third pereiopods, and constitutes the second rhynchocinetid from the Atlantic ocean.

Shrimps of the family Rhynchocinetidae differ from other caridean shrimps by having a typically movable rostrum, fine transverse striae on the surfaces of the carapace and abdominal somites, first two pairs of pereiopods robust, fingers bearing long lateral and terminal spines, and second pereiopod with carpus entire, not subdivided. Holthuis (1995) divided the genus *Rhynchocinetes* s.l. into two subgenera, *Rhynchocinetes* H. Milne-Edwards, 1837 and *Cinetorhynchus* Holthuis, 1995. Okuno (in press) elevated these subgenera to generic rank, and included in *Cinetorhynchus* six species from the Indo-Pacific and one from the Atlantic Ocean.

During this study, I examined several specimens previously identified as *C. rigens* (Gordon, 1936) captured from various localities in the Atlantic Ocean. In these materials, two ovigerous female specimens of an undescribed species were found. The new species differs from the other seven congeners by the absence of arthrobranchs on the second and third pereiopods. I provide herein the description and illustrations for this second Atlantic rhynchocinetid shrimp.

Method of measuring follows Okuno (in press). The postorbital carapace length is abbreviated as CL. The abbreviation USNM indicates National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Cinetorhynchus manningi, new species
Figs. 1, 2

Rhynchocinetes rigens.—Manning, 1961:1 (in part) (not *Rhynchocinetes rigens* Gordon, 1936).

Material.—Caribbean Sea: USNM 277772, holotype, ovigerous female, 8.5 mm CL, Virgin Islands, Eagle Shoal, 10.5 m, 1 Feb 1961; USNM 277773, paratype, ovigerous female, 8.0 mm CL, Florida, off Elliot Key, Bache Shoals, 4.5 m, 4 May 1960, coll. C. R. Robins.

Description.—A rather robust rhynchocinetid shrimp of subcylindrical body form (Fig. 1).

Carapace with many fine transverse striae. Three acute teeth on dorsal carina behind rostral articulation, anterior tooth largest. Antennal spine sharply pointed, considerably exceeding anterior margin of carapace. Anterolateral angle of carapace rounded, without pterygostomian spine.

Rostrum (Fig. 2A) well developed, indistinctly articulated with carapace, distinctly overreaching apex of scaphocerite; length 1.7 times as long as carapace; lateral carina distinct, reaching end of proximal third of rostrum, continuous with upper orbital margin; dorsal margin with 2 large proximal

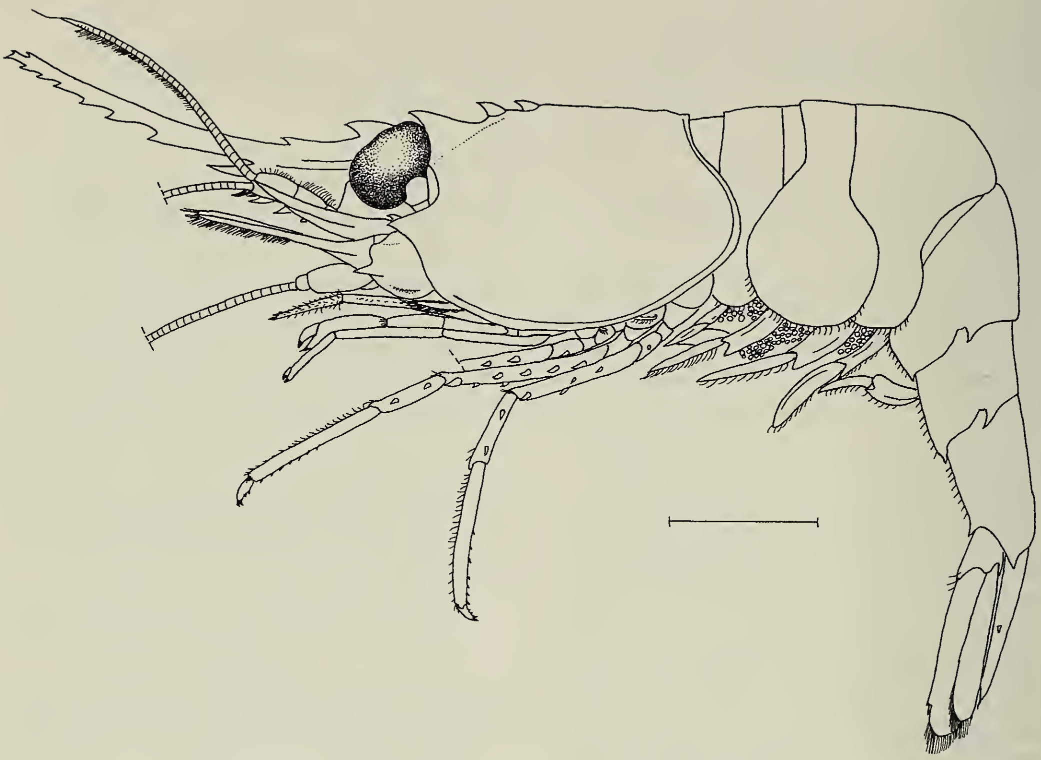

Fig. 1. *Cinetorhynchus manningi,* new species. Ovigerous female, holotype (USNM 277772, 8.5 mm CL), lateral view. Scale equals 5 mm.

teeth, 2 small teeth subterminally; ventral margin with 10 teeth, proximal 4 teeth strong, separated by distinct interval from proximal tooth of distal series, distal 6 teeth considerably smaller than proximal four teeth, decreasing in size distally.

Abdominal somites with fine transverse striae; pleura of first 3 somites rounded; fourth somite with small, distinct or indistinct protrusion posteroventrally; fifth somite with acute protrusion posteroventrally; posterolateral margin of fourth and fifth somites each with acutely pointed tooth directed posteriorly; sixth somite rather compressed, 0.6 times as long as carapace, 2.1 times as long as its width, with acutely pointed posteroventral spine directed obliquely backwards, with acute anal spine between uropodal basicerites.

Telson (Fig. 2B) 0.6–0.7 times as long as carapace, 1.1–1.2 times as long as sixth abdominal somite, rather convex dorsally; spination of dorsal surface in holotype abnormal, with 2 small spines on right side and a single small spine at left side, paratype has normal spination, armed with 3 pairs of small spines; posterior margin prominent, bearing 3 pairs of spinules at each side, intermediate spinules longest.

Eye with pigmented, rounded cornea, eyestalk much slenderer than cornea.

Antennular peduncle (Fig. 2C) reaching end of proximal third of rostrum; thickened part of the upper flagellum reaching to about rostral apex; proximal segment with distal margin acutely pointed, inner margin ventrally with acute spine, surface concave; stylocerite well developed, reaching distal margin of distal segment; statocyst longitudinally oval.

Scaphocerite (Fig. 2D) well developed, reaching midlength of rostrum, 0.8 times as

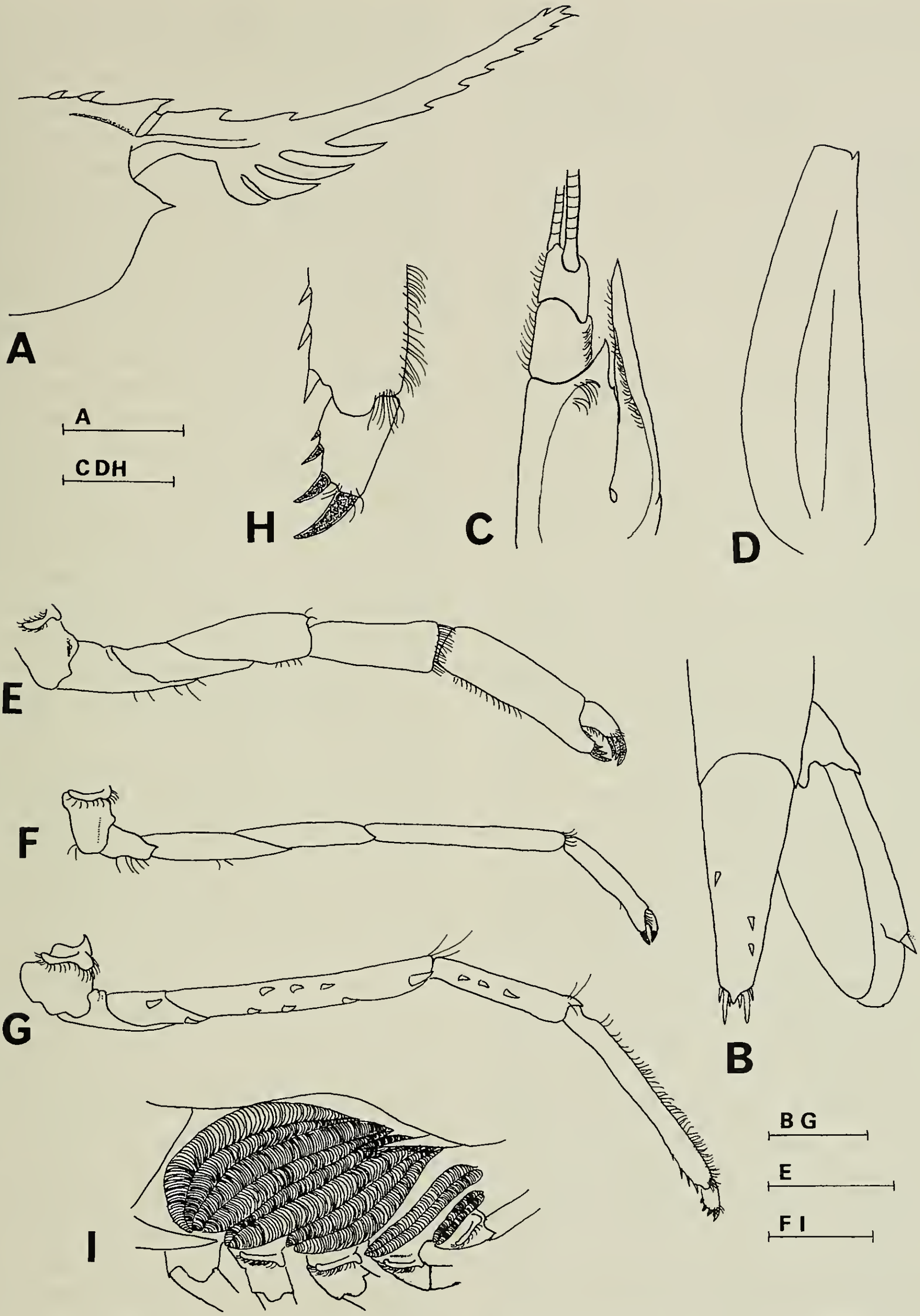

Fig. 2. *Cinetorhynchus manningi,* new species. A–H, ovigerous female, holotype (USNM 277772, 8.5 mm CL); I, ovigerous female, paratype (USNM 277773, 8.0 mm CL). A, anterior part of carapace with rostrum; B, telson and right uropod; C, antennular peduncle; D, scaphocerite; E, first pereiopod; F, second pereiopod; G, third pereiopod; H, dactylus of third pereiopod; I, gill complement of pereiopods. Scales equal 5mm (A), 2 mm (B–G, I), and 0.5 mm (H).

Table 1.—*Cinetorhynchus manningi,* new species. Branchial formula.

	Maxillipeds			Pereiopods				
	I	II	III	I	II	III	IV	V
Pleurobranchs	—	—	—	1	1	1	1	1
Arthrobranchs	—	—	2	1	—	—	—	—
Podobranchs	—	1	—	—	—	—	—	—
Epipods	1	1	1	1	1	1	1	—
Exopods	1	1	1	—	—	—	—	—

long as carapace, 3.3–3.4 times as long as its maximum width; external distal spine acute, reaching level of distal margin of lamella; basicerite covered with fine transverse striae, with acute spine directed anteriorly and terminal rounded lobe just above spine; carpocerite reaching end of proximal third of scaphocerite.

Branchial formula as shown in Table 1.

Mouthparts typical of genus. Mandible with three-segmented palp, distal segment rounded distally, with short dense setae, intermediate segment longest of all, distal margin with long sparse setae; incisor process stout, with sharp distal teeth; molar process subcylindrical, broad, with feeble distal setae and numerous corneous slits. First maxilla with feebly bifid slender palp, with denticulate long setae distally; distal lacinia broad, lateral margin convex, with sparse setae, distal margin straight, with 2 rows of small, stout spinules; proximal lacinia broader than distal lacinia, feebly square distally. Second maxilla with distinct palp, proximally broad, distally slender; coxal endite broad, distal margin truncate, with numerous long setae distally; distal endite bilobed, upper lobe feebly square distally, broader than lower lobe, with dense setae distally, lower lobe with rather straight distal margin, with dense setae; scaphognathite well developed, anterior lobe with feebly square distal end, posterior lobe very slender, inner margin convex, elongated posteriorly, reaching anterior part of third pleurobranch. First maxilliped with elongate, 3-segmented palp, intermediate segment longest of all, distal segment very small; distal endite expanded distally, broader than proximal endite, with distal margin with dense setae; proximal endite rounded, with dense setae distally; exopod well developed, caridean lobe slender, flagellum with numerous setae distally; epipod large, rounded. Second maxilliped with oval epipod having well developed podobranch; distal margin of dactylus almost straight, with long dense setae; propodus with distal margin rounded, inner margin feebly expanded. Third maxilliped reaching distal third of scaphocerite; antepenultimate segment with acute spine distolaterally; penultimate segment 0.3 times as long as carapace, with sparse setae on outer surface; ultimate segment 0.5 times as long as carapace, 1.5–1.6 times as long as penultimate segment, with 6-8 dark horny claws at apex, covered uniformly with dense setae except distal fourth.

First pereiopod (Fig. 2E) stout, reaching end of proximal third of scaphocerite; chela slightly compressed, 0.4 times as long as carapace, 1.6–1.7 times as long as carpus, palm with short dense setae on proximal ventral margin, both fingers slightly curved mesially, with dark claws terminally; carpus 0.2 times as long as carapace, distal margin truncate, with dense cluster of rather long setae.

Second pereiopod (Fig. 2F) slenderer than first pereiopod, falling short of midlength of scaphocerite; chela 0.3 times as long as carapace, both fingers slightly curved inside, with dark horny claws terminally; carpus long, 0.4–0.5 times as long as carapace, 1.5–1.6 times as long as chela.

Third to fifth pereiopods rather slender, similar; dactyli (Fig. 2H) with three horny claws posterior to terminal largest claw, decreasing in size proximally; propodi with slightly dense setae on upper margin, with sparse spinules at distal ⅖ of lower margin, terminal spinule largest of all; ischia with 2 articulated spines on outer surface and lower margin. Third pereiopod (Fig. 2G) reaching level of distal end of scaphocerite; merus 0.6–0.7 times as long as carapace, 2.0

times as long as carpus, with 4–5 articulated spines on outer surface, proximal spines equidistant, distal spine subterminal, distinctly separated from proximal series, with 3 spines on lower margin, and sparse long setae dorsodistally; carpus 0.3 times as long as carapace, with 2–3 articulated spines on outer surface, with sparse long setae at upper margin preterminally; propodus 0.5–0.6 times as long as carapace, 1.7 times as long as carpus. Fourth pereiopod falling short of distal end of scaphocerite; merus 0.6 times as long as carapace, with 4–5 articulated spines on outer surface, 2–3 articulated spines on lower margin; carpus 0.3–0.4 times as long as carapace, with 2 articulated spines on outer surface, with sparse long setae at upper margin preterminally; propodus 0.6 times as long as carapace, 1.6–1.8 times as long as carpus. Fifth pereiopod reaching midlength of scaphocerite; merus 0.5–0.6 times as long as carapace, 1.5–1.6 times as long as carpus, with three articulated spines on outer surface, a single spine situated at distal third of lower margin; carpus 0.4 times as long as carapace, spination similar to that of fourth pereiopod; propodus 0.6 times as long as carapace, 1.6 times as long as carpus.

Uropodal exopod (Fig. 2B) with articulated and non-articulated spines at distal third of outer border.

Coloration.—Unknown.

Etymology.—The present new species is named for Dr. Raymond B. Manning, in honor of his valuable contributions to our knowledge of western Atlantic rhynchocinetid shrimp.

Distribution.—Known only from the Virgin Islands and Florida.

Remarks.—Cinetorhynchus manningi differs from the other seven congeners by the absence of arthrobranchs on the second and third pereiopods (Fig. 2I), whereas other species of *Cinetorhynchus* have an arthrobranch on each of the first three pereiopods. *Cinetorhynchus manningi* is the second species of Rhynchocinetidae from the Atlantic Ocean. The present new species is distinguished from the other Atlantic species, *C. rigens* (Gordon, 1936), by having three accessory claws on the inferior margin of the dactyli of the third to fifth pereiopods, a small posteroventral protrusion on the fourth abdominal somite, a well developed podobranch on the second maxilliped and the distinct interval between the proximal four teeth and the distal smaller teeth on ventral margin of rostrum. *Cinetorhynchus rigens* possesses only two accessory claws on the dactyli of the ambulatory pereiopods, unarmed, rounded posteroventral angle of the fourth abdominal somite, an oblong vestige of podobranch on the second maxilliped, and ventral teeth on the rostrum decrease regularly in size distally (Gordon 1936, Okuno 1996).

The dorsal spination of the telson in the holotype is an abnormal condition, and can be attributed to intraspecific variation. The paratype does exhibit the normal condition.

The holotype of the present new species was included in the various specimens reported as *Rhynchocinetes rigens* (= *C. rigens*) by Manning (1961). In his report, Manning (1961) mentioned that there are two patterns of colorations in the western Atlantic population of *C. rigens.* However, the type specimens of *C. manningi* had lost their color pattern when I examined them. In some publications, beautiful underwater photographs have been included of an unidentified Atlantic rhynchocinetid species, the coloration of which definitively disagrees with that of *C. rigens* (see Baensch & Debelius 1992; Debelius 1983, 1984; Humann 1992). This unidentified species has the red ground color on the whole body surface covered with fine pale white spots on the carapace, and five pale white transverse bands on the abdominal somites. I have not seen any specimen having the coloration mentioned above. Although the coloration is diagnostic in rhynchocinetids (Nomura & Hayashi 1992; Okuno 1994a, 1994b, 1996; Okuno & Takeda 1992), I could not determine that of the new species during this study.

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Systematics, distribution, and host specificity of *Edrabius* Fauvel (Insecta: Coleoptera: Staphylinidae)

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Abstract.—Systematics, distribution, and host relations of the amblyopinine genus *Edrabius* (Coleoptera: Staphylinidae) are reviewed. Herein, we recognize 11 species in the genus *Edrabius,* all of which are obligate associates of South American caviomorph rodents of the families Caviidae, Ctenomyidae, and Octodontidae (Mammalia: Rodentia), and restricted to the southern cone of the continent. Three new species are described: *Edrabius grandis* (host: *Ctenomys coyhaiquensis* and *C. haigi*); *Edrabius australis* (host: *Ctenomys maulinus maulinus*); and *Edrabius chilensiformis* (host: *Octodon degus*). New distribution and host records are given for *E. alticolus* Seevers, *E. argentinus* Seevers, *E. chilensis* Scheerpeltz, *E. peruanus* Seevers, *E. philippianus* Fauvel, and *E. weiseri* Seevers. Occurrence of *Edrabius* on octodontid rodents is reported for the first time (*E. chilensis* from *Aconaemys* and *E. chilensiformis* from *Octodon*). The genus *Edrabius* was formerly known to occur in association with various species of *Ctenomys,* with the exception of one species, *E. kuscheli,* associated with *Galea musteloides* (Caviidae).

Resumen.—Se presenta una revisión de la sistemática, la distribución y las relaciones de los hospederos de los amblyopininos del género *Edrabius* (Coleoptera: Staphylinidae). Se reconocen 11 especies de *Edrabius,* todas parásitos obligados de roedores caviomorfos sudamericanos de las familias Caviidae, Ctenomyidae y Octodontidae (Mammalia: Rodentia). Se describen tres nuevas especies: *Edrabius grandis,* hospedador: *Ctenomys haigi*); *Edrabius australis,* hospedador: *Ctenomys maulinus maulinus*); y *Edrabius chilensiformis,* hospedador: *Octodon degus*). Se entregan nuevos registros distribucionales y de hospederos para *E. alticolus* Seevers, *E. argentinus* Seevers, *E. chilensis* Scheerpeltz, *E. peruanus* Seevers, *E. philippianus* Fauvel y *E. weiseri* Seevers. Por primera vez se reporta la presencia de *Edrabius* en roedores octodóntidos (*E. chilensis* en *Aconaemys* y *E. chilensiformis* en *Octodon*). El género *Edrabius* anteriormente se conocía solamente asociado a diferentes especies de *Ctenomys,* con la excepción de una especie, *E. kuscheli,* asociada a *Galea musteloides* (Caviidae).

Perhaps the most interesting and enigmatic of all insect-vertebrate interactions are those of rove beetles of the tribe Amblyopinini (Coleoptera: Staphylinidae) and their mammal hosts. Amblyopinine beetles are unique members of the family Staphylinidae because of their obligate association with mammals; most of the 40,000 described species of staphylinids are free-living predators (Ashe & Timm 1987b). All known species of amblyopinines have been most often found attached to the fur of mammalian hosts or in the hosts' nests. Six genera and more than 55 species have been described in the tribe Amblyopinini; five genera are restricted to the Neotropical region and one is found in the Australian region (Ashe & Timm 1988). Those restricted to the Neotropical region include: *Amblyopinodes* Seevers, *Amblyopinus* Solsky, *Chilamblyopinus* Ashe and Timm, *Edrabius* Fauvel, and *Megamblyopinus* Seevers; a single monotypic genus, *Myotyphlus* Fauvel, is restricted to Australia and Tasmania (Ashe & Timm 1988, 1995; Seevers 1944, 1955).

Amblyopinines were, until recently, believed to be obligate, blood-feeding ectoparasites. However, the Central American *Amblyopinus* have a mutualistic relationship with their hosts rather than a parasitic one, and the conclusion that other amblyopinines are parasitic is not supported by available evidence. Beetles living on various rodents that have different nesting biologies show significantly different behaviors, and nesting biology of the hosts undoubtedly played a major role in the evolution of this mutualistic relationship (Ashe & Timm 1987a, 1987b, 1988; Timm & Ashe 1987, 1988, 1989).

Hosts of amblyopinines are primarily cricetine and caviomorph rodents and South American marsupials. The evolution of this association is exceptionally interesting, both in terms of the ecology, evolution and biogeography of the beetles themselves, and also of the mammals with which they are associated. Members of each amblyopinine species are host specific, and members of the genera and intergeneric higher taxa have a tendency to be associated with a particular group of mammals. Our concerted field efforts in recent years have uncovered a high degree of host specificity in these rather large, active beetles (Ashe & Timm 1987a, 1995; Timm & Ashe 1987, and see below).

One of the most poorly known of the amblyopinine genera is *Edrabius*. Currently, eight species of *Edrabius* are known from southern Peru, Argentina, and Chile. These are: *E. alticolus* Seevers; *E. argentinus* Seevers; *E. chilensis* Scheerpeltz; *E. kuscheli* Scheerpeltz; *E. pearsoni* Seevers; *E. peruanus* Seevers; *E. philippianus* Fauvel; and *E. weiseri* Seevers. Of the species of *Edrabius* currently recognized, most occur on species of *Ctenomys* (Rodentia: Ctenomyidae), the tuco-tucos. However, in this paper we also report their occurrence on two additional genera of rodents, *Aconaemys* and *Octodon* (Octodontidae). Ctenomyids and octodontids are caviomorph rodents that are found throughout southern South America. They occur in Argentina, Chile, southern Bolivia, and Peru and range in elevation from sea level to 4700 m (Mares & Ojeda 1982).

Little information is available about the life history or habits of the species of *Edrabius,* or about the nature of the beetle-mammal interaction. Fauvel (1900) reported the observations of Philippi that adults and larvae of *Edrabius philippianus* were found around the anus of a species of *Ctenomys* and caused damage to the skin. Fauvel received adult beetles that he subsequently described, but he did not mention the larvae in his description, and he may not have actually received them. There have been no subsequent reports of amblyopinine larvae on any host, although hundreds of mammals carrying adult amblyopinines have been examined. Timm & Ashe (1989) described larval *Edrabius* that were found in the nest of *Ctenomys* in Chile.

In this paper we: describe three new species of *Edrabius*; review previously published information about *Edrabius*; and provide new information on host and geographic distributions of *Edrabius.*

Materials and Methods

Recent field work in Chile by one of us (MHG) as part of his ongoing research on the systematics and biogeography of *Cten-*

omys, as well as that of other field workers provide significant new information about, and specimens of, *Edrabius.* The new material prompted us to review the systematic status of all the species of *Edrabius* in Argentina, Bolivia, Chile, and Peru.

In the course of this study, we examined the types and dissected aedeagi of all described species of *Edrabius* except *E. philippianus.* According to Seevers (1955) the holotype, and only known specimen, of *E. philippianus* is a female. He gives a detailed description of this specimen, including illustrations of distinctive pronotal features. None of the species described here match the description of *E. philippianus* given by Seevers. We also examined the specimens that Scheerpeltz (1957) identified as *E. philippianus* and that he used in his comparisons with other species. We are convinced that these specimens are incorrectly identified. They do not have the distinctive pronotal shape that Seevers (1955) described for *E. philippianus,* and other described features also do not fit Scheerpeltz's specimens very well (though these are more qualitative and less distinctive). In addition, all of Scheerpeltz's specimens are from Argentina, whereas the type of *E. philippianus* is from Antofagasta, in the Atacama Desert of Chile.

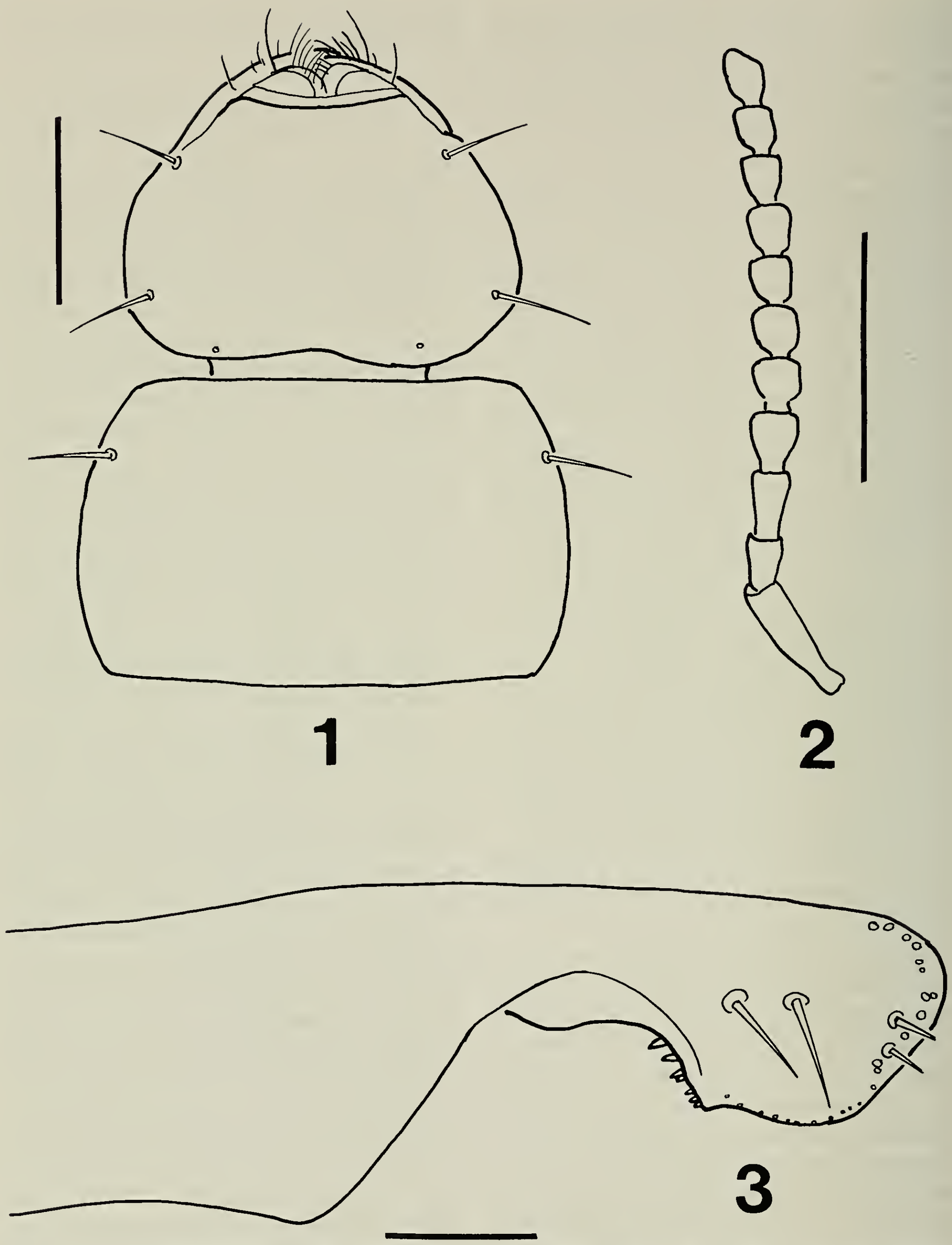
Specimens of *Edrabius* examined are deposited in: Instituto de Ecología y Evolución, Universidad Austral de Chile, Valdivia, Chile (IEEUACH); Field Museum of Natural History, Chicago, Illinois (FMNH); Snow Entomological Museum, University of Kansas, Lawrence (KSEM); and Naturhistorisches Museum Wien, Vienna, Austria (NHMW). The mammal hosts are deposited in: Instituto de Ecología y Evolución, Universidad Austral de Chile, Valdivia, Chile (IEEUACH); American Museum of Natural History, New York (AMNH); Field Museum of Natural History (FMNH); Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico (MSB); Museum of Vertebrate Zoology, University of California, Berkeley, California (MVZ).

Edrabius grandis, new species
Figs. 1–3

Description.—Length 9.0–10.5 mm. Uniformly light reddish-brown. Head shape variable, small males and females with lateral margins tapered uniformly from rounded posterior angles to front, heads of larger males with lateral margins inflated and broadly rounded in posterior half (Fig. 1); integument of head with dense, prominent, small-meshed, isodiametric microsculpture, surface not strongly shining; without micropunctures; microsetae on lateral margins behind eye very small and sparsely distributed. Antenna (Fig. 2) longer than head and pronotum together, article 2 slightly longer than, or subequal to, article 3, article 4 slightly elongate; article 5 quadrate to slightly elongate; articles 6-10 slightly to moderately elongate. Pronotum (Fig. 1), moderately transverse, about 1.5–1.6 times as wide as long; without postero-lateral macroseta; microsetae on antero-lateral margins very small and sparsely distributed, microsetae extended from near middle of lateral margin of pronotum to antero-lateral angles and very sparsely along lateral third of anterior margin; integument with dense, prominent, small-meshed, isodiametric microsculpture, sculpticells more prominent laterally than medially, surface not strongly shining (except in specimens in which the microsculpture has been eroded away due to abrasion); surface without micropunctures. Elytra with very fine, widely dispersed, golden-yellow microsetae, punctures very small. Abdomen uniformly covered with silky vestiture of moderately dense, very fine, yellowish microsetae.

Male.—Posterior margin tergum VIII emarginate. Posterior margin of sternum VIII broadly and evenly emarginate, maximum depth of emargination about 0.5 times width of emargination.

Aedeagus.—As in Fig. 3.



Figs. 1–3. *Edrabius grandis* n. sp. 1. Head and prothorax, dorsal (scale = 1.0 mm); 2. Antenna (scale = 1.0 mm); 3. Apex of aedeagus, lateral (scale = 0.1 mm).

Holotype.—Male, with labels as follows: "Argentina: Prov. Río Negro; 13 km WSW Comallo, el. 1150 m, 15 Nov 1987, A. K. and O. P. Pearson #OPP 7435, ex. *Ctenomys haigi* (MVZ 175156)." "HOLOTYPE, *Edrabius grandis* Ashe, Timm, & Gallardo, Designated J. S. Ashe, R. M. Timm, and M. L. Gallardo 1995." Deposited in the Snow Entomological Museum, University of Kansas, Lawrence, Kansas.

Paratypes.—6, from the following localities. Argentina: Río Negro Prov., 3-V-1986, M. H. Gallardo #833, ex. *Ctenomys haigi* (IEEUACH 1535) ♀, 2 males 2 females. Same locality, date, and collector, MHG #837, ex. *Ctenomys coyhaiquensis* (IEEUACH 1539), 1 male. Chile: Coyhaique Prov.; 4.5 km SE Coyhaique Alto, Fundo Los Flameneos, 750 m; M. H. Gallardo #1092, ex. *Ctenomys coyhaiquensis* ♂ (IEEUACH 4233), 1 male. Paratypes deposited in IEEUACH and KSEM.

Distribution.—Known from the Río Negro Valley in Argentina and adjacent Coyhaique in Chile.

Hosts.—Collected from *Ctenomys coyhaiquensis* in Coyhaique, Chile, and *C. haigi* in Río Negro Province, Argentina.

Discussion.—Specimens of this species are among the largest of any described species of *Edrabius.* They can be recognized by: large size; relatively elongate antenna with elongate antennomeres; head and pronotum densely reticulate with isodiametric sculpticells; integument of head and pronotum without micropunctures; microsetae on lateral margins of head and pronotum very small and sparsely distributed; and, the distinctive aedeagus.

Edrabius australis, new species
Figs. 4–6

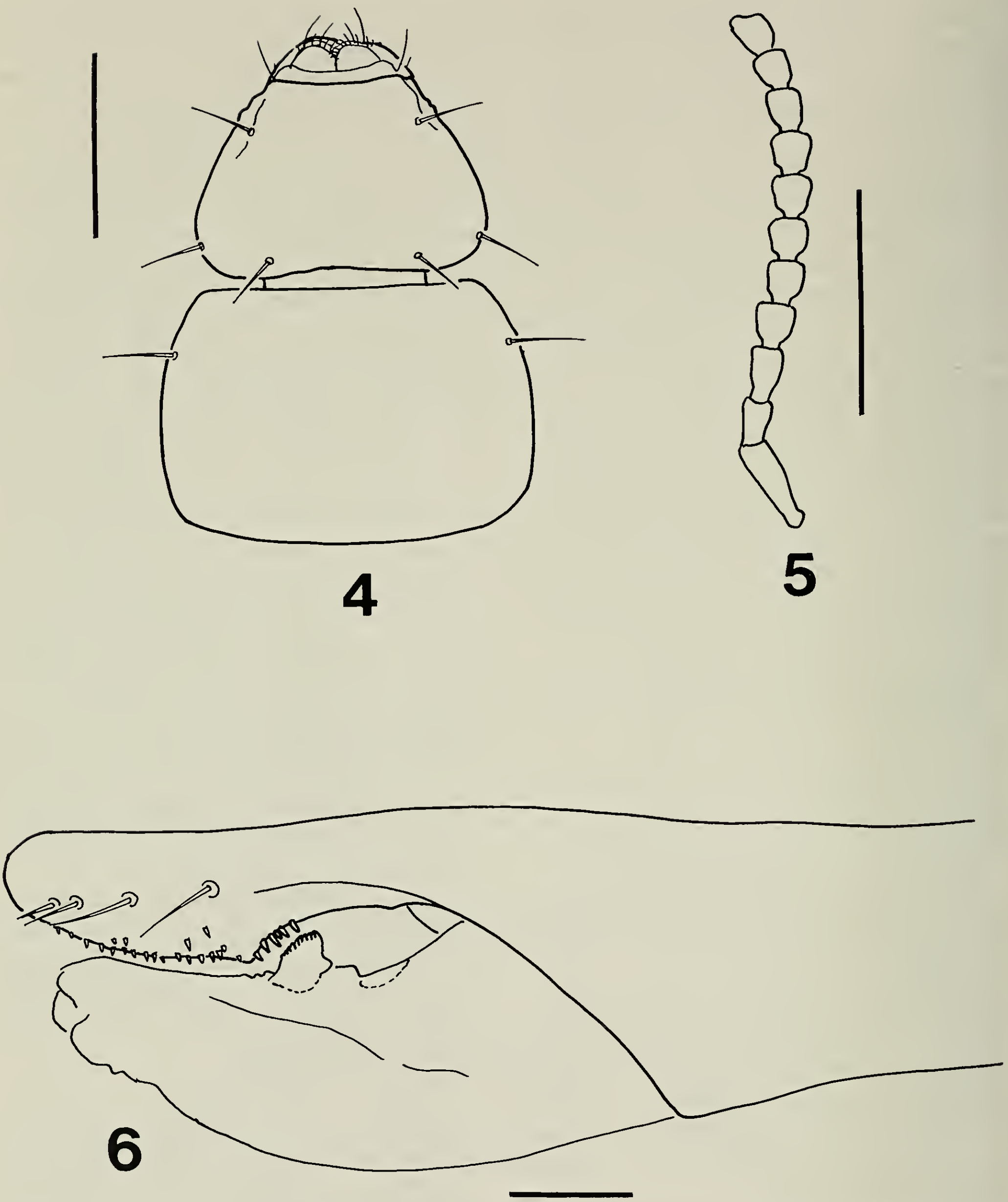
Description.—Length 7.0–9.0 mm. Uniformly light reddish-brown. Head shape (Fig. 4) with lateral margins uniformly tapered from rounded posterior angles anteriorly; integument of head with faint, isodiametric microsculpture, microsculpture obsolete to absent postero-medially, surface strongly shining; micropunctures extremely fine and inconspicuous; microsetae on lateral margins of head behind eye sparse to moderate in size and number. Antenna (Fig. 5) longer than head and prothorax together; article 2 slightly shorter than, to subequal to, length of article 3, article 4 quadrate to slightly elongate, articles 5–10 quadrate to slightly elongate. Pronotum (Fig. 4) moderately transverse, about 1.4–1.5 times as wide as long; without postero-lateral macroseta; microsetae on antero-lateral border variable from sparse and located in antero-lateral half, to moderately dense and extended along lateral margin from near posterior third of pronotum to antero-lateral angles and along lateral third of anterior margin; integument with faint microsculpture, sculpticells isodiametric laterally but slightly elongate medially, surface strongly shining; micropunctures extremely fine and inconspicuous. Elytra with moderate sized, uniformly distributed, yellowish microsetae, punctures small. Abdomen uniformly covered with silky vestiture of moderately dense yellowish microsetae.

Male.—Posterior margin of tergum VIII broadly and moderately emarginate. Posterior margin of sternum VIII broadly and deeply emarginate, emargination broadly rounded internally, width of emargination about 2.3 times depth.

Aedeagus.—As in Fig. 6.

Holotype.—Male, with labels as follows: "Chile: Bío-Bío Prov.; Laguna Laja, 21-III-1987, M. H. Gallardo 1011 & 1012, ex. *Ctenomys maulinus maulinus* (IEEUACH 1640 & 1641)." "HOLOTYPE, *Edrabius australis* Ashe, Timm, & Gallardo, Designated J. S. Ashe, R. M. Timm, and M. H. Gallardo 1995." Deposited in Zoological Collections of the Universidad Austral de Chile, Valdivia, Chile.

Paratypes.—12, same data as holotype; 11, Chile: same locality, date, and collector, MHG #1017, ex. *Ctenomys maulinus mau-*



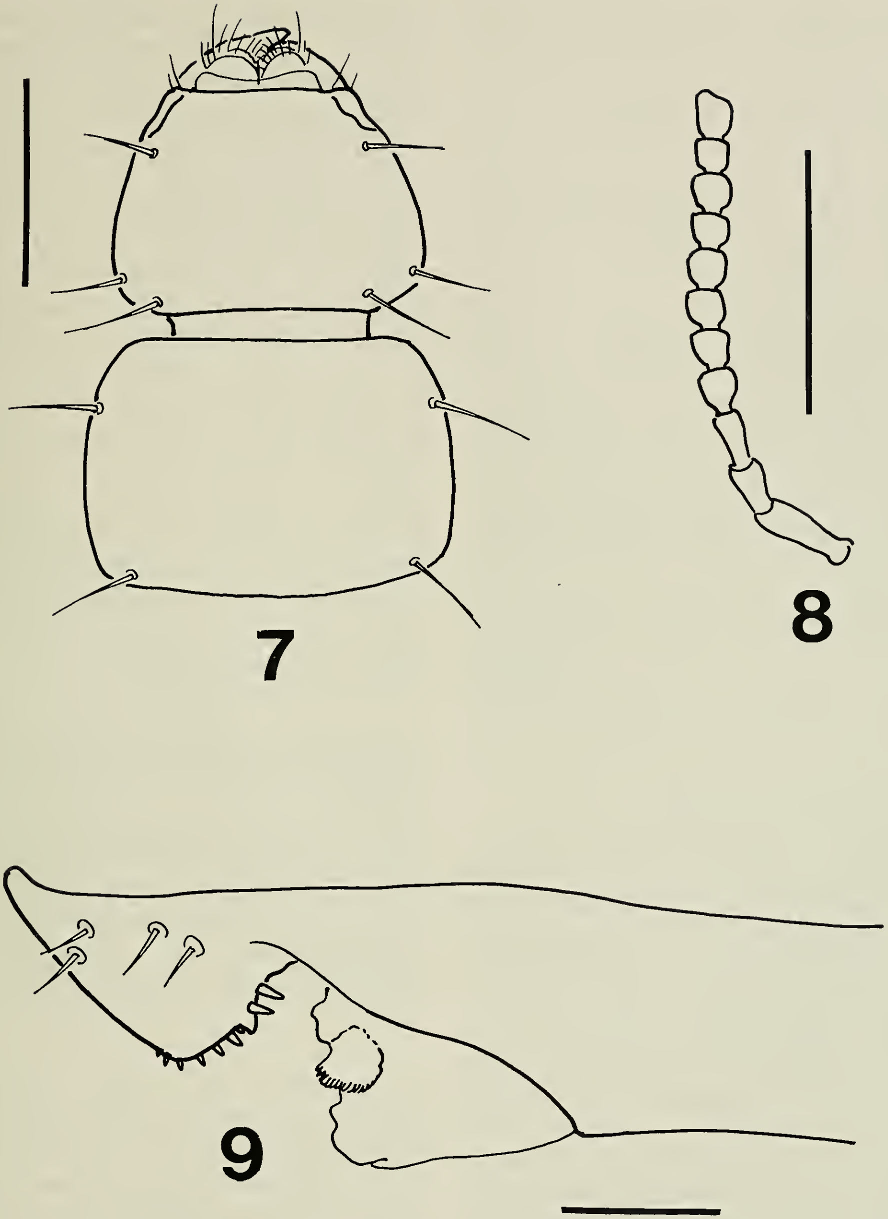
Figs. 4–6. *Edrabius australis* n. sp. 4. Head and prothorax, dorsal (scale = 1.0 mm); 5. Antenna (scale = 1.0 mm); 6. Apex of aedeagus, lateral (scale = 0.1 mm).

linus (IEEUACH 1646). Paratypes deposited in IEEUACH and KSEM.

Distribution.—Known only from Petronquines, Laguna Laja, Bío-Bío Province, Chile.

Host.—Collected only from *Ctenomys maulinus maulinus.*

Discussion.—This species can be distinguished by the relatively faint reticulation of the head and prothorax with extremely



Figs. 7–9. *Edrabius chilensiformis* n. sp. 7. Head and prothorax, dorsal (scale = 1.0 mm); 8. Antenna (scale = 1.0 mm); 9. Apex of aedeagus, lateral (scale = 0.1 mm).

fine and inconspicuous micropunctures, and the distinctive aedeagus.

Edrabius chilensiformis, new species

Figs. 7–9

Description.—Length 5.0–6.0 mm. Reddish-brown. Head shape (Fig. 7) rounded and tapered from broadly-rounded posterior angles to anterior margins; integument with moderate, elongate, irregularly wavy microsculpture, sculpticells obsolete to absent medially, integument strongly shining; micropunctures numerous, very minute; microsetae on lateral margins behind eye moderately dense. Antenna (Fig. 8) about as long as head and pronotum together; article 2 subequal in length to article 3, articles 4–10 quadrate to subquadrate. Pronotum (Fig. 7) moderately transverse, about 1.4 times as wide as long; with postero-lateral macroseta; microsetae on antero-lateral margin prominent and more or less densely distributed in anterior half of lateral margins and along anterior third of anterior margins, integument with faint, irregular wavy microsculpture, sculpticells obsolete to absent medially, surface strongly shining; micropunctures numerous, very minute. Elytra with moderately dense, yellowish microsetae, punctures moderate in size. Abdomen uniformly covered with silky vestiture of very densely distributed, yellowish microsetae.

Male.—Posterior margin of tergum VIII very shallowly and broadly emarginate. Posterior margin of sternum VIII broadly and deeply emarginate, emargination broadly rounded; width of emargination about 2.0 times depth.

Aedeagus.—As in Fig. 9.

Holotype.—male, with labels as follows: "Chile: Coquimbo Prov.; 10 km N Puente Los Molles, 32°09′S, 71°31′W, 26-VII-1976, R. E. Martin #1470, ex. *Octodon degus* ♀ (FMNH 119659)." "HOLOTYPE, *Edrabius chilensiformis* Ashe, Timm, & Gallardo, Designated J. S. Ashe, R. M. Timm, and M. L. Gallardo 1995." Deposited in the Field Museum of Natural History, Chicago, Illinois.

Paratypes.—3, same data as holotype. Paratypes deposited in FMNH and KSEM.

Distribution.—Known only from Coquimbo Province, Chile.

Host.—Collected from *Octodon degus* (Octodontidae).

Discussion.—This species is closely related to *Edrabius chilensis* Scheerpeltz from which it can be distinguished by the denser abdominal setation and distinctive aedeagus of *E. chilensiformis. Edrabius chilensis* and *E. chilensiformis* appear to form a distinctive monophyletic group within *Edrabius* characterized by the synapomorphous condition of an upturned and apically pointed aedeagus (see Fig. 9, and fig. 2C in Scheerpeltz 1957). In contrast, these two species appear to retain several plesiomorphic characteristics not found among other known *Edrabius.* These apparent plesiomorphies include: presence of a postero-lateral seta on the pronotum (also found among many free-living quediines, as well as the amblyopinines—*Amblyopinodes, Amblyopinus, Megamblyopinus,* and *Myotyphlus,* but not present on other known *Edrabius*), and the very weakly developed cluster of long aciculate setae on the apex of the lateral plates of abdominal segment 9 (very strongly developed among other known *Edrabius*—see Seevers 1955, fig. 44G). This suggests that these two species occupy a relatively basal position in the phylogeny of *Edrabius.*

It is also interesting that both of these species are known from caviomorph rodents other than *Ctenomys* in the family Octodontidae: *Edrabius chilensis* from the rock rat, *Aconaemys fuscus* and *E. chilensiformis* from the degu, *Octodon degus.* In contrast, most other *Edrabius* are known from *Ctenomys* (the only exception is *E. kuscheli* from the nest of a cui, *Galea musteloides* (Caviidae), but see below).

New Records

Edrabius alticolus Seevers. Bolivia: Dept. Oruro; 3.5 km E Huancaroma, 6-VIII-1984, ex. *Ctenomys opimus opimus* ♀, NK 11550 (MSB 55377), 1 male. Oruro; 2.5 km NE Huancaroma, 3720 m, 6-VIII-1984, ex. *Ctenomys opimus opimus* ♀, NK 11566 (AMNH 260837), 2 males. Oruro; 1 km N, 5 km W Pomata Ayte, Río Barros, 11-IX-1986, ex. *Ctenomys opimus opimus* ♂, NK 14549 (AMNH 263040), 1 male 1 female. Oruro; Huancaroma, 2-X-1986, ex. *Ctenomys opimus opimus* ♀, NK 14765 (MSB 57197), 2 males. Chile: Parinacota Prov.; D. Reise #2710, ex. *Ctenomys opi-*

mus (IEEUACH 4332), 2 males 2 females (KSEM and IEEUACH).

Edrabius argentinus Seevers. Argentina: Mendoza Prov.; 5.7 km NW Villavicencio, 2800 m, 31 December 1981, Richard D. Sage #10656, ex. *Ctenomys haigi* (MVZ 162936), 1 male (KSEM). Seevers (1955: 258) described *E. argentinus* from "ex nido de *Ctenomys*" from Argentina: Catamarca; Hualfin (near Tucumán). On the basis of the locality, we believe the host to be *Ctenomys tucumanus.*

Notes.—This specimen differs from the type series of *Edrabius argentinus* in having a slightly longer antenna with longer articles 4–10, more uniformly rounded lateral margins of the pronotum and mostly isodiametric microsculpture on pronotum (more wavy on specimens in type series). However, the aedeagus is highly distinctive and cannot be distinguished from the aedeagus of the holotype of *E. argentinus.* Therefore, we have chosen to assign the specimen from Mendoza Province to *E. argentinus* in spite of the minor differences noted above. It is possible that a new subspecies should be established for the Mendoza population; however, until more specimens of *E. argentinus* are known from the original population, the Mendoza Province population, and other intervening populations, it would be premature to describe such a subspecies.

Edrabius chilensis Scheerpeltz. Chile: Cautín Prov.; Quetropillán; F. Mondaca #439, ex. *Aconaemys porteri* (IEEUACH 4119), 1 male 1 female. Malleco Prov.; Parque Nacional Nahuelbuta, 10-I-1976, Robert E. Martin #1339, ex. *Aconaemys fuscus,* 1 male (IEEUACH and KSEM).

Notes.—The specimen from Malleco Province has an aedeagus that is slightly more robust apically than that of the specimens from Cautín and that shown in Scheerpeltz's (1957) figure. However, this slight difference does not seem sufficient to assign this specimen to a new species.

Edrabius peruanus Seevers. Chile: Parinacota Prov.; ex. *Ctenomys opimus,* 3 males 4 females (IEEUACH and KSEM).

Edrabius philippianus Fauvel. Fauvel (1900) described *E. philippianus* from *Ctenomys* sp. from Antofagasta, Chile. We herein correct the type host identification to be *C. fulvus* as that is the only species of tuco-tuco occurring in Antofagasta (Gallardo 1991).

Edrabius weiseri Seevers. Bolivia: Dept. Oruro; 7 km S, 4 km E Cruce Ventilla, 3450 m, 30-IX-1986, ex. *Ctenomys opimus opimus* ♀, NK 14748 (MSB 57194), 1 male. Dept. Potosí; 2 km E ENDE Camp, Laguna Colorado, 4280 m, 16-IX-1986, ex. *Ctenomys opimus opimus* ♀, NK 14571 (AMNH 263051), 1 male. Potosí; 2 km E ENDE Camp, Laguna Colorado, 4278 m, 16-IX-1986, ex. *Ctenomys opimus opimus* ♀, NK 14572 (MSB 57204), 7 males 20 females (KSEM).

Discussion

Two major groups of *Edrabius* are apparent. One, represented by *E. chilensis* and *E. chilensiformis,* is found on *Aconaemys* and *Octodon* respectively, both in the family Octodontidae (Table 1). These two small species of *Edrabius* share the synapomorphy of a sharply pointed and upturned apex to the aedeagus. However, they share a number of plesiomorphic features not found in other *Edrabius* (see discussion under *E. chilensiformis*).

The second major *Edrabius* lineage is made up of those species that have the apomorphic conditions of the following characteristics: that is, pronotum without a postero-lateral macroseta, and a very distinct and prominent "pencil" of aciculate setae on the apices of the lateral styli of abdominal tergum IX. This lineage includes all the other known species of *Edrabius.* Members of this second lineage are found primarily on various species of the genus *Ctenomys,* the sole genus in the family Ctenomyidae, though all known specimens of *E. kuscheli*

Table 1.—Summary of known general distribution and hosts of *Edrabius* species (Staphylinidae, Amblyopinini).

General distribution	Host	Reference
E. alticolus Seevers		
Peru: Tacna Prov.	*Ctenomys fulvus*	Seevers, 1955
Bolivia: Oruro Prov.	*Ctenomys opimus*	this paper
Chile: Parinacota	*Ctenomys opimus*	this paper
E. argentinus Seevers		
Argentina: Catamarca	"nest of *Ctenomys*" [*Ctenomys tucumanus*]	Seevers, 1955
Argentina: Mendoza Prov.	*Ctenomys mendocinus*	this paper
E. australis Ashe, Timm, & Gallardo		
Chile: Bío-Bío Prov.	*Ctenomys maulinus maulinus*	this paper
E. chilensiformis Ashe, Timm, & Gallardo		
Chile: Coquimbo Prov.	*Octodon degus*	this paper
E. chilensis Scheerpeltz		
Chile: Curicó	"An Ratten"	Scheerpeltz, 1957
Chile: Malleco Prov.	*Aconaemys fuscus*	this paper
Chile: Cautín Prov.	*Aconaemys porteri*	this paper
E. grandis Ashe, Timm, & Gallardo		
Argentina: Río Negro Prov.	*Ctenomys haigi*	this paper
Chile: Coyhaique Prov.	*Ctenomys coyhaiquensis*	this paper
E. kuscheli Scheerpeltz		
Chile: Arica-Lipiche	"nest of *Galea musteloides*"	Scheerpeltz, 1957
E. pearsoni Seevers		
Peru: Puno Prov.	*Ctenomys opimus nigriceps*	Seevers, 1955
E. peruanus Seevers		
Peru: Puno Prov.	*Ctenomys peruanus*	Seevers, 1955
Chile: Parinacota Prov.	*Ctenomys opimus*	this paper
E. philippianus Fauvel		
Chile: Antofagasta	*Ctenomys fulvus*	Seevers, 1955
E. weiseri Seevers		
Argentina: Jujuy	host unknown	Seevers, 1955
Bolivia: Dept. Oruro	*Ctenomys opimus opimus*	this paper
Bolivia: Dept. Potosí	*Ctenomys opimus opimus*	this paper

were found in the nest of a cui, *Galea musteloides* (but see below) (Table 1).

Scheerpeltz (1957), illustrated specimens of *Edrabius kuscheli, E. philippianus,* and *E. chilensis* showing a posterolateral seta on the pronotum. However, our examination of the holotype of *E. chilensis,* all paratypes of *E. kuscheli,* and specimens labeled *E. philippianus* (almost certainly misidentified, see above) from Scheerpeltz's collection clearly show that specimens of both species lack posterolateral pronotal setae, whereas all three specimens of the type series of *E. chilensis* have such setae.

Furthermore, Seevers (1955), in a quote from O. P. Pearson (page 254), notes that *Galea musteloides* frequently use old *Ctenomys* burrows. If true, then movement of individuals of *Galea* into *Ctenomys* burrows that already had a population of *Edrabius* could account for this unusual host record.

Members of the genus *Ctenomys,* the tuco-tucos, are small to mid-sized (100–

1500 g), strictly fossorial rodents forming a complex assemblage of species with fairly uniform morphology, but extremely variable in chromosome number (Gallardo 1991, Reig et al. 1990). The genetic variation found in the family Ctenomyidae is nearly as great as is found in all other mammals (Gallardo & Köhler 1992, Gallardo & Palma 1992). Although there are 56 available species names of *Ctenomys,* the number of valid species recognized by recent authors ranges from 32 to 44 (Kelt & Gallardo 1994, Mares & Ojeda 1982, Nowak 1991, Reig et al. 1990, Woods 1993). There is consensus that the genus is in need of revision. Tuco-tucos, being strictly fossorial, subterranean dwellers, are restricted to particular soil types and are poor at long distance dispersal and dispersal over water, as is true for other groups of fossorial rodents occupying grasslands on other continents (i.e., the pocket gophers of North America (Geomyidae); the African mole-rats (Bathyergidae); and the mole-rats of Eurasia (Spalacidae)). The subterranean ecotype limits dispersal and produces a population structure characterized by demic fragmentation that facilitates extensive chromosomal variation (Gallardo 1991). In the few species of tuco-tucos studied to date, all maintain extensive underground tunnel systems and have a well-formed, grass-lined nest chamber (Gallardo & Anrique 1991). Reig et al. (1990) suggested that the extensive distribution of tuco-tucos in the southern cone of South America and the lack of morphological differentiation, suggested that the major radiation of the genus was almost certainly post-Pleistocene, although the geologic age of the family goes back to the Pliocene; however, given the diversity, the time of divergence must certainly have been longer. The ctenomyids are believed to be the sister group to the Octodontidae, and it has been suggested that they are more properly classified as a subfamily of the Octodontidae (Reig et al. 1990).

The caviomorph family Octodontidae contains six genera and 11 living species, all with very restricted Andean or pre-Andean ranges. Their habits are diverse. *Octodon degus* is similar to a ground squirrel in behavior, diet, and ecology. *Aconaemys fuscus* is fossorial and similar in size and shape to *Ctenomys,* though less specialized for burrowing (Gallardo & Reise 1992). Other octodontids (*Octomys*) have habits that are similar to woodrats or are strictly fossorial (*Spalacopus*). The biology, ecology, and geographical distributions of most species of octodontids are very poorly known and phylogenetic relationships among the genera are uncertain (Mares & Ojeda 1982, Nowak 1991). Contreras et al. (1987) discussed known aspects of the ecology, distribution, and biogeography of the Octodontidae.

Reig et al. (1990) note that the families Ctenomyidae and Octodontidae (they treated these taxa as subfamilies rather than families) are sister taxa. The Octodontidae are known from the Oligocene of Argentina (Mares & Ojeda 1982, Nowak 1991, Contreras et al. 1987), and it seems possible that the association of *Edrabius* with this lineage of caviomorph rodents may date to at least this time period.

The relatively recent differentiation of *Ctenomys* (Reig et al. 1990) is reflected in evolution of the *Edrabius* found on *Ctenomys* into a number of poorly differentiated species. It is virtually impossible to separate the species of *Edrabius* based exclusively on external characteristics. Aedeagal characteristics are more distinctive, but some (*E. peruanus, E. pearsoni,* and *E. alticolus*) are also only weakly differentiated by aedeagal features. A clear understanding of patterns of species limits and geographic variation of *Edrabius* species associated with *Ctenomys* will require much more extensive collecting.

Few other amblyopinines are known from caviomorph rodents. The only two known species of *Megamblyopinus* are found on *Ctenomys—M. germaini* Fauvel on *C. peruanus* Sandborn & Pearson and

M. mniszechi on *C. opimus nigriceps* Thomas. In addition, *Amblyopinus fuegensis* Seevers occurs on *Ctenomys magellanicus, A. pacae* Seevers is known from *Agouti taczanowskii,* and *Amblyopinodes caviae* Martínez & Prosen is known from *Cavia* species (Caviidae) (Seevers 1955, Machado-Allison 1963).

Given the extensive radiation of *Ctenomys* in southern South America and the relatively few collections of *Edrabius* from these rodents, we strongly suspect that numerous new species of *Edrabius* remain to be collected. In addition, other species of *Edrabius* may be associated with other genera of the Octodontidae. Because of the relatively basal phylogenetic position of those *Edrabius* currently known to be associated with octodontids, it is likely that additional collections of *Edrabius* from octodontids will prove pivotal to understanding the phylogeny and evolution of association of *Edrabius* with caviomorph rodents.

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A new species of rainfrog, *Eleutherodactylus phasma* (Anura: Leptodactylidae), from Montane Costa Rica

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Abstract.—*Eleutherodactylus phasma* (Leptodactylidae), a new rainfrog from the Cordillera de Talamanca, Costa Rica is described. The new form belongs to the *Eleutherodactylus fitzingeri* group, and can be distinguished from the other members of this group from Lower Central America by the combination of basal toe webbing, no heel tubercle, and its distinctive gray-white ghost-like coloration.

Resumen.—Se describe una nueva especie, *Eleutherodactylus phasma,* de la Cordillera de Talamanca al sureste de Costa Rica. Esta nueva forma puede ser distinguida de las otras por las membranas interdigitales en lo base de los dedos, la ausencia de un tubérculo del talón, y la coloración inusual de blanco y gris.

In March 1992 the first author collected an unusually colored frog of the genus *Eleutherodactylus* in the southern Cordillera de Talamanca of Costa Rica. Aside from the black eyes and a scattering of black markings on the head and hindlimbs, the dorsal and ventral surfaces were a uniform ghost-like gray-white.

Initially we thought this specimen might be a partial albino of one of the several species of the genus from the same region. However, further study indicated that this frog differed from all congeners in significant morphological features.

Subsequent fieldwork in the same area in 1993 and 1994 failed to uncover additional examples of this form which we now believe represents a distinctive taxon. Consequently, we describe this specimen below in order that it may be included in the second author's handbook on the herpetofauna of Costa Rica. Because of its ghost-like appearance, this specimen is to be called:

Eleutherodactylus phasma, new species
Fig. 1

Holotype.—CRE 5331 (Costa Rican Expeditions, the private collection of JMS housed at the University of Miami, to be deposited in the LACM) an adult female from Costa Rica: Puntarenas Province, Canton Coto Brus, Zona Protectora Las Tablas, Finca Jaguar, 8°55′N, 82°44′W on the Río Coton; ca. 20 km NNE of La Lucha, 1850 m elevation; taken 1 March 1992 by Karen R. Lips.

Etymology.—The species name is derived from the Greek *phasma* meaning an apparition or spirit, in reference to the ghost-like appearance of this white frog.

Diagnosis.—The new species is a member of the *Eleutherodactylus fitzingeri* series and *fitzingeri* species group as defined by Savage (1987). Within the *fitzingeri* group it shares with a number of taxa (*Eleutherodactylus cuaquero, E. emcelae, E. monnichorum,* and *E. rayo*) the features of basal toe webbing and emarginate disk covers on some digits. The webs between toes III–IV extend at most only slightly distal to the proximal subarticular tubercles in these forms. In most other members of the *fitzingeri* group from Lower Central America (*Eleutherodactylus andi, E. crassidigitus, E. fitzingeri, E. longirostris,* and *E. raniformis*) the toe webs are moderate to extensive

Fig. 1. Holotype of *Eleutherodactylus phasma* (CRE 5331) in life.

and minimally encompass the proximal subarticular tubercles on all toes. The new form differs from *E. emcelae, E. monnichorum,* and *E. rayo* most obviously in lacking a definite large heel tubercle.

Eleutherodactylus phasma also differs from *E. talamancae,* a lowland species of the *fitzingeri* group having basal toe webs, in the predominantly gray-white dorsum, flanks, limb surfaces, and venter. In *E. talamancae,* the upper surfaces are tan to dark brown with some darker markings, the posterior thigh is uniform, pale yellowish-brown to reddish and suffused with red in life, as is the groin region. *Eleutherodactylus phasma* differs from *E. talamancae* in that it has a weak tarsal fold, the skin of the dorsum smooth, and it lacks a dark eye mask. *Eleutherodactylus talamancae* by comparison, lacks a tarsal fold and has a finely tuberculate dorsum and black eye mask.

The only other form with which the new species might be confused is *E. cuaquero* of the Cordillera de Tilaran of northwestern Costa Rica (Savage 1980). *Eleutherodactylus phasma* differs from that species (characters for *E. cuaquero* in parentheses) in having smaller disks on fingers III–IV, their width being less than the length of the inner metatarsal tubercle (greater in *E. cuaquero*), and in having a uniform gray-white ventral and posterior thigh surface (venter bright yellow, suffused with pink posteriorly and posterior thigh with yellow-white lines and spots on dark brown ground color). *Eleutherodactylus melanostictus,* a member of the *fitzingeri* group that is sym-

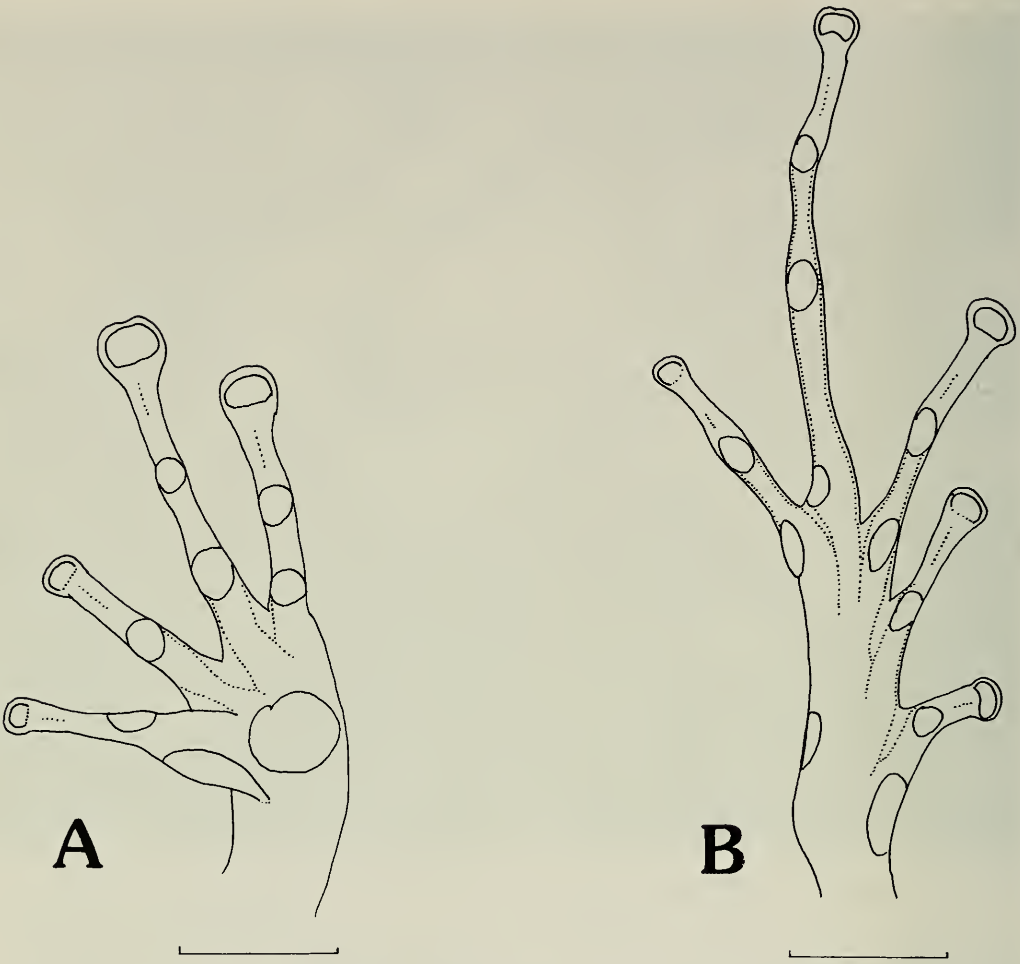

Fig. 2. Diagram of A) hand and B) foot of holotype, showing characteristics of webbing, tubercle, and disk shape. Bar indicates A) 3 mm and B) 5 mm.

patric with *E. phasma,* is easily distinguished from it by lacking any trace of toe webbing and having a distinct heel tubercle, granulate venter and the posterior thigh surface marked with vertical bars and scarlet interspaces.

General characteristics.—Head relatively narrow, slightly longer than broad; snout subovoid in dorsal outline; snout profile obtuse. Canthus rostralis sharp. Loreal region obtuse, upper lip not flared in cross section. Choanae ovoid, slightly smaller than vomerine tooth patches; posterior but internal to choanae, widely separated on midline. Surface of head smooth, without pustules; upper eyelid smooth. Tympanum distinct, elliptical, vertical diameter slightly more than ½ length of orbit; bordered above and posteriorly by a distinct glandular ridge. Dorsum, flanks and upper limb surfaces smooth. Finger I longer than II when adpressed together; relative finger lengths III > IV > I > II (Fig. 2a). Disk on finger I rounded, slightly wider than finger. Disk on finger II slightly expanded and truncate. Disks on fingers III and IV expanded, that of III truncate, emarginate, almost twice as wide as finger, width equals that of tympanum; disk pads broadened and truncate. Subarticular tubercles under fingers round in outline, globular in profile, and slightly projecting; no supernumerary tubercles; thenar tubercle large, elongate; palmar tubercle very large, cordate; no obvious accessory palmar tubercles. No distinct heel tubercle or calcar. Toe disks smaller than finger disks, disk on III larger than disks on other toes, equal to disk on finger II; disks on toes II–IV truncate, palmate and only slightly expanded on toes I and V. Relative toe lengths IV > III > V > II > I; toe III much longer than toe V (Fig. 2b). Slight basal toe webbing between toes I–IV; toe webbing formula I2 -2¾II2 -3¼III3 -4¼IV4¼ -2¾V. Subarticular tubercles under toes round, slightly projecting, globular in profile. No supernumerary nor plantar tubercles; inner metatarsal tubercle well-developed, elongate; outer metatarsal tubercle moderate and low; weak inner tarsal fold present. No inguinal gland; venter smooth.

Coloration.—Dorsal ground color dirty white to faint gray-brown. Scattered small brown punctuations contribute to gray-brown tint of dorsum. Scattering of 15–20 small black spots forming dark blotches posterior and medial to eyes. Upper lips pale gray-brown to black, color becoming more distinct along edges of canthus and nasal area. Black line extending from just anterior to eyes, along edge of upper eyelid and posterior to eye; upper ¾ of tympanum colored similarly, with eye line continued posterior to tympanum, but interrupted dorsally. Two black spots on posterior tibia and knee of left leg. Right knee slightly suffused with same dark gray-brown color. Tubercles of feet also colored gray-brown. Remainder of all dorsal, ventral and lateral areas dirty white to light gray-brown. Jaw muscle formula (after Savage 1987) dfsqt + e.

Measurements.—Measurements were taken following Lynch and Duellman (1980). Standard length (SL) 47.9 mm (all measurements in mm, those in parentheses given as percent of SVL); head length 19.5 (40.8); head width 18.5 (38.6); length of eye 6.2 (13.0); snout length 6.6 (12.7); loreal length 14.8 (30.8); vertical tympanum diameter 3.7 (7.6); hind limb length 89.9 (187.7); tibia 31.7 (66.3).

Distribution.—Known only from the type locality in the Lower Montane Rainforest (Holdridge 1982) in the Cordillera de Talamanca of Costa Rica near the Panama border at 1850 m elevation.

Remarks.—The type specimen was collected from the rocky banks of the Río Coton during a rainy afternoon in the early wet season. This site is within a transect that was monitored at intervals of 1–4 d over a period of 24 months from July 1991–June 1994. No other specimens were ever seen.

The addition of E. *phasma* brings the total number of *Eleutherodactylus* species at this site to seven: *E. crassidigitus, E. cruentus, E. hylaeformis, E. melanostictus, E. phasma, E. podiciferus, E. punctariolus.*

Discussion

On the basis of external morphology *Eleutherodactylus phasma* clearly belongs to the *fitzingeri* species group (Savage 1987), agreeing with most other members of this stock in habitus and in having a smooth venter, inner tarsal fold, and some toe webbing. This assignment is further confirmed by an examination of the jaw muscles. As noted by Lynch (1986) and Savage (1987), the *fitzingeri* group is part of the Middle American clade or "subgenus Craugaster", characterized by having only an externus superficialis mandibular adductor muscle. *Eleutherodactylus phasma* has a mandibular depressor arrangement (dfsqt) typical of the *fitzingeri* group.

Relationships among the species within the *fitzingeri* group remain obscure. *Eleutherodactylus melanostictus* of montane Costa Rica and western Panama (no toe webs, granulate venter) and *E. talamancae* of the Atlantic lowlands from Nicaragua to eastern Panama, (no tarsal fold) are outliers in the range of interspecific variation in these characters. Lynch (1985) suggested that the emarginate disks of *E. emcelae* and

E. monnichorum, both of montane western Panama, and *E. melanostictus* formed a synapomorphy for this subset of species. Savage (1987) noted that most species in the *fitzingeri* group have some emarginate digital disks, and that marked differences exist in toe webbing (absent to moderate), heel tuberculation (present or absent) and posterior thigh coloration (uniform to large light spots or dark bars) among these species. While these features in various combinations aid in species recognition, we lack confidence that their occurrence in two or more species contains phylogenetic information (i.e. are non-homoplasious).

Although *E. phasma* is similar in morphological features to *E. cuaquero* (see diagnosis above), they differ markedly in coloration and to a lesser extent in habitus. *Eleutherodactylus cuaquero* appears to be a more robust species but has much longer legs (227–230% of standard length) than *E. phasma.* In these features and in the size of finger disks III–IV, the new form most closely resembles the sympatric *E. crassidigitus,* a wide-ranging (40–1800 m elevation) species found in Costa Rica and Panama. *Eleutherodactylus crassidigitus* differs markedly from *E. phasma* in having more toe webbing than any other member of the *fitzingeri* group (modal formula: I2$^-$ -2II1½ -3$^-$III2 -3½IV4$^-$ -2½V), predominantly brown upper surfaces and a uniform brown to reddish brown posterior thigh.

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The systematic status of Guatemalan populations of snakes allied with *Ninia maculata* (Reptilia: Colubridae)

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Abstract.—The Guatemalan colubrid snake, formerly recognized as *Ninia maculata pavimentata,* is elevated to a full species. This species is closely related to *N. maculata* of southern Central America, but differs in segmental counts, relative tail length, various measures of head shape, and ventral coloration. Three recently collected specimens of *N. pavimentata* represent significant range extensions of this snake in Guatemala. *Ninia pavimentata* is re-described and ecological notes are provided.

Resumen.—El colúbrido guatemalteco conocido como *Ninia maculata pavimentata* es elevado al nivel de especie. Esta especie se encuentra cercanamente relacionada a *Ninia maculata,* del sur de Centro America, pero difiere de esta en número de segmentos, largo relativo de la cola, medidas cefálicas y coloración ventral. Tres especímenes de *Ninia pavimentata* recientemente colectados representan extenciones de rango significativas para esta serpiente en Guatemala. Se redescribe *Ninia pavimentata* y se provee datos ecológicos.

The apparent distribution of the colubrid snake known as *Ninia maculata* has been an enigma to biogeographers. Peters (1861) originally described *N. maculata* from a single specimen taken in Costa Rica. Bocourt (1883) noted similarities between four specimens from Alta Verapaz, Guatemala, and snakes from Costa Rica, and described the Guatemalan specimens as a new subspecies, *N. maculata pavimentata.* In his revision of the genus, Dunn (1935) did not consider the taxonomic position of this subspecies, and apparently never examined the types. Stuart (1948) noted the large hiatus between the provenance of *N. maculata pavimentata* in Alta Verapaz and the northernmost record of *N. m. maculata,* given by Dunn (1935) as Jinotega, Nicaragua. Stuart (1948) predicted that intergrades would eventually be collected in the intervening area. Savage & Lahanas (1991) noted that no such specimens had been forthcoming, and they anticipated that *N. m. pavimentata* would eventually be elevated to full specific status.

The senior author, as part of an ongoing study of the genus *Ninia,* has examined 14 specimens of *N. m. pavimentata* housed in collections, including several specimens from Guatemala collected far from the type-locality. It has become clear that these specimens share certain unique similarities with each other, but differ from the more southern populations, indicating that the northern population deserves full species status.

Materials and Methods

Material from the Museum National d'Histoire Naturelle (MNHNP), Carnegie Museum (CM), Los Angeles County Museum (LACM), Museum of Vertebrate Zoology (MVZ), University of Michigan Museum of Zoology (UMMZ), Florida State Museum (UF), the University of Texas at Arlington (UTA), and the Universidad del Valle of Guatemala (UVG) was examined.

Standard scale counts and measurements of the head and body were taken on all specimens. Counts of paired characters were made on both sides of the body. The following counts were made: number of dorsal scale rows one head-length behind the angle of the jaw, at mid-body, and one head length anterior to the anal plate; number of ventrals (method of Dowling 1951); number of subcaudals (counted on the left side, beginning with the first subcaudal in contact with an opposite subcaudal, the "best" method of Peters 1964); the number and position of supralabials, infralabials, supraoculars, loreals, preoculars, postoculars, anterior temporals, posterior temporals, chin tubercles (males only); and dark bands on the left side of the body. Ventral color pattern was scored using the categories of Savage & Lahanas (1991:43, their figure 4). Several measurements of the head were made to the nearest 0.1 mm using a vernier caliper, and the following variables were normally distributed: head length from the front face of the rostral to the angle of the jaw on the left side of the head, head width at the level of the angle of the jaw, snout length from the tip of the snout to the anterior margin of the orbit, head width at the widest point (immediately behind the orbit), length of the prefrontal suture, length of the parietal suture, and length and width of the frontal scale. Three juvenile *Ninia pavimentata* were used in the species description, but were not used in statistical analyses. Other head scale measurements used in the description of head scale shape included rostral height-width and loreal length-height. Measurements of paired cephalic scales were taken on the left side of the head only. Measurements of snout–vent length and tail length were made with a standard metric ruler to the nearest 1 mm.

To assess the differences between the Costa Rican and Guatemalan populations, a subset of morphometric measurements were entered into a multivariate analysis of covariance (MANCOVA), using snout–vent length as a covariate. Variables that were found to be not normally distributed were dropped from this analysis, as noted above. Ventral and subcaudal scale counts are sexually dimorphic in species of *Ninia* (Savage & Lahanas 1991), with slightly higher ventral counts in females, and slightly higher subcaudal counts in males. Ventral and subcaudal counts added together form the segmental count, a variable that was used in a study of Costa Rican *N. maculata* (Savage & Lahanas 1991) as a non-dimorphic measure of vertebral number. In our study, we used segmental counts in a Mann-Whitney U test to compare populations of *Ninia maculata* (sensu lato). Our analysis indicates that *Ninia pavimentata* is distinctive from *N. maculata* and we suggest that these taxa are specifically distinct. Table 1 provides the range of variation for standard scale counts in *N. pavimentata.* Statistical analyses were performed using Statistica version 3.1 (Statsoft, Inc. 1991).

Results and Discussion

Ninia pavimentata is a small colubrid snake from Guatemala (snout–vent length of largest male, 265 mm; largest female, 275 mm). It is characterized by a head slightly distinct from the neck; dorsal scales keeled and heavily striated, in 19 rows throughout; ventrals 142–147 in males, 136–147 in females (except as noted for UVG 382); and subcaudals 68–76 in males, 63–75 in females (except as noted for UVG 382). See Table 1 for standard scale counts. The subcaudals are paired and the anal plate is single. Insufficient data exist to document sexual dimorphism in ventral and subcaudal counts of *N. pavimentata.* The head scalation follows a typical colubrid pattern of nine large, platelike scales. The rostral is 1.35–2 times broader than high, and the internasals are paired, about half the size of the paired prefrontals. The frontal suture is 1.5–1.85 times as long as the prefrontal suture, except for one individual (MVZ 159860) in which the frontal scale is only slightly longer than the prefrontal suture.

Table 1.—Selected features of *Ninia pavimentata* (* tail incomplete, # chinshields dessicated, chin tubercles observed but not counted).

Museum no.	Sex	Snout-vent length (mm)	Tail length (mm)	Ventrals	Subcaudals	Segmental count	Chin tubercles
UTA R-7099	♂	225	83	144	68	214	91
MNHNP 1192	♂	226	82	147	70	217	#
MNHNP 1994.226	♂	209	83	142	74	216	63
MVZ 159860	♂	222	95	143	76	219	79
MVZ 159861	♂	265	103	142	75	217	75
UF 96321	♂	106	40	141	74	215	—
UVG 382	♀	215	62	130	49	179	—
MNHNP 1994.227	♀	275	101*	145	66*	211*	—
MNHNP 1994.228	♀	195	71	144	70	214	—
UMMZ 89083	♀	255	69*	144	49*	193*	—
CM 43954	♀	203	75	147	75	222	—
UTA R-37590	♀	266	81*	136	53*	189*	—
LACM 40055	♀	154	49	142	63	205	—

There is a single frontal, about as long as wide, in all specimens. The suture between the paired parietals is about as long as the frontal scale in all specimens examined. There is a single supraocular, a pre- and postnasal, and the loreal scale is 1.5–2 times as long as high, except for three individuals (LACM 40055, MNHNP 1192, and UMMZ 89083) in which the loreal scale is nearly square. Stuart's (1948) statement that the loreal is distinctively high and short appears to be relative, based on comparisons with other species with horizontally elongate loreals. There is no preocular (in MVZ 159860, one small scale is present on the left side and two small scales on the right side; on both sides the loreal still contacts the eye), two postoculars (rarely three or, more rarely, one), one anterior temporal, and two posterior temporals. Supralabials and infralabials usually 7 (rarely 6), with supralabials 3 and 4 in contact with the eye except for UF 96321, in which only supralabial 3 contacts the eye on the left side, and only supralabial 4 contacts the eye on the right side. The eye is moderately large, usually just slightly smaller in diameter than the loreal length. The mental is about twice as wide as long, and the first pair of infralabials are in contact, separating the mental and anterior chinshields. The first four infralabials are in contact with anterior chinshields (except in LACM 40055, in which the third and fourth infralabials are fused on the right side). The fourth infralabial is in contact with the posterior chinshields (except as noted above for LACM 40055). The anterior chin shields are 1.4–1.8 times longer than the posterior chinshields. Males have prominent raised chin tubercles on both chinshields and the first four pairs of infralabials. There are 63–91 chin tubercles on the anterior chinshields and first pair of infralabials.

In alcohol the dorsal ground color is usually reddish brown, with the exception of UTA R-37590, which is badly formalin-blackened, obfuscating any dark dorsal crossbands. The other specimens we examined have 34–50 well-defined black crossbands. Approximately two-thirds of these crossbands are continuous across the dorsum, others end at the mid-dorsal scale row. The anterior band is always continuous across the dorsum. Immediately in front of this band is a pale nuchal collar, indistinct and narrow, which is usually no wider than one or two scale rows at mid-dorsum, and slightly wider laterally. In seven of 12 snakes this collar is not continuous across the dorsum. The supralabial and infralabial scales are cream colored, with black edges. The distinctive checkerboard ventral pattern is diagnostic for the species. Costa Rican

N. maculata can be similar (see Savage & Lahanas 1991: their fig. 4G and 4H, for illustrations of venters similar to *N. pavimentata*), but Guatemalan specimens are much more boldly marked than any Costa Rican specimens that we have examined.

Ninia pavimentata can be distinguished from its close relative *N. maculata* by having a broader, blunter, more spatulate head. The upper lips of *N. pavimentata* are somewhat flared compared to *N. maculata,* and are easily seen in dorsal view. Additionally, the dorsal pre-orbital surface of the head of *N. pavimentata* is distinctively convex, while this surface in *N. maculata* is nearly flat. The snout of *N. pavimentata* is fairly blunt, whereas that of *N. maculata* is more angular.

The statistical analyses, while not robust with such small sample sizes, assist in indicating the nature of the differences between the two species. The MANCOVA results separate the species using the following variables: *Ninia pavimentata* has a relatively longer tail than *N. maculata* ($f = 29.17$, $P = 0.000039$, $df = 1{,}18$); *N. pavimentata* has a narrower head at the level of the angle of the jaw ($f = 5.55$, $P = 0.030$, $df = 1{,}18$), probably reflective of the spatulate shape of the head of *N. pavimentata*; and *N. pavimentata* has relatively larger parietal scales ($f = 4.59$, $P = 0.046$, $df = 1{,}18$). In addition, *N. pavimentata* has a significantly higher segmental count than *N. maculata* (Z-adj $= -2.97$, $P = 0.0030$). There is little overlap between segmental counts of *N. pavimentata* and *N. maculata* (Table 1).

Three snakes warrant special mention. Two of these are significant extensions of the range of *Ninia pavimentata,* which had previously been known only from the highlands of Alta Verapaz and adjacent Baja Verapaz. One specimen (UTA R-37590) was recently collected in the province of San Marcos, the first specimen of *N. pavimentata* to be collected on the Pacific versant of Guatemala. Examination of this specimen reveals that it is dark (probably formalin-blackened) but otherwise it agrees with *N. pavimentata.* Another specimen (LACM 40055) from near Barillas in the Sierra Cuchumatanes, Huehuetenango, is fairly typical of the species.

Finally, a specimen from near La Francia, Izabal, near the Honduran border (UVG 382) is unusual not only because it is the only *Ninia pavimentata* known from the lowlands of Guatemala, but also because it shows a combination of features typical of either *N. maculata* or *N. pavimentata.* This snake has a smooth and level surface on the dorsal pre-orbital portion of the head, similar to *N. maculata,* but it has large parietal scales typical of *N. pavimentata.* The snout is fairly blunt like *N. pavimentata,* but ventral and subcaudal counts are more similar to *N. maculata.* This specimen apparently represents an isolated population restricted to the lowlands of eastern Guatemala and perhaps adjacent Honduras. Despite its morphology, we do not consider it an "intergrade" in the sense of Stuart (1948). This population is separated from the most geographically proximate populations of *N. maculata* in Costa Rica by about 600 km and may have become isolated relatively soon after the vicariant event that separated *N. maculata* and *N. pavimentata.* The area in which this specimen was collected is not well known, and further specimens from this area are needed to fully resolve the status of this snake. We tentatively allocate this specimen to *N. pavimentata,* but recognize that it may ultimately prove to be distinct.

With respect to the ecology and habits of *Ninia pavimentata,* very little is known. Most specimens have come from pine-oak or cloud forest at elevations of 1120 to 1825 meters (Fig. 1). A single lowland specimen was collected below 300 m. *Ninia pavimentata* is rarely encountered, either because it is rare or because of secretive behavior. Specimens have been found most frequently in the highlands of Alta Verapaz (with one specimen from nearby Baja Verapaz), but recent specimens collected in the

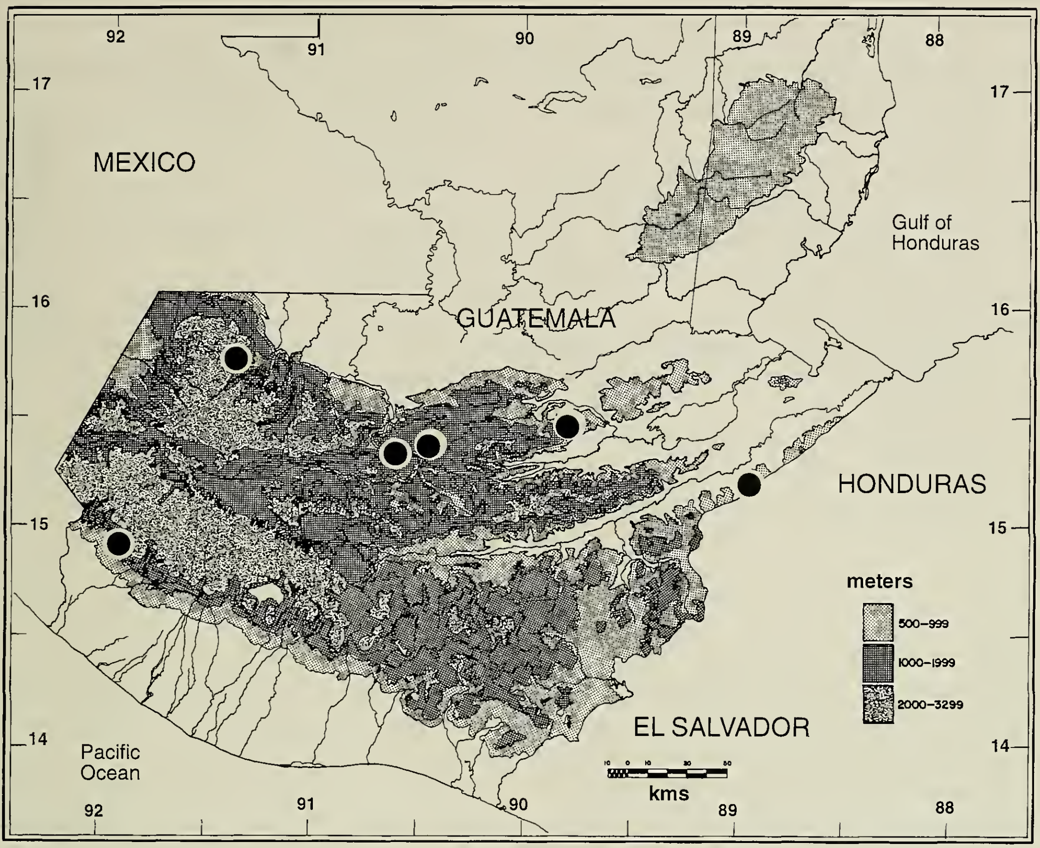

Fig. 1. Localities for *Ninia pavimentata* in Guatemala.

departments of San Marcos and Huehuetenango indicate that this species ranges more widely throughout the Guatemalan highlands than previously thought.

Material examined of Ninia pavimentata.—Guatemala: Alta Verapaz: Municipio de San Cristóbal Verapaz, Baleu, 1350 m (CM 43954); 11 km W San Cristóbal Verapaz, 1120 m (UF 96321); Finca Chichén, 1410 m (UMMZ 89083); Finca Volcán, 25 km by road NW Senahú, 1300 m (MVZ 159860, 159861); no specific locality (MNHNP 1192, 1994.226, 1994.227, and 1994.228—syntypes). Baja Verapaz: Cerro Verde, ca. 1500 m (UTA R-7099). Huehuetenango: Sierra de los Cuchumatanes, Barillas, 1700 m (LACM 40055). Izabal: Finca Santa Isabel, near La Francia (UVG 382). San Marcos: Aldea La Fraternidad, Finca La Esperanza, 1825 m (UTA R-37590).

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Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 1. Characterization of *Calypte anna* × *Stellula calliope* and the possible effects of egg volume on hybridization potential

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Abstract.—Plumage pattern, plumage color, and external morphology of two specimens of hybrid hummingbird (*Calypte anna* × *Stellula calliope*) are described. The parental species differ substantially in size, and the hybrids are similar to the averages of character means of the parental species. Expression of parental plumage characters in the hybrids varies, particularly the color and configuration of the frontlet and gorget. The possible effects of egg volume on hybridization potential are discussed.

The possibility of hybridization among North American species of hummingbirds (Trochilidae) was mentioned by Jeffries as early as 1888. The first published notice of such hybridization was buried in Fisher's monograph on Death Valley birds (1893), and Suchetet (1896) did not list any hybrid Trochilidae in his review of avian hybrids. Subsequently, a few additional cases were reported (e.g., Thayer & Bangs 1907, Berlioz 1930), but Banks & Johnson (1961) were the first to evaluate critically the known hummingbird hybrids from North America. The latter authors, in an exemplary study that set the standard for future work on this subject, documented five hybrid combinations based upon the direct examination of specimens and noted three other probable combinations for which they were unable to locate the pertinent specimens. Additional hybrids were reported by Short & Phillips (1967), Lynch & Ames (1970), Wells et al. (1978), and Newfield (1983). To date, a total of 13 hybrid combinations (Table 1) have been documented by specimens among the hummingbird species that regularly breed north of Mexico.

On 19 June 1926, Chester C. Lamb collected an adult male hummingbird in the Sierra San Pedro Martir (7500 ft elevation [2287 m]), Baja California del Norte, Mexico. Grinnell (1928:134) noted that Lamb's specimen (Museum of Vertebrate Zoology [MVZ], University of California No. 47983; 3.1 g), "... shows hybrid origin, apparently *Stellula calliope* × *Calypte anna*," but left Berlioz (1930) to describe it formally. Three decades later, Banks & Johnson (1961) reexamined the specimen and elaborated on Berlioz's description. Neither Berlioz nor Banks and Johnson discussed alternative parental hypotheses.

A second hybrid hummingbird, also possibly *Calypte anna* × *Stellula calliope*, recently was collected by Newfield in Baton Rouge, Louisiana, on 22 December 1993 (Louisiana State University Museum of Natural Science, Louisiana State University (LSUMZ) No. 154189; testes minute, skull 10% ossified, light neck molt, 3.7 g, light fat, insect parts in stomach, frozen tissue saved (B-19447), prepared by Steven W. Cardiff).

Here we present a hybrid diagnosis of the two specimens and discuss the field identification of hummingbird hybrids. Finally, we briefly address the possible constraints

Table 1.—Hybrids reported among species of hummingbirds that breed north of the Mexican-U.S.A. border. References indicate the earliest publication of the identification of hybrid parentage that is currently accepted.

Hybrid combination	References
Amazilia violiceps x *Cynanthus latirostris*	Griscom 1934
Archilochus alexandri x *Calypte anna*[a]	Thayer and Bangs 1907
Archilochus alexandri x *Calypte costae*	Fisher 1893
Archilochus alexandri x *Selasphorus platycercus*[a]	Banks and Johnson 1961
Archilochus alexandri x *Selasphorus sasin*	Lynch and Ames 1970
Calypte anna x *Calypte costae*	Wells et al. 1978
Calypte anna x *Selasphorus sasin*[a]	Thayer and Bangs 1907
Calypte anna x *Stellula calliope*[a]	Grinnell 1928
Calypte costae x *Selasphorus platycercus*	Huey 1944
Calypte costae x *Stellula calliope*[a]	Hartert 1900
Cynanthus latirostris x *Eugenes fulgens*	Short and Phillips 1966
Selasphorus rufus x *Stellula calliope*	Thayer and Bangs 1907
Selasphorus rufus x *Selasphorus sasin*	Newfield 1983

[a] Specimens examined by Banks and Johnson (1961).

on hybridization imposed by interspecific differences in egg volume.

Materials and Methods

For the hybrid diagnosis, we considered the geographic pool (sensu Graves 1990) from which potentially hybridizing species may be drawn to include all hummingbird species ($n = 15$) that breed regularly north of Mexico or in Baja California del Norte (AOU 1983, see Appendix 1). Neither of the putative hybrid specimens possesses striations or corrugations on the upper rhamphotheca (Ortiz-Crespo 1972), indicating that both birds were "adult." The hybrids (hereafter referred to as "Baja" or "Louisiana" hybrids) were compared with large series of adult males of all North American species of hummingbirds in the National Museum of Natural History (USNM), Smithsonian Institution. Plumage color was evaluated under Examolites (MacBeth Corp.). Measurements of wing chord, lengths of the first (central), third, and fifth rectrices (from point of insertion of central rectrices), greatest widths of the first, third, and fifth rectrices, and bill length (from anterior edge of nasal flange) were made with digital calipers to the nearest 0.1 mm (Table 2). We used bivariate plots of size variables to display morphological variation in two dimensions.

For purposes of the hybrid diagnosis, we used the methodological assumptions outlined by Graves (1990). The hybrid diagnoses followed a two-step procedure. First the presumed parental species of each hybrid were hypothesized through comparative analysis of plumage pattern and color. These hypotheses were then examined with quantitative analyses of external measurements. Concordance of results is regarded as strong support for the presumed parentage of the hybrids (Graves 1990, Graves & Zusi 1990).

Results

Plumage characters.—Neither putative hybrid specimen can be assigned to any known taxon of hummingbird, even after considering the possibility of plumage aberrancy due to mutation or environmental induction. Both specimens possess a distinctive combination of characters that can be found among the assemblage of species in the geographic pool (Appendix 1), but not in a single species, which itself is evidence suggestive of hybridization. Three characters of the hybrids permit their parental species to be identified: (1) a brilliant,

Table 2.—Ranges and means (± one standard deviation) of measurements (mm) of adult male *Calypte anna*, *Stellula calliope*, and their male hybrids (MVZ 47983, LSUMZ 154189).

Character	*Calypte anna* (n = 12)	*Stellula calliope* (n = 12)	Hybrids	
			MVZ	LSUMZ
Wing chord	47.9–51.0 49.3 ± 1.0	38.0–40.7 39.2 ± 0.8	44.3	43.6
Bill length	17.4–19.4 18.1 ± 0.6	13.1–15.1 14.0 ± 0.5	16.4	16.8
Rectrix 1 length	22.9–26.5 24.5 ± 1.0	17.5–18.7 18.2 ± 0.4	21.2	20.0
Rectrix 3 length	26.2–28.5 27.6 ± 0.7	18.7–20.2 19.6 ± 0.6	24.5	23.1
Rectrix 5 length	30.3–32.5 31.3 ± 0.9	18.2–20.3 19.3 ± 0.6	25.7	25.8
Rectrix 1 width	7.6–10.5 8.9 ± 0.8	4.1–4.9 4.5 ± 0.2	5.6	5.7
Rectrix 3 width	5.3–7.4 6.4 ± 0.6	4.9–5.6 5.2 ± 0.2	6.1	6.4
Rectrix 5 width	3.0–3.7 3.4 ± 0.2	3.4–3.8 3.6 ± 0.1	3.3	3.6

contrasting frontlet; (2) parallel or slightly concave margins of the central rectrices; and (3) rufous margins of rectrices 1, 2, and 3 (Figs. 1–3).

Only two species in the geographic source pool, *Calypte anna* and *C. costae*, have brilliant frontlets that contrast with the remainder of the capital feather tract in color and iridescent intensity (the crown but not the frontlet of *Eugenes fulgens* is brilliant). With the exception of the gorget and frontlet, the plumage color of *C. anna* and

Fig. 1. Lateral view of adult males, from top to bottom: *Stellula calliope; Calypte anna* × *S. calliope* (LSUMZ 154189); *C. anna* × *S. calliope* (MVZ 47983); *C. anna.*

Fig. 2. Ventral view of adult males, from top to bottom: *Stellula calliope; Calypte anna* × *S. calliope* (LSUMZ 154189); *C. anna* × *S. calliope* (MVZ 47983); *C. anna.*

C. costae is similar, but neither species has rufous pigmentation on the rectrices. This means that a species of *Calypte* is a parent of both hybrids, but that neither hybrid could have been produced by an intrageneric union (see Wells et al. 1978).

Adult males of 5 species in the source pool (*Amazilia yucatanensis, Stellula calliope, Selasphorus platycercus, Selasphorus rufus, Selasphorus sasin*) have rufous pigmentation on the rectrices. Of these, only *Stellula calliope* has subspatulate central rectrices with parallel or concave margins (as in the hybrids). Although the Louisiana hybrid superficially resembles *S. platycercus* in gorget color, neither it nor the Baja hybrid exhibits any evidence of the extremely attenuated outermost primary found in males of that species. The hybrids lack extensively rufous or buffy sides, flanks, or rump, as would be expected if *S. rufus* or *S. sasin* were involved (a more detailed description of the plumage is presented in Appendix 2). *Amazilia yucatanensis* can be rejected as a parental species for several reasons, most notably the color of its throat, belly, and fleshy rhamphotheca. Thus, plumage characters suggest that the parentage of both hybrids is *Calypte* sp. × *Stellula calliope.*

Mensural characters.—Assuming additive genetic variance (see Graves 1990, 1996), measurements of the hybrids should fall within the cumulative ranges observed in large samples of the parental species. *Calypte costae* and *S. calliope* are among the smallest species (body mass, wing length) in the geographic pool. Data in Table 2 and values for *C. costae* (Wells et al. 1978), indicate that the length of rectrix 5 of the hybrids exceeds those of *C. costae* and *S. calliope* by a minimum of 12% and 27%, re-

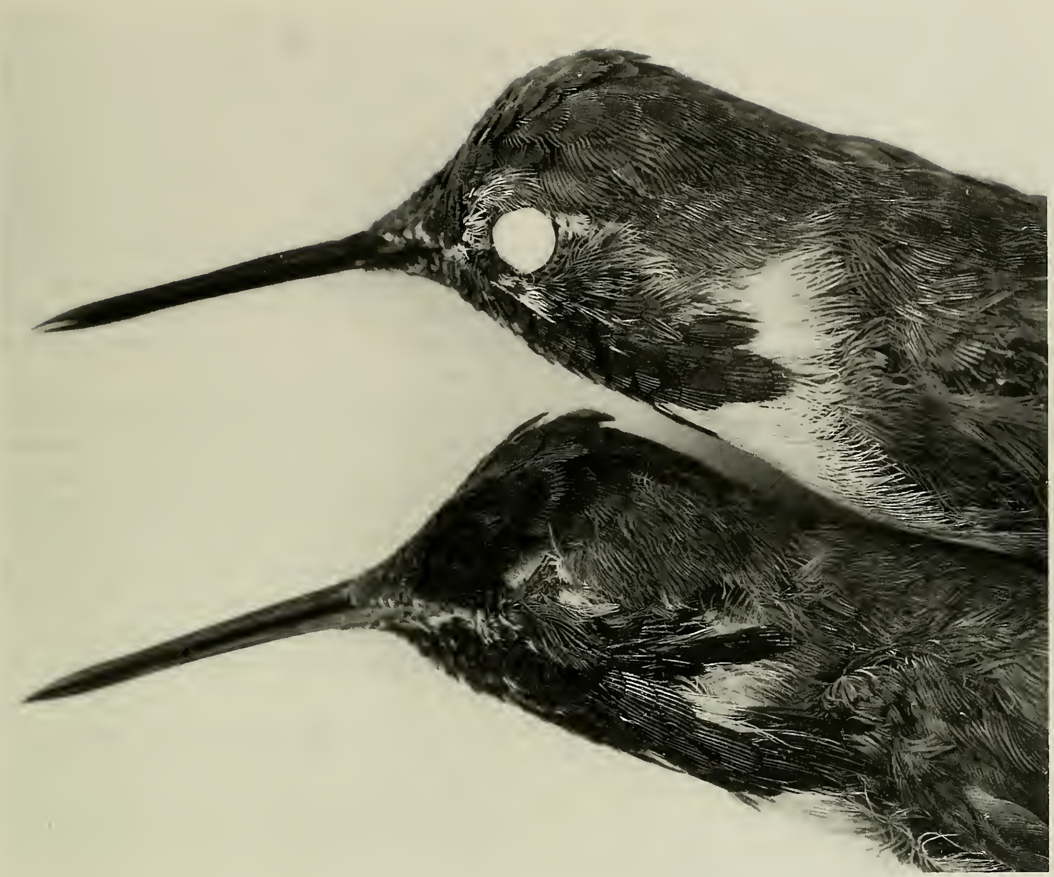

Fig. 3. Lateral view of *Calypte anna* × *Stellula calliope* hybrids: LSUMZ 154189 (top) and MVZ 47983. Note difference in shape of lateral gorget feathers.

spectively. As morphological luxuriance (where a hybrid is larger than either of its parental species) is unknown among trochiline hybrids (Graves, unpubl.), these comparisons effectively rule out *C. costae* as a parental species and suggest that both hybrids are the result of matings between *Stellula calliope* and the larger *C. anna.*

The hybrids are similar in size and shape (Table 2, Fig. 4). Wing, bill, and rectrix length measurements of the hybrids differ from the biparental character means by 0.1 to 6.8%, whereas rectrix width measurements differ by 2.9 to 19.6% from the averages of the character means of the parental species.

Discussion

Field identification of hybrids.—Case histories of the two known *Calypte anna* × *Stellula calliope* hybrids strongly suggest that the parentage of hybrid hummingbirds cannot be determined under field conditions.

Lamb, an experienced field collector, identified the Baja hybrid as "Costa Hummingbird" (*Calypte costae*) in his field catalog. We concur that the hybrid bears more than a superficial resemblance to *C. costae,* particularly in the color and shape of the gorget.

The Louisiana hybrid was studied at close range by experienced observers for

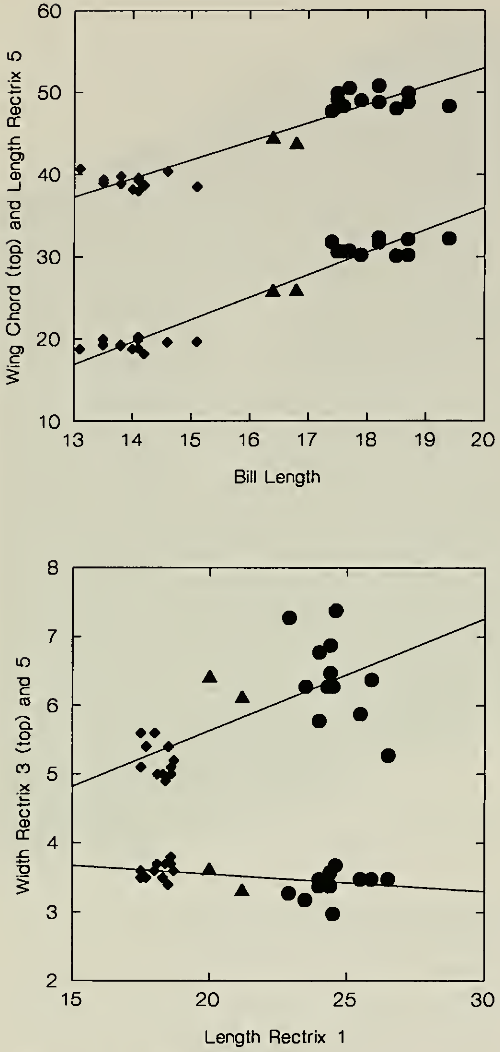

Fig. 4. Bivariate plots of male *Calypte anna* (circles), *Stellula calliope* (diamonds), and their hybrids (triangles, MVZ 47983 and LSUMZ 154189). Least squares regression lines are illustrated for comparison.

several weeks in the vicinity of a nectar feeder before it was collected. The hybrid emitted a high-pitched song similar to that of *C. anna* and loud call notes ("tsick, tsick, tsick . . .") (Paul McKenzie, field notes). McKenzie (19 November 1993, field notes) wrote, "looks more like a Broad-tailed [*Selasphorus platycercus*] in some respects but suggests Anna's [*C. anna*] in others . . . no sign of any reflective feathers on the crown or sides of face . . . [which] should be conspicuous for adult ♂ Anna's . . . cannot see any rufous along the edges of the tail while the bird is perched . . . which would be easily visible for an adult ♂ Broad-tailed . . . the color of the gorget appears more along the shade for Broad-tailed rather than Anna's . . . the shape of the gorget is odd . . . there appears to be a few incomplete feathers on the chin and feathers protrude out on the edges of the gorget . . . almost Costa's like."

McKenzie noted that a second observer saw rufous in the tail, whereas a third believed "the bird to be a typical Anna's." Finally, McKenzie (24 November) reported, "some birders have apparently seen rose-red on the crown and face but I can't see it although (again) the sun is not out." He speculated that the hummingbird might be a hybrid between *C. anna* and *S. platycercus.*

Understandably, none of the field observers suggested the possibility that the hybrid was *C. anna* × *S. calliope.* Subtle shape and color characters that permitted the identification of parental species from specimens would not have been visible on free-living birds, nor could the hybrids have been conclusively diagnosed solely from plucked rectrices or photographs.

Both *C. anna* and *S. calliope* are occasional winter vagrants to the Gulf coast from Texas to Florida (Newfield 1984, unpubl.); perhaps it is not surprising that a hybrid of the two species might occur there as well. However, at least three additional presumed hybrids (*S. rufus* × *S. sasin*) have been collected in this general region in recent years (see Newfield 1983). This seems unusual and suggests an alternative hypothesis that the migratory orientation and behavior of trochiline hybrids is faulty. In other words, the proportion of hybrids may be higher outside the "normal" geographic range of the parental species. Another possibility is that the prevalence of hybrids is geographically invariant, but that hummingbirds are scrutinized more closely in eastern North America.

Are there limits to size differences among hybridizing species?—The body mass ratio (larger divided by smaller) of *Calypte anna* and *Stellula calliope* is approximately 1.6, regardless of which species is female (mass data from Stiles 1971). Although this size difference is striking, the mass ratio is well below the maximum observed among interspecific hybrids of birds (Graves, unpubl.). Mayr and Short (1970) reported a possible hybrid between *Lampornis clemenciae* and *Calypte costae* or possibly *C. anna.* If this combination is correct, the minimum body mass ratio (i.e., ♂ *Calypte costae* × ♀ *Lampornis clemenciae*) would be approximately 2.3 (mass data from Stiles 1971, R. L. Zusi, unpubl.).

This raises the question of paternal effects on avian hybrid viability. Heritability (h^2) of egg size is moderately high in wild birds (Buckley 1982), and the volume of nutritive components of the egg are naturally controlled by the female of a hybridizing pair. In cases in which the smaller of two hybridizing species is female, the egg may not be large enough to support the metabolic and volumetric needs of the developing embryo after factoring in additive genetic effects of the male.

The ratio of average egg volume of *C. anna* and *S. calliope* is approximately 1.2, calculated from the data in Bent (1940). Curiously, however, the range of egg volume for *S. calliope* (ca. 299–611 mm^3) completely overlaps that of the larger *C. anna* (342–591 mm^3) (calculated from the dimensions of size extremes reported in Bent 1940). Thus, despite the specific difference in body mass, egg volume per se appears not to inhibit hybridization between the species. On the other hand, egg volumes of *C. costae* (ca. 276–572 mm^3) and *L. clemenciae* (ca. 662–857 mm^3) are non-overlapping, suggesting that viable hybrids of those species may only be fathered by *C. costae.* Egg volumes of the pairs of hybridizing species listed in Table 1 overlap.

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Appendix 1

Species that regularly breed in Baja California and/or in the United States and Canada: *Cynanthus latirostris, Hylocharis xantusii, Amazilia yucatanensis, Amazilia violiceps, Lampornis clemenciae, Eugenes fulgens, Calothorax lucifer, Archilochus colubris, Archilochus alexandri, Calypte anna, Calypte costae, Stellula calliope, Selasphorus platycercus, Selasphorus rufus, Selasphorus sasin.*

Appendix 2

Comparative description of male *Calypte anna, Stellula calliope,* and their hybrids collected in Baja California (MVZ 47983) and Louisiana (LSUMZ 154189). Descriptions of structural colors are unusually subjective, as color seen by the observer varies according to the angle of inspection and direction of light. For this reason we use general color descriptions.

The forecrown, superciliary, crown, hindneck, back and rump of *calliope* are green with bronzy toning; the loral streak is pale grayish-white. In *anna,* the forecrown, loral region, and crown (anterior from a line drawn across the crown 3–5 mm behind the eye) are feathered with brilliant, iridescent rose-red discs; plumage from the hindneck to the rump is green, slightly bronzier on the hindneck and scapulars than in *calliope.*

In the Baja hybrid, feathers above the nostrils are brownish-gray and dimly reflective (rose-purple) under 10× magnification; iridescent reddish-purple discs extend from the forecrown laterally along the margins of the crown to the rear of the orbits; a few feathers on the crown (between the eyes) are tipped with dull purplish spots. The loral area is buffy-white with dark terminal spots on some feathers. The frontal reflective display in the Baja hybrid is more subdued than in *anna*; the "plate-like" arrangement of barbules of iridescent discs is less well-developed, and several reddish-purple discs exhibit greenish iridescence near the distal margins. The remainder of the crown, hindneck, back, and rump are indistinguishable from *calliope.*

Feathers of the forecrown and crown (to 3 mm behind the eye) of the Louisiana hybrid have terminal discs that emit a dull coppery-rose iridescence when viewed head-on in direct light. The frontal reflective display is less brilliant than in the Baja hybrid (much less so than in *anna*). Under magnification, disc feathers are banded: gray basally, bordered distally in succession by narrow iridescent bands of shining green and reddish-purple merging into a broad terminal band of bronzy- or coppery-rose, with faint greenish reflections. Feathers of the loral area are buffy-white, occasionally tipped with small and indistinct dark spots. Feathers of the hindcrown, back, and rump are green, nearly identical in appearance to *calliope* and most specimens of *anna,* but finely margined with buff, perhaps reflecting the freshness of plumage.

The gorget in *calliope* covers the chin and throat and extends laterally along the sides of the lower throat to form a fringed but tapered point. Gorget feathers are tricolored; proximally white, bordered with a very narrow transitional band of bronzy-green, and broadly tipped with brilliantly iridescent discs (purplish-red).

The purplish-red portions of feathers are greatly elongated in the lateral tails of the gorget. White feather bases result in conspicuous streaking, especially on the center of the throat. A subocular stripe of grayish-buff feathers extends from the loral area to the auriculars. The gorget is bordered posteriorly by a band of white plumage across the lower throat and upper breast. The sides, flanks, and belly are buffy-gray, palest along the midline; feathers on the sides tipped with bronzy-green spots. The undertail coverts are very pale buffy-white or white, some with a few indistinct grayish spots.

The rose-red gorget in *anna* has a similar shape, but the iridescent discs are more imbricated than in *calliope* and extend to the subocular region. Lateral discs are less elongate than in *calliope* and all gorget feathers are dark gray to bronzy-gray basally. Feathers just posterior to the gorget are dull brownish gray with pale gray tips. The remainder of the underparts are dark gray; feathers of the sides, flanks, belly, and undertail coverts have dull bronzy-green subterminal spots. Some males exhibit traces of rosey iridescence on the sides and flanks.

The distribution, shape, and disc color of gorget feathers in the Baja hybrid are intermediate between those of *calliope* and *anna.* Basally, gorget feathers are white or very pale grayish-white, and hence, more like *calliope* than *anna.* A very narrow transitional band of green separates the white base from the terminal purplish-red disc. A buffy-gray subocular stripe separates the eyering from the gorget as in *calliope.* The remainder of the underparts are nearly intermediate to that of *calliope* and *anna.* The throat, immediately adjacent to the gorget, is white, darkening to medium gray on the lower breast, sides, flanks, and belly; feathers on the sides and flanks have green subterminal spots. The undertail coverts (white with a large but nearly imperceptible grayish subterminal spot) are most similar to those of *calliope.*

The gorget of the Louisiana hybrid lacks well-developed lateral extensions observed in *calliope, anna,* and the Baja hybrid, and superficially resembles that of *Selasphorus platycercus* in color and shape. Gorget feathers are pale grayish-white basally (darker near the rachis). A narrow bronzy-green band separates the white feather base from the brilliantly iridescent terminal disc. On most discs, the dominant reflected color varies proximally from coppery purplish-red to coppery rose-red distally. The reddish portions of lateral gorget feathers are not as elongate as those of *calliope, anna,* or the Baja hybrid. White feather bases are visible at the sides of the throat, and especially on the chin and upper throat. The pale grayish-buff subocular stripe is sprinkled with tiny reddish discs; gorget discs extend dorsally to the eyering and auriculars as in *anna.* The gorget is bordered posteriorly by a white band that darkens to light gray on the upper breast and along the midline. Feathers of the sides and flanks have large green subterminal spots and pale buffy margins (especially prevalent on the flanks). The undertail coverts are very pale grayish-white with pale greenish-gray subterminal spots (a few with buffy-white margins), more pronounced than those of *calliope* or the Baja hybrid.

Wing color of *calliope, anna,* and the hybrids is similar. Primary shape in the hybrids is intermediate between that of *calliope* ("squared" primaries 5, 6, 7, and 8) and *anna* (tapered) (see Banks and Johnson 1961).

Rectrices in *calliope* are dull brownish-black with a bronzy sheen, slightly greener on the distal ⅓ of rectrix 1 and 2; the proximal half of the medial and lateral webs of rectrix 1, 2, 3, and 4 (medial web only) are margined with rufous. The central pair of rectrices (1) are semispatulate (web margins proximal to the tip are concave); the margins of rectrix 2 are slightly concave.

Rectrix 1 of *anna* is bright bronzy-green, rectrix 2 is slightly darker. The outer rectrices (3, 4, and 5) are gray along the margins (especially medially), grading to grayish black along the rachis and toward the distal tip. Rectrices lack rufous pigmentation or concave margins.

Shape and pigmentation of rectrices in the hybrids are intermediate between those of *calliope* and *anna.* Overall, the pattern of pigmentation on the rectrices of the Baja hybrid more closely resembles that of *calliope*; the central rectrices are only slightly greener than the outer rectrices, and rufous occurs on the medial (rectrix 1, 2, 3, and 4) and lateral (rectrix 1, 2, and 3) margins. Rectrices of the Louisiana and Baja hybrid are similar, but rectrix 1 and 2 of the Louisiana specimen are greener (approaching the color of *anna*).

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Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 2. Hybrid origin of *Eriocnemis soderstromi* Butler

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Abstract.—*Eriocnemis soderstromi* (Butler 1926) is shown to be a hybrid between *E. nigrivestis,* an endemic of the Volcán Pichincha region in Ecuador, and *E. luciani,* an inhabitant of timberline Andean forest from southern Colombia to Bolivia. This is the first report of intrageneric hybridization among the nine species of *Eriocnemis.* Plumage characters of the hybrid appear to be a blended intermediate of those of the parental species. External measurements of the hybrid are intermediate of those of parental species.

Butler (1926) described *Eriocnemis soderstromi* from a unique specimen [The Natural History Museum, formerly British Museum (Natural History) (BM(NH)) 97.11.12.98] collected by Ludovico Söderström at Nono, on the western slope of Volcán Pichincha, Ecuador, in January 1890. This taxon was the last in a series of enigmatic or questionable Trochiline species discovered in the environs of Quito. Opinions on the taxonomic status of *E. soderstromi* have varied. Peters (1945) listed *E. soderstromi* with a question mark, whereas Meyer de Schauensee (1966) suggested that it might represent an aberration of *E. godini.* Morony et al. (1975) considered it a valid species without elaboration. Sibley and Monroe (1990) listed three possibilities—that it might be an aberrant specimen of *E. godini,* a valid race of *E. godini,* or a distinct species. Fjeldså & Krabbe (1990: 275) regarded *E. soderstromi* as a possible hybrid or "at least not a valid taxon," and Collar et al. (1992) omitted it from their compilation of threatened birds of the Americas. Here I report that *E. soderstromi* represents an intrageneric hybrid between *Eriocnemis nigrivestis* and *E. luciani.*

Methods

I employed the analytical methods of hybrid diagnosis outlined in Graves (1990). Because of the specimen's size and shape and general configuration of plumage elements, *Eriocnemis soderstromi* cannot be attributed to mutation or a rare genetic variant of any known taxon. Assuming its hybrid origin, the geographical source pool of potential parental species may be drawn from the list of hummingbird species ($n = 47$, see Appendix 1) that inhabit the Andes of northern Ecuador above 2000 m elevation (see Fjeldså & Krabbe 1990). The type specimen of *E. soderstromi* appears to be fully adult by plumage characters and lacks striations on the rhamphotheca at 10× magnification. Söderström sexed the bird as male and there is no evidence to suggest otherwise. The type was compared to large series of all source pool species in The Natural History Museum. Plumage colors were compared under natural light. Wing chord, bill length (from anterior extension of nasal feathering), and rectrix length (from the point of insertion of the central rectrices) of males of several species were measured with digital calipers and rounded to the nearest 0.1 mm (Table 1).

I used principal components analysis (PCA) on $\log_{10}$ transformed rectrix length to reduce the dimensionality of tail data to a single value. Unrotated principal compo-

Table 1.—Ranges and means (± one standard deviation) of measurements (mm) of adult male *Eriocnemis nigrivestis, E. luciani, E. vestitus* from Ecuador, and the hybrid, *E. nigrivestis* x *E. luciani* (= *E. soderstromi* Butler).

Character	*nigrivestis* (*n* = 15)	*luciani* (*n* = 15)	*vestitus*[a] (*n* = 15)	Hybrid BM(NH) 97.11.12.98
Wing chord	57.6–60.5	69.1–72.5	57.8–61.3	65.6
	58.9 ± 0.9	70.7 ± 1.1	59.4 ± 1.1	
Bill length	14.4–15.8	19.2–20.8	15.9–18.8	19.2
	15.1 ± 0.5	20.1 ± 0.5	17.5 ± 0.8	
Rectrix 1	25.7–28.5	25.5–29.0	26.2–29.7	27.4
	26.8 ± 1.0	27.8 ± 0.9	28.4 ± 1.1	
Rectrix 2	26.8–29.8	29.1–33.6	28.0–31.5	29.8
	28.1 ± 1.1	32.0 ± 1.3	29.9 ± 1.0	
Rectrix 3	28.8–33.1	38.5–44.1	31.1–35.3	33.5
	31.0 ± 1.5	41.5 ± 1.7	33.1 ± 1.4	
Rectrix 4	32.0–37.1	49.4–53.1	35.3–39.7	41.0
	34.2 ± 1.9	51.8 ± 1.3	37.9 ± 1.5	
Rectrix 5	34.9–39.3	55.4–60.2	40.6–45.3	46.6
	37.1 ± 1.3	58.0 ± 1.3	42.7 ± 1.4	

[a] Includes 10 specimens from the Eastern Cordillera of the Colombian Andes.

nents were extracted from covariance matrices (Wilkinson 1989).

The hybrid diagnosis followed a two-step procedure. The presumed parental species of *Eriocnemis soderstromi* were hypothesized through the comparative analysis of plumage pattern and color, as well as the shape of external keratinized structures (bill and feathers). Then, the restrictive hypothesis was further examined with quantitative analyses of size and shape. As pointed out in a series of hybrid diagnoses (e.g., Graves 1990, 1993, 1996; Graves & Zusi 1990), I consider the concordance of results as strong support for the hypothesis of presumed parentage. Atavism or hybrid luxuriance has not been demonstrated in hybrid hummingbirds Banks & Johnson 1961, Graves 1990.

Results

Butler's (1926:62) description of the type of *Eriocnemis soderstromi* was brief but generally accurate:

> "Forehead greenish-blue, crown darker and more bronze than the back, turning to velvet-black when viewed from in front, whereas in *E. godini* the forehead and crown are of the same colour as the back, remaining green when viewed from in front; back of a darker shade; lower rump and upper-tail coverts dark steel-blue, only margined with green (in *E. godini* they are entirely shining grass-green); blue throat-patch much larger, and lower surface darker without the strong golden gloss of *E. godini.*"

Unfortunately, Butler's description compared the type of *E. soderstromi* with that of *E. godini* (also in The Natural History Museum) rather than the six species of *Eriocnemis* that occur in northern Ecuador. Recent examination of the type of *E. godini* suggests that it too is a hybrid (Graves, in prep.).

Key plumage characteristics of *E. soderstromi* (Fig. 1) that permit its parental species to be identified include: elongated, silky tibial plumes (commonly referred to as "leg puffs"); small poorly-defined gorget; unmarked and forked tail (depth = 19.2 mm); steel-blue upper-tail coverts margined with green; brilliant purplish-blue under-tail coverts; and bluish-green forecrown (Fig. 1).

Well-developed, silky leg puffs are the

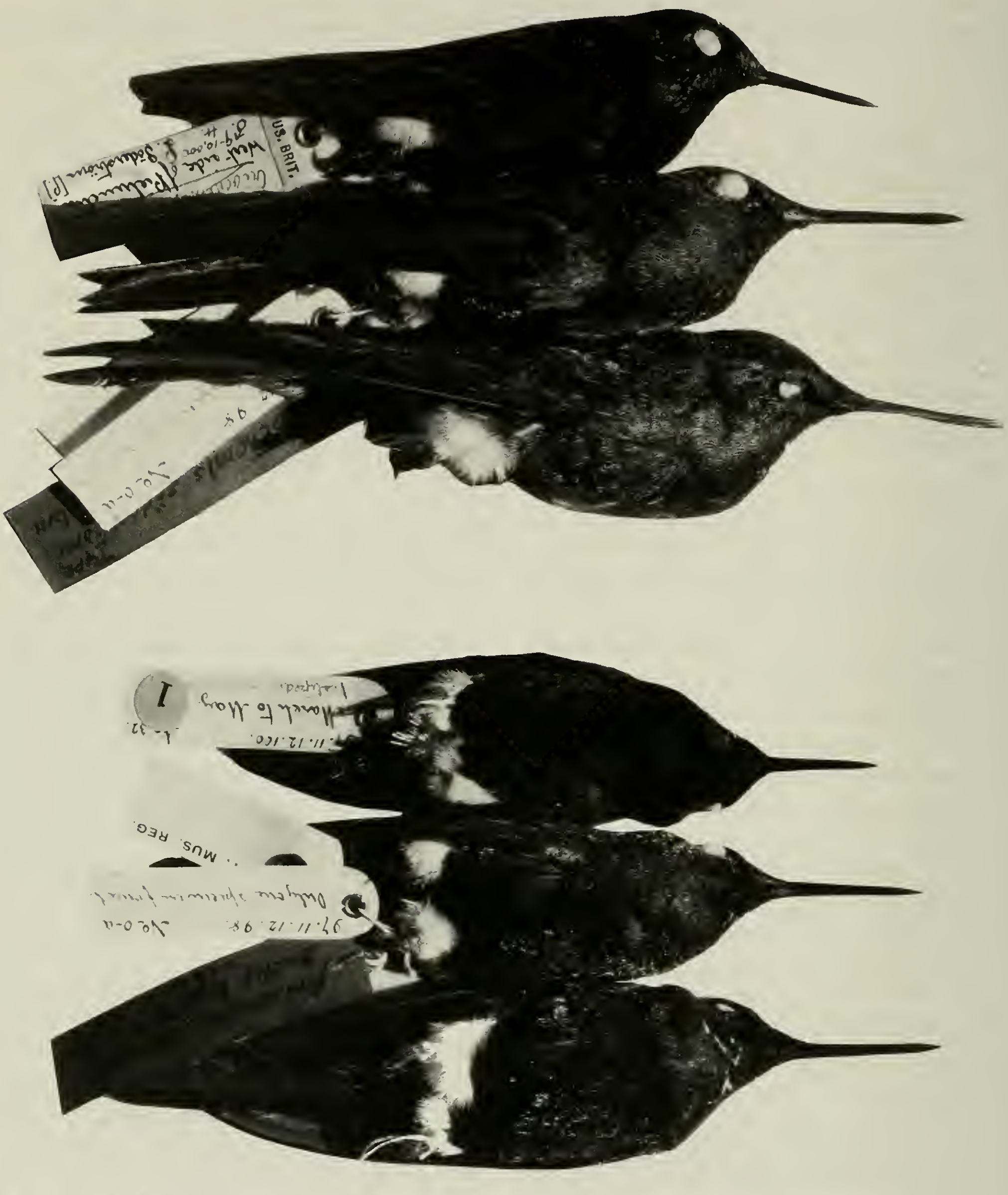

Fig. 1. Lateral and ventral views of male *Eriocnemis nigrivestis* (top), *E. luciani* (bottom), and their hybrid (= *E. soderstromi* Butler, BM(NH) 97.11.12.98).

most distinctive character of *E. soderstromi.* Species in three genera from the Ecuadorian Andes (*Eriocnemis, Haplophaedia, Ocreatus*) possess leg puffs (see Appendix 1). *Ocreatus* can be eliminated from consideration because the hybrid lacks evidence (even as traces) of racket-tipped rectrices. Both species of *Haplophaedia* may be excluded from the pool of potential parental species because the breast, belly and flanks of *E. soderstromi* lack grayish-white or buffy margins, its leg puffs are pure white, and its nostrils are obscured by adpressed feathers. Based on this evidence, both of the parental species of *E. soderstromi* can be drawn from the assemblage

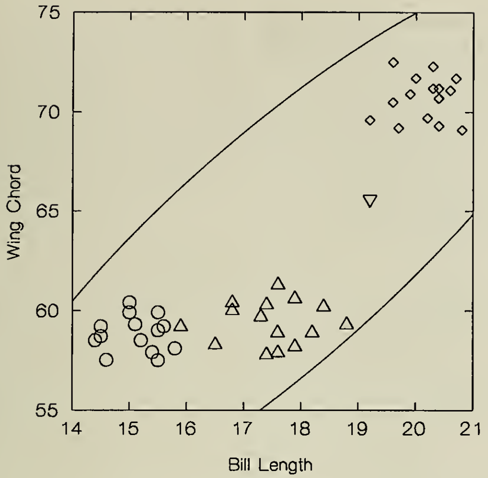

Fig. 2. Bivariate relationship of wing chord and bill length (mm) in males of *Eriocnemis nigrivestis* (circles), *E. vestitus* (triangles), *E. luciani* (diamonds), and the hybrid, *E. nigrivestis* × *E. luciani* (BM(NH) 97.11.12.98) (inverted triangle). Curved lines represent the boundaries of the 95% confidence ellipse.

of five Ecuadorian species of *Eriocnemis* with white leg puffs (*nigrivestis, vestitus, luciani, mosquera, alinae*). The uniformly steel-blue tail and brilliant, blue under-tail coverts of *E. soderstromi* nullifies the inclusion of *E. mosquera* and *E. alinae* in the pool of potential parental species.

Only two of the remaining triad of species could have contributed the unique combination of characters exhibited by *E. soderstromi.* The bluish-green forehead of *E. soderstromi* is found only in *E. luciani,* while the steel-blue upper-tail coverts are found in *E. nigrivestis* but not in *E. luciani* or *E. vestitus.* I conclude from plumage characters, that *E. soderstromi* represents a hybrid between *E. nigrivestis* and *E. luciani* (see Appendix 2). Hybridization between other combinations of species could not have produced the characters present in the type of *E. soderstromi.*

External measurements.—Measurements of *Eriocnemis soderstromi* fell within the character means of the hypothesized parental species (Table 1). However, *E. nigrivestis* and *E. vestitus* are so similar in size and shape, that *E. nigrivestis* × *E. luciani* and *E. vestitus* × *E. luciani* hybrids may not be distinguished by mensural characters alone (Table 1, Figs. 2, 3).

Table 2.—Factor loadings from a principal components analysis (PCA) of rectrix length in male specimens (see Table 1) of *Eriocnemis luciani, E. nigrivestis,* and their hybrid (= *E. soderstromi* Butler, BM(NH) 97.11.12.98).

Variables	PCA I
Rectrix 1 (innermost)	0.006
Rectrix 2	0.024
Rectrix 3	0.056
Rectrix 4	0.078
Rectrix 5	0.081
Percent variance explained	95.4%

Remarks

Eriocnemis nigrivestis has one of the most restricted geographic ranges of any avian species in South America and valid records are limited to Volcán Pichincha and Volcán Atacazo, Pichincha Province, in northwestern Ecuador (Collar et al. 1992). This taxon was locally abundant in the late 19th century as judged by the number of specimens in museums (e.g., Oberholser 1902, Lonnberg & Rendahl 1922, Chapman 1926), but populations are currently threatened by grazing, agriculture, and wood cutting (Bleiweiss & Olalla 1983, Collar et al. 1992).

Notwithstanding the plumage and morphological evidence, the possibility that *E. soderstromi* represents the only known specimen of a valid species is diminished by the fact that the avifauna of Volcán Pichincha is well known, and that no additional specimens or sight records have been obtained in that region (Chapman 1926, Meyer de Schauensee 1966, Bleiweiss & Olalla 1983, Fjeldså & Krabbe 1990). The specimen of *Eriocnemis nigrivestis* × *E. luciani* is the first intrageneric hybrid reported for the genus, although a number of presumed intergeneric hybrids between *Heliangelus amethysticollis* and *E. cupreov-*

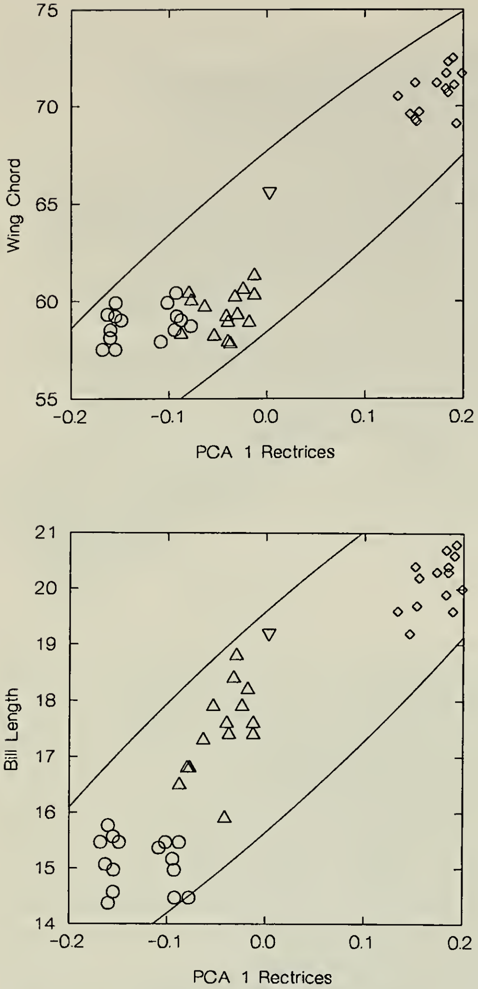

Fig. 3. Bivariate relationship of wing chord (top) and bill length (bottom) with factor scores from the first principal component (PCA 1) of an analysis of rectrix length in males of *Eriocnemis nigrivestis* (circles), *E. vestitus* (triangles), *Eriocnemis luciani* (diamonds), and the hybrid, *E. nigrivestis* × *E. luciani* × (BM(NH) 97.11.12.98) (inverted triangle) (see Table 2). Curved lines represent the boundaries of the 95% confidence ellipse.

entris have been documented (Graves 1990).

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Appendix 1

Species of hummingbirds that occur regularly above 2000 m in the northern Ecuadorian Andes: *Phaethornis syrmatophorus, Doryfera ludoviciae, Colibri thalassinus, C. coruscans, Chlorostilbon mellisugus, Adelomyia melanogenys, Heliodoxa rubinoides, H. leadbeateri, Urochroa bougueri, Oreotrochilus chimborazo, Patagona gigas, Aglaeactis cupripennis, Lafresnaya lafresnayi, Pterophanes cyanopterus, Coeligena coeligena, C. torquata, C. lutetiae, Ensifera ensifera, Boissonneaua flavescens, B. matthewsii, Heliangelus strophianus, H. exortis, H. viola?, Eriocnemis nigrivestis, E. vestitus, E. luciani, E. mosquera, E. alinae, E. derbyi, Haplophaedia aureliae, Ocreatus underwoodii, Lesbia victoriae, L. nuna, Ramphomicron microrhynchum, Metallura williami, M. tyrianthina, Chalcostigma ruficeps?, C. stanleyi, C. herrani, Opisthoprora euryptera, Aglaiocercus kingi, Schistes geoffroyi, Philodice mitchellii, Myrtis fanny, Acestrura mulsant, A. bombus, A. heliodor.*

Appendix 2

Comparative description of plumages of adult male *Eriocnemis luciani* and *E. nigrivestis* from Volcán Pichincha, Ecuador, and their hybrid, BM(NH) 97.11.12.98 (= "*Eriocnemis soderstromi*" Butler 1926). Descriptions of structural colors are unusually subjective, as color seen by the observer varies according to the angle of inspection and direction of light. For this reason I use general color descriptions.

Nasal feathering and forecrown of *luciani* are shining blue, shading to bluish-green on the lores when viewed head-on in direct light. These plumage regions in *nigrivestis* are black with very faint green reflections. The forecrown of the hybrid exhibits pronounced bluish-green reflections, surrounded by matte black when viewed from in front. The frontal profile of the hybrid is intermediate between that of *nigrivestis* and the more sloping profile of *luciani* (see Fig. 1).

The crown, back, wing coverts, and upper-tail coverts are green in *luciani.* In *nigrivestis* the crown, back, and wing coverts are black with faint greenish-blue reflections; the upper-tail coverts are shining steel blue (brilliant pale green in *vestitus*). The crown and back of the hybrid are green, but of a darker shade than in *luciani*; a few feathers on the lower back are shaded with steel-blue, whereas the upper tail coverts are steel-blue with green margins. The rectrices of *luciani* are black with faint blue reflections in strong light, whereas the more angular rectrices of *nigrivestis* are somewhat more glossy and bluer. Rectrices of the hybrid are intermediate in color and shape.

The chin, throat, breast and belly are green in *luciani*; white feather bases are exposed on the throat. In *nigrivestis,* these plumage regions are black with green reflections on the sides of the throat, and with narrow green feather margins on the sides and flanks; a small, brilliant, purplish-blue gorget is present on the center of the throat. The throat, breast and belly of the hybrid are darker than in *luciani* and exhibit fewer and less intense reflections when viewed head-on. A shining (but diffusely defined) turquoise gorget (ca. 12 feathers) occurs on the throat of the hybrid. A coppery-gold sheen on some feathers adjacent to the gorget can be observed at certain angles. The bases of the brightest, most differentiated, gorget feathers are gray with buffy-white margins separated from the broad turquois tip by a narrow transitional band of greenish gray.

Tibial plumes (leg puffs) of *luciani, nigrivestis,* and the hybrid are well developed and silky white. Undertail coverts of *luciani, nigrivestis,* and the hybrid are brilliant purplish-blue.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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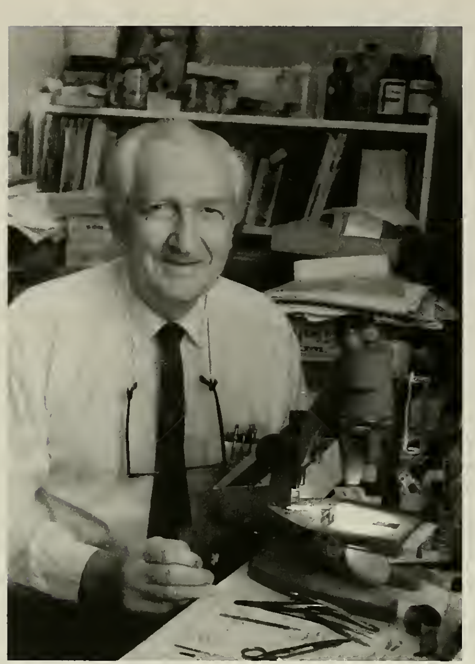

George C. Steyskal (1909–1996)

George Constance Steyskal, since 1975 Editor for Classical Languages for the *Proceedings of the Biological Society of Washington,* died on May 30, 1996 in Gainesville, Florida. His wife preceded him in death in 1991. He is survived by a son, Neil Morgan Steyskal, and by two grandchildren, two great grandchildren and two brothers.

George was born in Detroit, Michigan on March 30, 1909. He was the oldest of seven children and early on entered factory work to help the family, graduating from the Henry Ford Trade School in Detroit. He worked for many years as a tool-and-die maker, and finally became superintendent of a plant, traveling around the country to estimate jobs. He joined the Systematic Entomology Laboratory, USDA, at the Smithsonian in 1962, retiring in 1979. After the death of his wife, he moved to Florida and became a resident Research Associate of the Florida State Collection of Arthropods.

During his working career he was interested in many aspects of natural history, and he became knowledgeable especially in insects, snails, and botany. His major interests early turned to the true flies (Diptera) and especially to the typically small flies of the Acalyptrate Diptera. His competence in botany would be useful as he later worked on insects attacking plants, the Tephritidae (fruit flies) and the Agromyzidae (leaf miners). His first paper was published in 1938 and he continued to publish until serious illness overtook him after a long and generally healthy life.

Although an amateur, his publications, often accompanied by his own drawings, attracted attention. When a vacancy occurred in the taxonomic organization now known as the Systematic Entomology Laboratory of the U.S. Department of Agriculture, he applied and was hired, although at first as Agriculture Research Technician because of the lack of formal academic qualifications required for the position of Research Entomologist. Ultimately he was promoted to Research Agriculturist. At the time he was hired, he had already published 101 papers, more than many people have in a career. At the time of his retirement in 1979, this total had swelled to 360. A complete bibliography has been prepared for the Proceedings of the Entomological Society of Washington to accompany a more detailed record of his work.

One remarkable facet of this multi-talented amateur was his interest in languages, both classical Latin and Greek and modern languages. Blessed with a phenomenal memory and a facility with languages, he translated all—I believe "all" is a fair statement—the European languages, and studied others such as Arabic and Japanese. This background, and the generous helpfulness that was an important part of his character, made him a natural advisor on scientific names for the *Proceeding of the Biological Society of Washington,* which he served faithfully for over twenty years, as well as for the *Proceedings of the Entomological Society of Washington,* and as Translation Editor (1980–1996) for Scripta Technicas *Entomological Review* (the translation of the Russian serial, *Entomologicheskoe Obozrenie*).

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(retired)

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CONTENTS