PROCEEDINGS

of the

Biological Society of Washington

VOLUME 108
1995

Vol. 108(1) published 24 March 1995
Vol. 108(2) published 22 June 1995
Vol. 108(3) published 19 September 1995
Vol. 108(4) published 28 December 1995

WASHINGTON
PRINTED FOR THE SOCIETY

All correspondence should be addressed to the
Biological Society of Washington, Smithsonian Institution
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WASHINGTON

VOLUME 108 NUMBER 1
24 MARCH 1995

ISSN 0006-324X

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PROCEEDINGS

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Known office of publication: National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Printed for the Society by Allen Press, Inc., Lawrence, Kansas 66044

Second class postage paid at Washington, D.C., and additional mailing office.

POSTMASTER: Send address changes to PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON, P.O. Box 1897, Lawrence, Kansas 66044.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(1):1–5. 1995.

The karyotypes of two South American mouse opossums of the genus *Thylamys* (Marsupialia: Didelphidae), from the Andes, and eastern Paraguay

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Abstract.—The karyotypes of *Thylamys macrura,* from eastern Paraguay and adjacent Brazil, and *T. pallidior,* from the Andean Altiplano in Argentina and Bolivia, are reported for the first time. The karyotypes of somatic tissues from female *T. macrura* and female *T. pallidior* consist of 2N = 14. However, the diploid number found in somatic cells in males of *T. pallidior* exhibits 2N = 13 because the Y chromosome is missing. The missing Y phenomenon might represent another case of chromosome mosaicism in American marsupials, although this time detected in didelphids.

Tate (1933) recognized five species groups in the genus *Marmosa* Gray, 1821 (sensu lato) based on phenetic characters. Subsequent morphologic, chromosomic, and serologic studies have shown that these assemblages approximate genera (Reig et al. 1985, 1987; Gardner & Creighton 1989). Among these, *Thylamys* Gray, 1843, has the southernmost distribution of mouse opossums in South America encompassing elevations as high as 3500 m, as well as lower temperate and subtropical habitats (Cabrera 1958). *Thylamys* differs from other marmosines in having a characteristic tricolored dorsal pattern, and the capacity to store fat in the tail (Tate 1933, Mann 1978) Recent revisions of the genus recognize five species (Gardner & Creighton 1989, Gardner 1993): *Thylamys pusillus* (Desmarest 1804), *Thylamys macrura* (Olfers 1818), *Thylamys elegans* (Waterhouse 1839), *Thylamys velutinus* (Wagner 1842), and *Thylamys pallidior* (Thomas 1902). *Thylamys pallidior* occurs on the rocky slopes of the Altiplano of Bolivia and Argentina (Tate 1933; fig. 1), whereas, the subtropical form *T. macrura* is found in the humid forests of eastern Paraguay and adjacent Brazil (Gardner 1993; fig. 1). This constitutes the sixth published record of this species for Paraguay, since the original description by Olfers (1818) based on Azara's (1801) "Micouré à queue longue," or "Colilargo" (Azara 1845). Tate (1933) referred to this species as *Marmosa marmota,* and Cabrera (1958) as *Marmosa grisea.* The name *macrura* (Olfers 1818) is available and *T. macrura* is used by Gardner (1993). In this study, the karyotypes of *T. macrura* and *T. pallidior* are reported for the first time. This is the first study documenting the absence of one of the sex chromosomes of somatic cells in didelphid marsupials.

Methods

Chromosomal preparations were obtained directly from bone marrow using the standard velban technique described in Anderson et al. (1987). A minimum of 10 metaphase spreads were counted for each specimen. Nomenclature for chromosome morphology and fundamental number (FN) follows Patton (1967). Five specimens of *T. pallidior* from two localities in Bolivia were analyzed. The karyotype of *T. macrura* was

Fig. 1. Map showing the distribution of *T. pallidior* along the Andes of Argentina and Bolivia, and *T. macrura* in eastern Paraguay. The boxes and dot represent the collecting site given in the text.

obtained from a specimen from eastern Paraguay. Voucher specimens, chromosome slides, and cell suspensions are deposited in the Museum of Southwestern Biology (MSB) and the American Museum of Natural History (AMNH). Collection localities are (Fig. 1): Bolivia: Department of Chuquisaca, Camargo, 68 km (by road) N of Camargo, 3400 m, 20°09′S, 65°17′W (3 males MSB 57003, AMNH 262406, and AMNH 262407; 1 female AMNH 262405); Department of Tarija, Serranía Sama, 3200 m, 21°27′S, 64°52′W (1 female, AMNH 263555). Paraguay: Department of Concepción, Escuela Agropecuaria, 7 km (by road) NE from Concepción, 23°21′S, 57°23′W (1 female, MSB NK 27536).

Results and Discussion

The autosomes of *T. macrura* (2N = 14, FN = 20; Fig. 2a) consist of three pairs of large submetacentrics (1–3), one pair of medium-sized metacentrics (4), and two pairs of small acrocentrics (5–6). The X chromosome is a small acrocentric. The autosomes of *T. pallidior* (Fig. 2b) are not distinguishable from those of *T. macrura,* although the three males of the Andean species present 2N = 13, FN = 20; the Y chromosome was absent in all counted plates. The female *T. pallidior* exhibited the complete set of chromosomes, 2N = 14. A male of *T. macrura* was not available for karyotype.

The autosomic complement of the species of *Thylamys* reported here is similar to those documented previously for other species of the genus, such as *T. elegans* from Chile and Bolivia, which possess the identical three group pattern of autosomes and morphology (Reig et al. 1972, Palma & Yates 1995). *Micoureus cinereus* and *M. constantiae* have similar diploid and fundamental number (2N = 14, FN = 20; Palma & Yates 1995). *Marmosa* (sensu stricto), *Marmosops,* and *Gracilinanus,* have 2N = 14, however the fundamental number in these taxa is FN = 24 (Reig 1968, Palma & Yates 1995).

The mouse opossum karyotypes presented in this paper reinforce the concept of chromosomic conservatism in marsupials, and support the fact that marsupial species that occur in remarkably different habitats share a common karyotype (Reig et al. 1977, Hayman 1990). The common 2N = 14 is shared by most of the marmosines in the Neotropics. *Marmosa canescens* (2N = 22), is the only known exception (Engstrom & Gardner 1988).

The conclusive evidence of the absence of the Y chromosome in *T. pallidior* is difficult to determine under the methodology followed in this study. It is possible that the Y has been translocated to another chromosome, or this condition may be another example of chromosome mosaicism, i.e., a difference in sex-chromosome presence between the germ line and cells of the somatic tissues (Hayman 1990). Similar patterns of absence of the Y chromosome for somatic

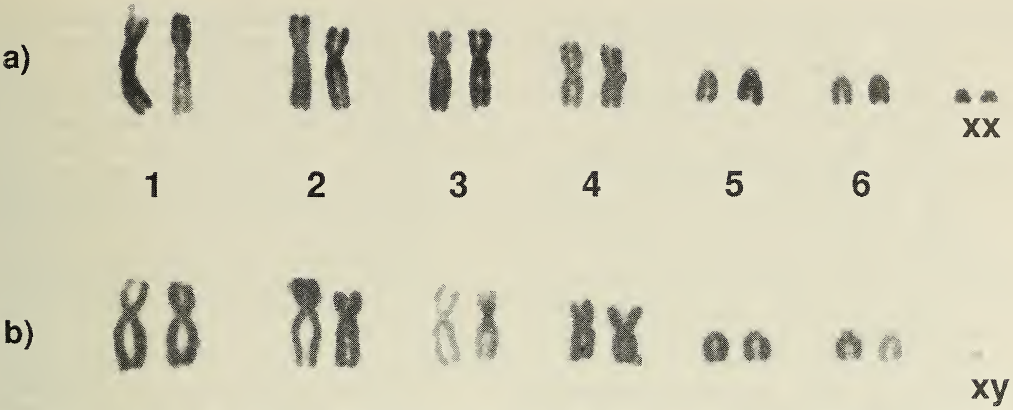

Fig. 2. a, Standard karyotype of a female *Thylamys macrura* from Concepción, Paraguay, 2N = 14, FN = 20. b, Standard karyotype of a male *Thylamys pallidior* from Camargo, Chuquisaca, Bolivia, 2N = 14, FN = 20.

cells have been found for *Chironectes minimus* (Palma & Yates 1995) and *Dromiciops australis* (Gallardo & Patterson 1987). Additional reports of chromosome mosaicism have been also made for Australian marsupials of the family Peramelidae, where one of the X chromosomes is missing in somatic cells of females, and in *Petauroides* (Petauridae), where the Y chromosome is missing from the majority of cells obtained from bone marrow (Murray et al. 1979, Hayman 1990).

The missing Y chromosome found in *Dromiciops australis* (Gallardo & Patterson 1987), caused these authors to suggest that the microbiotheriid would be more related to Australasian marsupials than to American metatherians, supporting Szalay's (1982) contention that *Dromiciops* and Australian marsupials constitute the cohort Australidelphia. Data from this study and from Palma & Yates (1995), prove that the Y chromosome is missing not only in *Dromiciops* and Australasian marsupials, but in American marsupials as well. This scenario fits a typical case of parallelism or represents a plesiomorphic condition in the evolution of metatherian sexual chromosomes of both geographic regions. Hence, this character cannot be used as evidence for inferring phylogeny between Australian and American marsupial lineages.

Acknowledgments

Mike Bogan, Jennifer K. Frey, Jorge Salazar, and Terry L. Yates provided valuable comments on a draft of the manuscript. Special thanks to Lucy Aquino from CITES-Paraguay, and Carl Shuster; to Flaviano Colman and Luis Morán of the National Museum of Natural History of Paraguay, Maribé Robles, and to the National Parks Office of the Ministry of Agriculture and Livestock of Paraguay. Funding support was provided by a NSF Research Improvement Grant PDS-105-774, the Latin American Institute, University of New Mexico, and Sigma Xi. Field work in Bolivia was supported by NSF grants BSR-83-16740 to the American Museum of Natural History (S. Anderson), and BSR-84-08923 to the University of New Mexico (T. L. Yates). The map was prepared by Beth Dennis.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(1):6–17. 1995.

Rediscovery and redescription of *Sphenomorphus beyeri* Taylor (Reptilia: Lacertilia: Scincidae) from the Zambales Mountains of Luzon, Philippines

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Abstract.—Sphenomorphus beyeri Taylor, 1922, long known from a single specimen, is redescribed on the basis of newly acquired material from the herpetologically unsurveyed area of the Zambales Mountains, west central Luzon Island, Republic of the Philippines. Phenotypically most similar to its distantly allopatric congener *S. diwata,* the holotype and our new series are distinguished from other Philippine *Sphenomorphus* by the combination of their small to moderate size (SVL = 46.6–67.1 mm), fused frontoparietals, 88–96 paravertebrals, 38–42 scales at midbody, 19–21 subdigital fourth toe lamellae, and unique coloration.

In his monograph on the lizards of the Philippine Islands, E. H. Taylor (1922a) recognized 16 Philippine species in the genus *Sphenomorphus* (Lacertilia: Scincidae). He later supplemented this work on Philippine lizards with descriptions of two more scincid species in a more general herpetological contribution (Taylor 1922b). One of these was *Sphenomorphus beyeri,* a skink described on the basis of a single specimen found on Mt. Banahao in the Laguna Province of southern Luzon. Brown & Alcala (1980) later recognized 22 species of Philippine *Sphenomorphus.* One of these was *S. diwata* Brown & Rabor (1967), which the authors hypothesized to be the closest relative of *S. beyeri.* Brown & Alcala reported *S. diwata* from the Diwata mountains of northern Mindanao Island, and placed it and *S. beyeri* into the two-species non-phylogenetic couplet "Group I *Sphenomorphus*" (1980:154). As presently understood, the genus *Sphenomorphus* contains over 120 species world-wide (Myers & Donnelly 1991) with 60 species in the Oriental and Australian zoogeographic regions alone (Brown & Alcala 1956, 1961a; Greer & Parker 1974; Greer 1979).

Sphenomorphus beyeri has, to date, only been known from the incomplete holotype, yet it invariably has been recognized as a valid species. In the course of a recent inventory of the fauna of the Philippines undertaken by the Cincinnati Museum of Natural History (CMNH) and the National Museum of the Philippines (PNM), we captured 16 additional specimens of *S. beyeri* in the mossy cloud forests of the Zambales Mountains of west central Luzon. Collection of this new material provided us with a unique opportunity to analyze intraspecific morphological variation of this endemic Philippine skink and to reconsider the validity of its specific rank.

Methods

We conducted field studies in the Zambales Mountain range from 17 February to 18 March 1992. Drift fences and pitfall traps (25 m of 0.65 ml black plastic, stretched to 15 cm above ground, supported with wooden stakes, with ≥50 cm deep plastic-lined pits spaced every 5 m for a total of six pitfalls per 25 m of drift fence at each 100 m interval on slope) and time-constrained searches were used to collect specimens. Specimens were photographed, then fixed in 10% buffered formalin; notes on coloration, behavior, and habitat (including elevation) were recorded at time of capture. Upon return to the U.S.A. (approximately one month later), specimens were transferred to 70% ethanol.

Detailed examination of all material was conducted at the Cincinnati Museum of Natural History and at the National Museum of Natural History. When possible (see character definitions below), we took measurements and scale counts following techniques detailed in Brown & Alcala (1980); illustrations of head scalation were made (by RMB) with a Wild microscope equipped with a camera lucida attachment.

Characters (measured to the nearest 0.1 mm) are defined as: snout-to-vent length (SVL), from tip of animal's snout to caudal margin of anal scale; tail length (TL), from caudal margin of anal scale to tail's tip (specimens with regenerated tails are not included in statistical analyses); axilla-groin distance (AGD), from caudalmost point where forelimb meets body to anteriormost point where hind limb meets body; hind leg length (HLL), from point where rear limb meets body to tip of longest (=4th) toe; head length (HL), from tip of snout to caudal edge of tympanum; head breadth (HB), width of head at its widest point (=ocular region) when viewed from above; snout length (SL), from anterior edge of bony orbit to tip of snout; eye diameter (ED), horizontal diameter across bony orbit; and tympanum diameter (TD), horizontal distance across the tympanic annulus.

Lateral head scales (e.g., labial scales) were examined on both sides of the head and numbers for each side are given separately with a dashed line (—) designating left from right respectively. Meristic and mensural data are given as means ± standard deviations (*SD*) and range.

Statistical analyses were carried out using the Statistical Analysis Software Program (SAS), version 6.03 (SAS Institute Inc. 1988a, 1988b), using UNIVARIATE procedure for standard statistics. Significance of moment statistics (skewness, g_1, and kurtosis, g_2) was calculated by hand (Sokal & Rohlf 1981:174–175).

Specimens are deposited in the California Academy of Science (CAS), Cincinnati Museum of Natural History (CMNH), and National Museum of the Philippines (PNM). Material Examined includes: Holotype (Luzon Island, Laguna Province, Mt. Banahao) CAS 61183, immature male, collected on a rock ledge on Mt. Banahao at 1500 m by E. H. Taylor (Taylor 1922b:285). Six females (CMNH 3652, 3653, and 3658; PNM 2307, 2301, and 2304), nine males (CMNH 3655, 3657, and 3659; PNM 2300, 2302, 2303, 2305, 2306; USNM 337768) and one immature juvenile or hatchling (CMNH 3654), all collected by RMB and JWF. All were taken from Luzon Island, Zambales Province, Municipality of Masinloc, Barangay of Coto, Zambales Mountain range, Mt. High Peak.

Study Sites

Until the present study, (PNM/CMNH Philippine Biodiversity Inventory) the Zambales Mountains (Zambales Province, Municipality of Masinloc) were completely unsurveyed herpetologically due to a combination of major insurgency in this area and its close proximity to the Subic Bay Naval Base, 70 km south in the town of Olongapo. Following the eruption of Mt. Pinatubo in 1991 and subsequent closing of

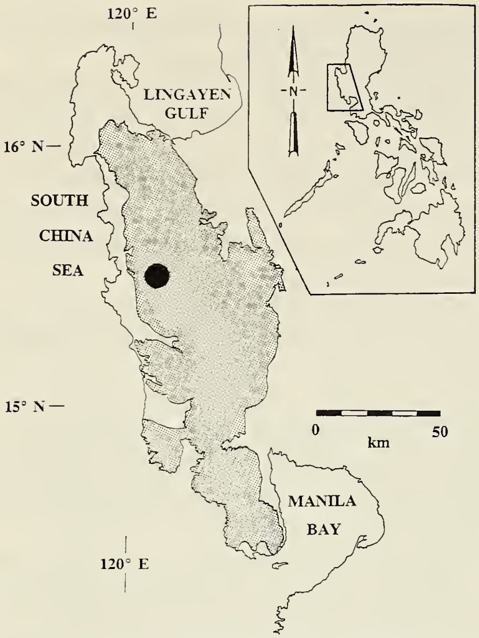

Fig. 1. The Zambales Mountains. Shaded area represents the major geologic formation constituting the Zambales Mountain range (see text). Darkened circle represents Mt. High Peak, and encompasses both localities sampled.

the United States military facilities at Olongapo, an opportunity was made available to naturalists to survey this largely unknown region.

The Zambales Mountains (Fig. 1) are an isolated coastal mountain range encompassing an area of approximately 6960 km^2 on west central Luzon; the Zambales range extends from west of the Lingayen gulf to the western border of Manila Bay at an orientation of 20° West of due North. To the east, the Zambales Mountains are isolated from the nearest mountain range, the Cordillera Central, by the Plains of Tarlac (also known as the Pampanga Plains). To the west and north, these mountains end in the South China Sea; to the south they separate Subic Bay from Manila Bay. The Zambales Mountain range currently is contiguous with mainland Luzon, connected to the latter by the wide Plains of Tarlac, believed to have been submerged below the Luzon sea during the Pliocene and Pleistocene (Rutland 1968; Hashimoto 1981a, 1981b; Auffenberg 1988). Geological evidence suggests that the Zambales Mountains were formerly isolated much farther west of their present position and were surrounded by water—not connected to mainland Luzon as they are today (Dickerson 1924, Auffenberg 1988). The Zambales currently represent a large "insular" massif, geologically isolated from the three other principal montane regions of Luzon (Bureau of Mines 1963; UNESCO/ECAFE 1971; Hashimoto 1981a, 1981b; Auffenberg 1988).

Site 1.—Zambales Mountains, 1100 m, 15°35′N, 120°09′W. Sampled from 17 to 26 February, the site is a tropical moist deciduous forest type (Whitmore 1984); virgin timber (predominantly Myrtaceae, Lauraceae, and Tiliaceae) begins at an elevation of ca. 1030 m. Presence of Mt. Pinatubo ash deposits throughout the area combined with noticeable signs of rattan gathering efforts undertaken by local residents precludes designation of the area as "undisturbed."

Site 2.—(Fig. 2) Zambales Mountains, 1500 m., 15°30′N, 120°08′W. Sampled between 11 and 18 March 1992, this area lies within the broad category of tropical moist deciduous forest type but remains, nonetheless, more typical of the upper montane (="mossy") rain forest (Whitmore 1984) due, presumably, to its somewhat higher elevation. Virgin timber predominates (Fagaceae, Myrtaceae, Magnoliaceae, and Pinaceae) and very little bamboo or other secondary or disturbance indicator species were encountered.

A more extensive description of these study sites and a discussion of their geologic importance is provided by Ruedas et al. (1994).

Results

Capture data.—A single specimen of *S. beyeri* collected at Site 1 was a mature male

Fig. 2. Typical habitat of *S. beyeri* between 1500 and 1600 m on Mt. High Peak, Zambales Mountains where most specimens of *Sphenomorphus beyeri* were found. The vegetation and forest floor in this area were coated with approximately 2–4 cm of volcanic ash from the eruption of Mt. Pinatubo. Photo from a color transparency by RMB, courtesy of CMNH.

(PNM 2300) collected under leaf litter on the forest floor at 1265 m. When disturbed, this lizard became alert, moved in a rapid serpentine manner and attempted to burrow under debris and leaf litter. A pair of pitfall trapped specimens (CMNH 3652, a gravid female; PNM 2301, a mature female without eggs) from Site 2 were captured during the day, at 1510 m, and 1610 m, respectively. The rest of the new series was captured by splitting open rotten logs lying horizontally in contact with the forest floor. One specimen (male, PNM 2305) was damaged when the machete used to split the log struck it. No specimens were taken at night despite extensive search efforts.

Sphenomorphus beyeri Taylor, 1922:283

Fig. 3, 4

Diagnosis.—A small to moderate-sized *Sphenomorphus, S. beyeri* is readily distinguished from its congeners by the following combination of characters: (1) prefrontals moderate, usually separate; (2) frontoparietals fused except in immature specimens; (3) usually 6–7 labials; (4) four large supraoculars (5) paravertebrals 88–96; (6) scales around midbody 38–42; (7) fourth toe lamellae 19–21; (8) body proportion ratios as follows, SL/HL = 0.25–0.37; SL/HB = 0.38–0.57; HB/HL = 0.60–0.69; HB/SVL = 0.13–0.17; ED/SL = 0.30–0.43; (9) unique coloration and color pattern.

Description (based on holotype and 16 referred specimens).—Details of the head scalation of an adult male (PNM 2302; captured by RMB on 16 March 1992 in montane cloud forest at 1460 m, between 1400 and 1630 hr) are shown in Fig. 3 from dorsal (A), ventral (B) and lateral (C) perspectives.

Head scalation.— Rostral 1.2–2.9 ($\bar{X}$ = 2.2 ± 0.4 *SD, n* = 14) mm wide (holotype

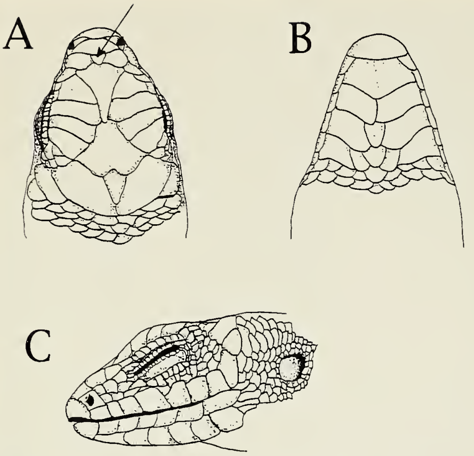

Fig. 3. Dorsal (A), ventral (B), and lateral (C) perspectives of head scalation of *Sphenomorphus beyeri* (PNM male 2302; HL = 12.0 mm). Arrow indicates the presence of the azygous interprefrontal scale on snout.

= 1.8). Frontonasals 1.7–2.4 ($\bar{X}$ = 2.2 ± 0.3 *SD, n* = 14) mm wide and 1.1–1.6 ($\bar{X}$ = 1.3 ± 0.2 *SD*; *n* = 14) mm long (holotype = 1.9 × 1.1). Ten of 17 specimens (including holotype) with separate prefrontals, four specimens with prefrontals in narrow to moderate contact, and three with prefrontals separated by an azygous interprefrontal (Fig. 3). Interprefrontals wider anteriorly; their caudal tip projecting slightly beyond prefrontal/frontal suture.

Frontal triangular, longer than wide, narrowed to a point caudally; in contact with two anterior supraoculars; length 2.8–3.7 mm ($\bar{X}$ = 3.3 ± 0.4 *SD, n* = 14) width 1.7–2.5 mm ($\bar{X}$ = 2.0 ± 0.4 *SD, n* = 14) (holotype = 3.1 × 1.9). Frontoparietals fused; 2.3–3.4 mm ($\bar{X}$ = 2.8 ± 0.4 *SD, n* = 14) long and 2.5–4.3 mm ($\bar{X}$ = 3.5 ± 0.4 *SD, n* = 14) wide (holotype = 2.7 × 3.2). Parietals behind interparietal in contact for a distance shorter than the parietal itself. Interparietals 1.5–2.8 mm ($\bar{X}$ = 1.9 ± 0.5 *SD, n* = 14) long and 1.2–1.6 mm ($\bar{X}$ = 1.3 ± 0.2 *SD, n* = 14) wide (holotype = 1.7 × 1.3).

Nasal large and single with nostril at center, bordered posteriorly by two pairs of overlapping (superimposed) loreals; most dorsal larger than ventral. Holotype with only 10 supraciliaries; supraciliaries varying considerably among and between our series of specimens: 11—12 (two specimens), 12—11 (1), 13—11 (1), 12—12 (2), 12—13 (2), 13—12 (2), 13—13 (3), 13—14 (1), 14—13 (1), and 14—14 (1); $\bar{X}$ = 12.6—12.5 ± 0.9—0.9 SD; range = 11–14—11–14; *n* = 16—16. All specimens with four large supraoculars; anterior most strongly triangular; the second widest. Caudalmost supraocular followed by three or four curved rows of very small scales, each with two or three scales. Tympanum exposed, not strongly depressed or sunken. Holotype with 6—7 upper labials and 6—6 lower labials. Our series varies considerably in both upper and lower labial scale counts: Upper labials: 6—5 (one specimen), 6—6 (10), 7—7 (4) or 7—6 (1); $\bar{X}$ = 6.3—6.6 ± 0.5—1.1 *SD*; range = 6–7—5–7; *n* = 16—16. Lower labials: 5—5 (1), 5—6 (1), 6—6 (12), 6—8 (1), 7—7 (1), or 8—7 (1); $\bar{X}$ = 6.3—6.4 ± 1.0—1.5 *SD*; range = 5–8—5–8; *n* = 16—16. Mental chin scale 2.3–3.4 mm ($\bar{X}$ = 2.8 ± 0.3 *SD, n* = 14) wide and 1.5–2.4 mm ($\bar{X}$ = 1.9 ± 0.3 *SD, n* = 14) long (holotype = 2.6 × 1.6); followed by one postmental, the latter in contact with two lower labials.

Dorsal scalation.—Nuchal scales undifferentiated. Scales (transversely) around midbody = 38 (two specimens), 39 (6), 40 (5, including holotype), 41 (1), and 42 (2); $\bar{X}$ = 39.9 ± 1.17 *SD, n* = 16. Paravertebrals = 88 (one specimen), 89 (2), 90 (2), 91 (2), 92 (6), 93 (1), 94 (holotype), and 96 (2); $\bar{X}$ = 91.5 ± 2.37 *SD, n* = 16.

Subdigital lamellae and ventral scalation.—All specimens with long digits, as reflected in lamellae scale counts. Both the holotype and our specimens display a longest to shortest toes rank of 4, 3, 2, 5, 1. Holotype has 19—19 fourth toe lamellae, whereas our series with 19—19 (two specimens), 19—20 (1), 20—20 (5), or 21—21 (8); $\bar{X}$ = 20.3—20.4 ± 0.8—0.7 *SD*; range

Table 1.—Measurements (in mm) from all known specimens of *Sphenomorphus beyeri* (character abbreviations in text). Standard univariate statistics, presented below, are abbreviated as follows: $\bar{X}$, mean; *SD*, standard deviation; *W*, Shapiro-Wilk test for normality (N = normal); g_1 = skewness statistic; g_2 = kurtosis statistic. None of the skewness or kurtosis statistics were found to be significant ($P > 0.05$). CMNH 3654 and the holotype were excluded from the analysis as they were not sexually mature. Tail length (TL) also was excluded from the analysis as several individuals showed scars indicative of caudal autotomy and regeneration.

		Character								
Specimen #	Sex	SVL	TL	AGD	HLL	HL	HB	SL	ED	TD
CMNH 3652	f	59.4	76.5	31.4	29.5	12.3	7.8	3.7	2.3	1.3
CMNH 3653	f	67.1	75.7	35.0	21.9	9.2	12.9	8.9	2.8	1.7
CMNH 3654	?	31.3	44.1	14.8	12.3	8.1	5.3	2.1	1.8	1.2
CMNH 3655	m	64.9	90.8[1]	31.3	24.3	14.4	9.8	4.7	3.1	2.0
USNM 337768	m	63.4	56.4[1]	31.8	24.3	13.0	8.7	4.0	3.1	1.5
CMNH 3657	m	66.7	100.0	34.6	25.0	14.1	8.9	4.6	3.2	1.7
CMNH 3658	f	51.2	33.5[1]	27.3	20.8	11.1	7.4	3.2	2.2	1.2
CMNH 2359	m	62.8	77.7	32.9	24.1	13.4	9.3	4.3	2.5	1.5
PNM 2300	m	56.6	70.8	27.9	22.9	12.0	7.6	4.6	1.7	1.3
PNM 2301	f	46.6	66.4	22.1	16.9	10.2	6.9	3.3	1.6	1.2
PNM 2302	m	62.7	91.6	33.3	23.5	13.1	9.1	4.6	3.1	1.5
PNM 2303	m	48.0	49.1[1]	21.8	20.3	10.8	6.5	3.7	2.6	1.1
PNM 2304	f	55.8	69.8	28.6	20.3	11.8	7.4	4.1	2.5	1.4
PNM 2305	m	56.5	80.4	29.8	22.9	12.5	8.2	4.5	2.8	1.5
PNM 2306	m	59.1	61.8[1]	30.3	22.4	12.7	8.2	4.1	2.6	1.3
PNM 2307	f	50.0	62.4	26.3	18.1	11.2	7.3	3.8	2.4	1.2
CAS 61183*	m	43.0	—	20.9	17.1	11.5	6.5	3.9	3.3	2.4
$\bar{X}$		58.9	—	30.2	22.3	12.5	8.2	4.2	2.7	1.5
SD		6.1	—	3.6	2.0	1.1	0.9	0.4	0.3	0.2
Range		19.2	—	13.7	7.0	3.6	3.3	1.5	0.9	0.9
n		14	—	14	14	14	14	14	14	14
W		N	—	N	N	N	N	N	N	N
g_1		−0.39	—	−0.83	−0.60	−0.05	−0.05	−0.67	−0.09	−0.66
g_2		−0.91	—	−0.86	−0.02	−0.66	−0.81	−0.07	−1.21	−0.42

[1] Tail recently autotomized or showing scars of caudal autotomy and subsequent regeneration.

* Holotype.

= 19–21—19–21; *n* = 16—16. Holotype with 5—5 first finger lamellae and ours have 5—5 (five specimens), 6—6 (7) or 7—7 (4); $\bar{X}$ = 6.4—6.4 ± 2.3—2.3 *SD*; range = 6–7—5–7; *n* = 16—16. Preanal scales strongly enlarged.

Body size.—Table 1 contains the morphological measurements taken from all known specimens of *S. beyeri*. Body size proportions of holotype and our new series are discussed below.

Coloration.—Color plates (Fig. 4) contain lateral views of male PNM 2302 in life. Dorsal surfaces dark umber to lavender brown. A mid-vertebral line of very dark brown to black spots variably obvious; vertebral spots (or line) at midbody usually encompassing one scale only, but occasionally two or three scale rows; spot series (or line) fading caudally on some specimens. Very dark brown to black series of irregular blotches laterally, usually forming a solid band, strongest at the pre-nuchal region, next strongest above hind limbs at pectoral girdle; band extending anteriorly through tympanum to rostral scale and caudally to thickest portions of tail base (⅓ total tail length). Dorsally, lateral band bordered by a thin golden yellow edge; ventrally, golden yellow edge becoming solid yellow on caudal por-

Fig. 4. *Sphenomorphus beyeri* in life before preservation (PNM male 2302; SVL = 62.7 mm). Note presence of grey volcanic ash on substrate. Photographs by RMB, courtesy of CMNH.

tions of body. Laterally, axilla-groin region bright orange with round yellow markings arranged in spots. Distinctive black tip on tail of all complete specimens. Undersides of arms and legs bright golden yellow. Posterior regions of hind limbs with distinct yellow spots surrounded with brown borders fading into a lavender brown background. Ventral side of body from nuchal region to tail golden yellow with pinkish tan, light grey, or very light sky blue flecks on nuchal region, ventral side of head, torso, and tail base. Lavender brown series of spots arranged into irregular, disjunct stripes of four to eight scales in length and one scale in width on ventral side of neck. Chin pinkish tan or translucent. Labial scales lavender to purplish, each with white spot in center or on ventral border of scale.

In alcohol: coloration generally faded throughout; ventral yellow and lateral orange fading to dull pinkish tan; ventral nuchal region devoid of blue tones; purple on labials fading to lavender or brown.

Comparisons.—Table 2 compares *S. beyeri* with closely related, sympatric, and/or morphologically similar species of *Sphenomorphus.*

Discrepancies with Taylor's original description.—Taylor's (1922b) description of *S. beyeri* stated that the holotype exhibited separated prefrontals, as do many of ours (10 of 16). However, three of our series have prefrontal scales in narrow to moderate contact and three others show the presence of an azygous interprefrontal (Fig. 3). In addition, Taylor (1922b) counted 40 scales at midbody in the holotype but did not record paravertebrals. Brown & Alcala (1980) and Alcala (1986) confirmed his midbody scale counts, and reported also that there were 94 paravertebral scales in the holotype. Our examination of the holotype confirms both of these reports, which fall within the range of variation for the new series (88–96; Table 2). Taylor (1922b) counted 17 lamellae under the holotype's longest (=fourth, rear) toe, but Brown & Alcala (1980) and Alcala (1986) reported that the holotype had 19 fourth toe lamellae. Our examination of the holotype confirms that the specimen has 19—19 subdigital lamellae under the fourth toe. Taylor (1922b) reported a SL/HL ratio for the holotype of 0.34; calculations for our series are remarkably close ($\bar{X} = 0.32$, range = 0.25–0.37; $n = 16$). Taylor (1922b) reported that the SL/HB ratio was 0.60 for the holotype; our series averaged 0.49 (range = 0.38–0.57; $n = 16$). Taylor's specimen had a HB/HL ratio of 0.57, and ours average 0.66 (range = 0.60–0.69; $n = 16$). Taylor reported a HB/SVL ratio of 0.15; our specimens average 0.14 (range = 0.13–0.17; $n = 16$). The holotype also had an ED/SL ratio of 0.50, but the eyes on our specimens seemed somewhat smaller on average ($\bar{X} =$ 0.37; range 0.30–0.43; $n = 16$). Disparities in these calculated ratios may reflect the small sample size ($n = 1$) available to Taylor; the distinctive black tip on the tails of all complete specimens undoubtedly would not have been missed by Taylor had he been able to recover the portion of the holotype's tail which was autotomized and lost in capture.

Remarks.—Two of the Zambales specimens were gravid females (CMNH 3652 and 3653), each containing two yellowish, thickly-shelled, oviductal eggs, the texture of which suggest oviparity. One of our specimens appears to be recently hatched (CMNH 3654). It is well within the range of morphological variation described here for *S. beyeri* except that it has unfused frontoparietals. As stated above (site descriptions), both areas surveyed in this study contained ash deposits from the June 1991 eruption of Mt. Pinatubo. This rendered the forest floor, vegetation, and much of the remaining habitat very dry (Fig. 2). Where water might be expected to collect (i.e., in *Pandanus* axils or other depressions in rocks or vegetation), the ash rapidly absorbed water deposited by rain or dew. Taylor (1922b) mentioned that he found the holotype on a rock ledge on Mt. Banahao; none of our

Table 2.—Comparisons of scale counts and other diagnostic characters species of Philippine *Sphenomorphus* allied to, morphologically similar to, or sympatric with *S. beyeri.* Data are from specimens reported in this study, from specimens examined at USNM, and from pertinent literature account (Taylor 1922a, 1922b; Brown & Alcala 1980; Alcala 1986; Brown et al. 1995).

Species	Para-vertebrals	Scales around midbody	Fourth toe lamellae	SVL (mm) at maturity	Prefrontals	Fused fronto-parietals	Tympanum exposed?	Approximate known distribution
S. steerei	52–64	30–32 rarely 28	9–14	26.5–36.0	in contact	yes	yes	Throughout the Philippines
S. decipiens	57–66	32–38	14–18	31.1–45.0	broad contact	yes	yes	Luzon, Mindanao, Tablas
S. arborens	64–75	36–39	18–22	45.0–66.3	broad contact	no	yes	Negros, Masbate, Pan de Azucar, Panay
S. luzonense	66–71	28	9–12	38.5–48.0	separate or in contact	yes	no	N. Luzon
S. lawtoni	57–62	28	13–15	45.8	moderately in contact	yes	yes	N. Luzon
S. leucospilos	63–68	32	16–18	52.0–55.0	broad contact	yes	barely	Luzon
S. acutus	51–63	26–30	8–10	51.0–76.0	broad contact	yes	yes	Mindanao, Leyte, Samar Bohol, and Dinagat
S. variegatus	66–76	38–44	19–25	49.9–62.6	narrowly separated	no	yes	Mindanao, Sulu Arch., Leyte Bohol, Dinagat, Camiguin
S. cumungi	75–87	48–54	22–27	115–143.2	widely separated	no	yes	Mindanao, Bohol, Leyte, Luzon, Sibuyan, Dinaget, Mindoro
S. a. abdictus	63–74	36–42	21–25	81.3–91.0	usually separated	no	yes	Mindanao, Camiguin, Bohol
S. a. aquilonius[a]	62–73	34–38	20–25	55.4–95.5	usually separated	no	yes	Luzon, Polilio
S. c. coxi	62–72	32–38	19–26	53.0–85.0	usually separated	yes	yes	Mindanao, Camiguin, Leyte, Samar
S. c. divergens[b]	64–75	38–40	21–26	63.0–90.0	usually separated	yes	yes	Luzon, Marinduque, Mindoro
S. jagori	63–73	38–40	24–30	70.9–108.8	separate	no	yes	Throughout the Philippines
S. llanosi	67–70	38–42	20–24	63.9–90.0	separated or in contact	no	yes	Leyte, Samar
S. laterimaculatus	72	40	18	52.5	broad contact	yes	yes	S. Luzon
S. diwata	90–93	40–42	13–14	51.4–58.5	moderately in contact	no	yes	N. Mindanao
S. beyeri	88–96	38–42	19–21	46.61–67.12	usually separate	yes	yes	Midwestern and southern Luzon
S. knollmanae[c]	73–83	34–39	17–20	47.5–51.0	separate or in contact	yes	yes	S. Luzon

specimens were collected anywhere near rocks or outcroppings in the Zambales but, instead, from inside moist rotten logs. Only two specimens were caught in our extensive pitfall trap system, suggesting either low levels of activity or semi-fossorial existence. However, due to the disturbed nature of the forest on Mt. High Peak, it is impossible to establish the true microhabitat of *S. beyeri.* The apparent semi-fossorial nature of this species in the Zambales could have been due to animals retreating from the aridity of the immediate area which was blanketed by Mt. Pinatubo's ash.

At present, *S. beyeri* is known to exhibit an allopatric insular montane distribution. However, little biogeographical information can be inferred from this fact alone due to lack of reliable survey data for southern Luzon, specifically the areas between the two localities discussed here. While the two mountain ranges included in this species' locality records are located on separate geologic components of Luzon, adequate habitat connecting these insular regions probably existed during the last glaciation (Rutland 1968; Hashimoto 1981a, 1981b; Auffenberg 1988). Mountains like Mt. Makiling and Mt. Arayat may support undocumented populations of *S. beyeri* as suggested by their intermediate placement between the two known localities (Mt. High Peak and Mt. Banahao). Studies of poorly known high elevation montane environments (e.g., Brown & Alcala 1961b, Custudio 1986, Auffenberg & Auffenberg 1988) are needed in such areas in and between these two disjunct localities to ascertain the true distribution of *S. beyeri* as well as other relict species. While elevational species succession of scincid lizards (Custudio 1986) and small mammals (McCoy & Connor 1980, Rapoport 1982, Rickart et al. 1991, Ruedas et al. 1994) has recently been documented in some areas of the Philippines, little is known about the potential effects of elevational gradients on lizard species stratification, diversity, and endemism in the Philippine archipelago. Our unpublished survey data suggest that species diversity is inversely proportional to elevation, but that endemism is positively correlated with elevation at least on the islands of Luzon, Panay, Mindanao, and Mindoro. The latter topic is subject of another work in progress (Ferner, pers. comm.).

Acknowledgments

Collecting permits were facilitated by the Protected Areas and Wildlife Bureau of the Philippines Department of the Environment and Natural Resources, especially by A. Alcala, A. Ballesfin, J. Caleda, and C. Catibog-Sinha. J. F. Barcelona, J. R. Demboski, R. E. Fernandez, and F. T. Wacdisen assisted in the collection effort and capture of several specimens. We thank R. I. Crombie for his help in obtaining the *S. beyeri* type specimen from the California Academy of Science, for facilitating our work at USNM, and for confirming the identity of our *S. beyeri* specimens along with W. C. Brown. Statistical analyses were carried out by L. A. Ruedas who also provided the map used in the manuscript. This study was funded by a grant from the John T. and Catherine C. MacArthur Foundation (to P. C. Gonzales and R. S. Kennedy) and by the following grants from the Miami University community (Oxford, Ohio) to RMB: The Zoology Student Enrichment Fund Grant, the Roschman Student Enrichment Fund Grant, the Undergraduate Research Fund Grant, and the Hefner Museum of Zoology Independent Studies Grant. JWF acknowledges the continued support of Thomas

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[a] Differs from *S. a. abdictus* by the presence of four (as opposed to five) supraoculars.

[b] Differs from *S. c. coxi* by the presence of four (as opposed to five) supraoculars and coloration.

[c] New species (Brown et al. 1995, this issue).

More College. Equipment was made available to us by H. Eshbaugh and G. Kritsky; outdoor apparel and other gear was provided by Outdoor Adventures in Cincinnati, Ohio. Comments on preliminary drafts of the manuscript were provided by R. I. Crombie, R. F. Inger, S. M. Moody, and L. A. Ruedas. This paper is Contribution No. 3 to the Results of the PNM/CMNH Biodiversity Inventory of the Philippines.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(1):18–28. 1995.

A new species of lygosomine lizard (Reptilia: Lacertilia: Scincidae; *Sphenomorphus*) from Mt. Isarog, Luzon Island, Philippines

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Abstract.—*Sphenomorphus knollmanae,* a new species, is described on the basis of recently collected material from Mt. Isarog, Bicol Peninsula, southeastern Luzon, Philippines. The small series ($n = 5$) differs from its congeners by the combination of its fused frontoparietals, relatively low number of paravertebrals (73–83) and midbody scales (34–39), the presence of 17–20 subdigital fourth toe lamellae, distinctive patterns of coloration, and a host of measurements related to its small body size (SVL = 47.5–51.0 mm). To better distinguish between the new species and two closely related congeners, univariate and multivariate analyses were performed on a suite of morphological characters. The three species were found to be well differentiated morphologically.

Worldwide, the genus *Sphenomorphus* contains over 120 species and is a "taxonomically residual" plesiomorphic taxon that "remains a convenient repository for . . . species, pending further phylogenetic analysis" (Myers & Donnelly 1991:2). Brown & Alcala (1961b) reported that Oriental and Australian zoogeographic regions contain over 60 scincid species in *Sphenomorphus.* In their key to Philippine Scincidae, Brown & Alcala (1980) recognized 22 species of *Sphenomorphus,* subdividing these into five groups based on external morphology. The Group I species of Philippine *Sphenomorphus* are *S. beyeri* (Taylor 1922) and *S. diwata* (Brown & Rabor 1967, see Brown & Alcala 1980, for review). Until recently, *S. beyeri* was known only from the holotype, collected by E. H. Taylor on Mt. Banahao, Laguna province, southern Luzon Island (Taylor 1922). During a recent biodiversity inventory of the Philippines conducted by the National Museum of the Philippines (PNM) and the Cincinnati Museum of Natural History (CMNH), we rediscovered and redescribed *Sphenomorphus beyeri* from specimens taken on Mt. High Peak, Zambales Mountains, west central Luzon Island (Brown et al. 1995). *Sphenomorphus diwata* also is currently known only from a small number of specimens collected in the Diwata Mountains, Surigao del Sur Province, northern Mindanao Island (Brown & Rabor 1967, Brown & Alcala 1980).

While examining material in the United States National Museum of Natural History (USNM), R. I. Crombie brought to our attention a small series of *Sphenomorphus* skinks that appeared very similar to our specimens of *S. beyeri* from the Zambales. At the time, we were not confident in the assignment of these specimens to our concept of *S. beyeri* (from the type locality or from Mt. High Peak) as several inconsistencies immediately were apparent. Following detailed examination of these specimens and a host of univariate and multivariate statistical analyses we concluded that differences between this series and its most closely-related congeners were sufficient to warrant its recognition as a distinct species.

Methods

Morphological characters and scale counts used here follow definitions and abbreviations in Brown & Alcala (1980) and Brown et al. (1995). Measurements were taken to the nearest 0.1 mm with digital calipers. All measurements are based on specimens preserved in 70% ethanol. In cases where scales of interest are found on both sides of the head (e.g., labials), scale numbers are given in pairs, separated with a long dash (—), designating left from right respectively. Mensural and meristic character abbreviations (defined in Brown et al. 1995) include: snout-to-vent length (SVL), tail length (TL), axilla-groin distance (AGD), hind leg length (HLL), head length (HL), head breadth (HB), snout length (SL), eye diameter (ED), tympanum diameter (TD), paravertebrals (PVS), midbody scales (MBS), supralabials (SUL), and infralabials (IFL). Specimens examined are deposited in the California Academy of Science (CAS) the Cincinnati Museum of Natural History (CMNH), the National Museum of the Philippines (PNM), and the United States National Museum of Natural History (USNM).

Statistical analyses were performed using the Statistical Analysis System software, version 6.03 (SAS Institute Inc., 1988a, 1988b). Sexually immature specimens (*S. beyeri,* PNM 2303 and CMNH 3654, CAS 61183; *S. diwata,* CAS 133514; *Sphenomorphus* sp., USNM 318343) were excluded from univariate and multivariate analyses. A Student-Newman-Keuls multiple range test was performed on both raw and log (base 10) transformed data to determine patterns of significant character variation. Two principal component analyses were performed, both on the correlation matrix of the variables. The first included only raw (untransformed) data; the second was carried out on the log (base 10) transformed data, in order to minimize the effects of size differences among the different populations examined herein; in the case of the log (base 10) transformed analysis, the size component of the variation is restricted to principal component axis one. In both instances, the first and second and the first and third principal component scores were then plotted in order to ascertain morphological differentiation among groups.

Results

Sphenomorphus beyeri, S. diwata, and *S.* n. sp., distinctly segregated into discrete groups in the principal component analysis (Fig. 1). In the PC analysis based on raw data (Fig. 1a, b), principal component one differentiates between *S.* n. sp. and *S. diwata* and between the new species and *S. beyeri.* This component loads heavily on HL, SVL, HB, HLL, AGD, and SL. Principal component two distinguishes between *S. diwata* and remaining Group I *Sphenomorphus.* This component loads heavily on fourth toe lamellae and MBS as well as TD, ED, and PVS. The third principal component differentiates between *S. beyeri* and remaining Group I *Sphenomorphus.* This component loads primarily on fourth toe lamellae, PVS, and TD. Together, the first three principal components account for 85.7% of the variation (PC I, 55.0%; PC II, 16.7%; PC III, 14%).

In the PC analysis based on the log transformed data (Fig. 1c, d), principal component one and two discriminate between *S.* n. sp. and *S. diwata,* while principal components two and three discriminate between *S. diwata* and *S. beyeri.* Principal component three also discriminates between *S. beyeri* and the new species. The first four principal components account for 91.6% of the variation (56.4, 16.8, 13.2, and 5.2, respectively). Factor loadings along the first prin-

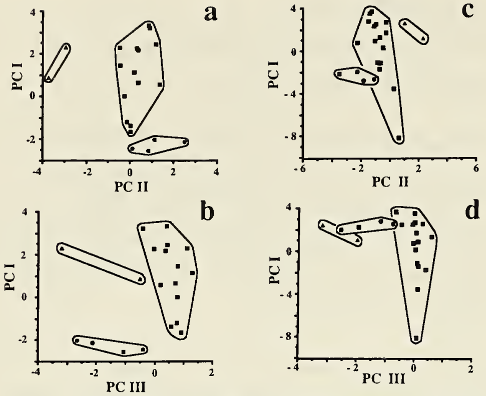

Fig. 1. Plots of principal component scores for two species of Group I *Sphenomorphus* and the new species examined in this study. Component I versus component II (a); component I versus component III (b); component I versus component III for log (base 10) transformed data (c); component I versus component III for log (base 10) transformed data (d). Symbols are: squares = *S. beyeri*; triangles = *S. diwata*; circles = *S. knollmanae*, new species.

cipal component are relatively homogeneous, indicating that the size variation generally has been isolated to this component, while shape is more important among remaining principal components. High loadings in principal component two are shown in discrete characters (scale row counts). An additional PC analysis carried out on the correlation matrix of the log (base 10) transformed variables but using only measurements (not shown), indicates that tympanum and eye diameters were the heaviest contributors to the variation in PC axes two and three.

An important point to make regarding these analyses concerns the orientation of the principal component axes of each putative species group's dispersion in multivariate space. Orthogonal orientation of the axes in multivariate space has been interpreted as indicative of differing allometric growth patterns (Voss et al. 1990, Voss & Marcus 1992); a corollary of the foregoing is that different orientations of the principal component axes are thereby good evidence of distinct specific status. In the case of the analyses of the populations of *Sphenomorphus* examined herein, it is quite clear that the orientation of the axes of dispersion are quite distinct both in analyses based on raw data as well as log (base 10) transformed data. This particular distinction is especially severe between *S. beyeri* and remaining *Sphenomorphus* examined and is clearly observed in the raw data plots, but more significantly in the log (base 10) transformed data, which minimizes the contribution of size to principal component axis one.

In view of the quantum separation in allometric growth patterns, as well as morphology between the Mt. Isarog *Sphenomorphus, S. beyeri,* and *S. diwata* in both multivariate (PCA) and univariate analyses (ANOVA) of discrete and continuously varying characters, we describe the series from Mt. Isarog as:

Sphenomorphus knollmanae, new species

Figs. 2, 3

Holotype.—PNM 2311 (formerly USNM 318342), adult male, collected by L. R. Heaney on 1 May 1988, in loose leaf litter alongside a fallen, partially decomposed log on the forest floor in primary mid montane forest at 1125 m on Mt. Isarog (Philippines, S. Luzon, Bicol Peninsula, Camarines Sur Prov.), 4.5 km N, 20.5 km E Naga City, 13°40′N, 123°22′E (map: fig. 1 in Goodman & Gonzales 1990).

Paratypes.—(4) USNM 318341 (female) and 318343 (juvenile), same data as above except as follows: USNM 318341, collected by L. R. Heaney on 29 Apr 1988; USNM 318343, collected by S. M. Goodman, 22 Mar 1988. USNM 318344 and CAS 191800 (formerly USNM 318345) collected by S. M. Goodman, 19 Mar 1988, and by R. C. B. Utzurrum on 20 Mar 1988 respectively, at 4 km N, 21 km E Naga City, 13°40′N, 123°22′E, at 1350 m in primary upper montane forest. All specimens collected in loose leaf litter and loose topsoil on forest floor; USNM 318344 and CAS 191800 associated with fallen, partially decomposed logs on forest floor.

Etymology.—Named in honor of the late Margy Knollman, friend and teacher, who guided the senior author through his first scientific experiment at age seven and continued to encourage his herpetological pursuits until the time of her death in November 1989.

Diagnosis.—A small to moderate species of *Sphenomorphus* (SVL, 47.5–51.0 mm) differing from its congeners by a combination of the following characteristics: frontoparietals fused; prefontals separate, in contact, or with azygous interprefrontal; 73 to 83 paravertebrals; 34 to 39 scales around midbody; 17 to 20 subdigital fourth toe lamellae; unique coloration (see below).

Description of holotype.—(PNM 2311) Total Length, 118.7 mm; SVL, 48.7 mm; TL, 70.0 mm; HL, 11.1 mm; SL, 3.9 mm; HB, 7.1 mm; ED, 3.1 mm; lower eyelid scaly with translucent window, oval in shape, arranged horizontally; ear opening and tympanum exposed, not deeply sunken, vertically oval, 1.2 mm in width; ear opening without spines or lobules; limbs pentadactyl, well developed; HLL, 18.3 mm; AGD, 22.7 mm; head (viewed from above) tapered, snout rounded dorsally and laterally; dorsal, lateral, and ventral scales smooth, unstriated; rostral large, visible from above, broader (1.8 mm) than long (0.7 mm), forming a curved suture with frontonasal; latter wider (1.5 mm) than long (1.1 mm); prefrontals in broad contact; frontoparietals fused (2.8 mm wide, 1.8 mm long) frontal moderate, rhomboidal, pointed caudally, 1.9 mm wide, 3.0 mm long, in contact with two supraoculars; interparietal moderate, pointed, 1.3 mm wide, 1.9 mm long; parietals in contact behind interparietal; nasals large and single with round nostril at centers, widely separated by frontonasal and nasal bordered caudally by two pairs of overlapping loreals, dorsal pair slightly larger than ventral; 3—3 large preoculars, most ventral contacts suture between third and fourth labial; 4—4 large supraoculars, anteriormost triangular, second widest; last supraocular followed by 3 rows of small scales clustered in postocular region, each row containing 2–3 scales; 3—3 temporals, dorsalmost wraps one-fourth of way around posterior edge of parietal scales; nuchals undifferentiated, except for most lateral pair which is very slightly enlarged; 2—2 rows of small scales between eye and labials; 12—12 supraciliaries; 15—16 lower ciliaries; 6—6 supralabials; 6—6 infralabials; 73 paravertebrals; 34 midbody scales; 20 subdigital fourth toe lamellae; 5 first finger lamellae; toe length (shortest to longest) 4, 3, 2, 5, 1; two strongly enlarged preanal scales apparent; mental chin scale followed by single postmental bordered caudally by two pairs of chin shields; subcaudals only slightly larger than ventrals. The holotype had a live weight of 3.0 g. Body size proportions and coloration discussed below.

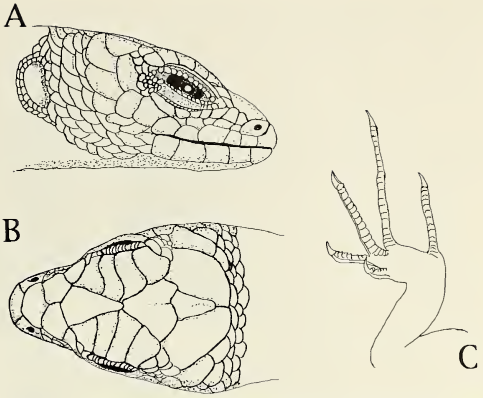

Fig. 2. *Sphenomorphus knollmanae* holotype (PNM 2311)—Lateral (A), and dorsal (B) head scalation and subdigital lamellae, right hind foot (C).

Coloration.—Field notes recorded by R. C. B. Utzurrum (courtesy L. R. Heaney, Field Museum of Natural History) state that in life CAS 191800 had a "golden venter, dark brown dorsum, mottled on sides." In alcohol, dorsal surfaces very dark brown with black spots and a darkly pigmented (=2–3 scale rows) black mid-vertebral line. Mid-vertebral line darkest on CAS 191800,

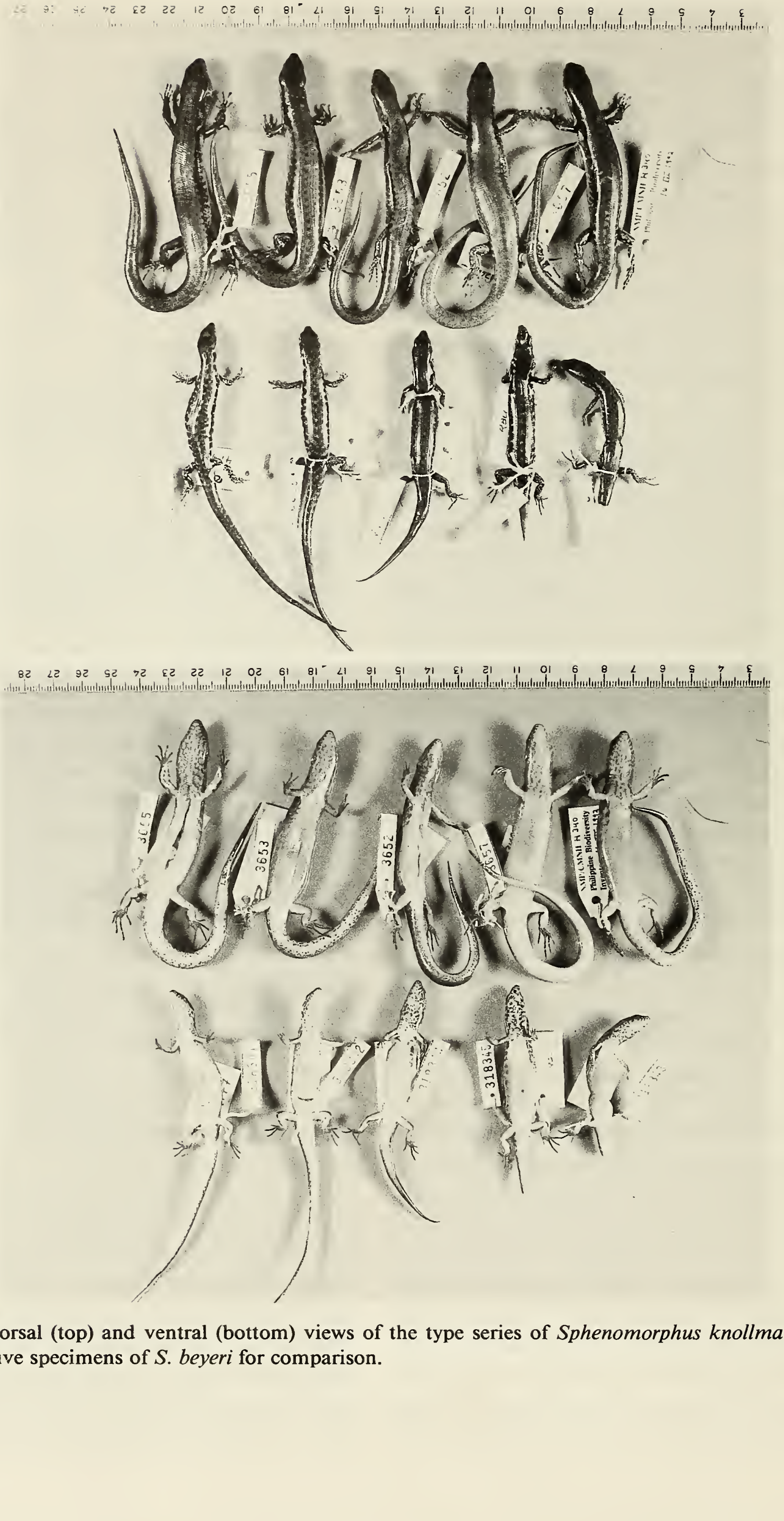

Fig. 3. Dorsal (top) and ventral (bottom) views of the type series of *Sphenomorphus knollmanae* placed underneath five specimens of *S. beyeri* for comparison.

Table 1.—Morphological measurements and scale counts taken from all known specimens of *Sphenomorphus knollmanae* (see text for abbreviations of characters). Standard univariate statistics are presented below as means ± one standard deviation (sexually mature specimens only).

		Character													
Specimen #	Sex	SVL	TL	AGD	HLL	HL	HB	SL	ED	TD	PVS	MBS	SUL	IFL	4th Toe
USNM 318342	f	49.8	71.5	24.9	18.5	10.0	6.2	3.6	2.5	1.2	76	39	7-7	6-6	19
PNM 2311[a]	m	48.7	70.0	22.7	18.3	11.1	7.1	3.9	3.1	1.2	73	34	6-6	6-6	20
USNM 318343	?	47.5	8.3[b]	24.8	15.9	10.0	6.0	3.5	2.5	1.2	83	39	7-7	6-6	19
USNM 318344	f	51.0	41.4[b]	26.5	17.2	10.0	6.4	3.5	2.7	1.4	76	37	7-7	6-6	17
CAS 191800	f	50.4	8.5[b]	28.7	18.3	11.0	6.4	3.2	2.7	1.8	76	35	6-6	7-7	18
Mean		49.1	—	25.3	18.4	10.5	6.6	3.5	2.7	1.3	77.0	36.5	6.5	6.3	18.5
SD		1.3	—	2.5	0.1	0.6	0.5	0.3	0.2	0.3	4.2	2.4	0.6	0.5	1.3

[a] Holotype.

[b] Tail autotomized and partially regenerated.

but also heavy on PNM 231 and USNM 318341, somewhat lighter (1–2 scale rows) on USNM 318343 and 318344. Mid-vertebral line ending abruptly at pectoral girdle where dorsal mottling coalesces into transverse bars that fade caudally (this pattern not apparent in USNM 318343). Laterally, with a heavy series of black blotches, forming a solid stripe in canthal region, and extending posteriorly from nostril, through eye and typanum, to groin. Lateral black stripe anteriorly bordered ventrally by a distinct white line intersecting the tympanum at one-half its height and extending from caudal edge of eye to region dorsal to forearm. Lateral white line on midsection breaking up into series of white spots that continue caudally through anterior one-third length of tail. Ventral surfaces in complete specimens pale yellow from chin to tip of tail (USNM 318344 has a regenerated tail that is completely black; USNM 318343 and CAS 191800, with autotomized tails). Throat pale yellow with dark umber flecks (darkest on CAS 191800 and almost invisible on holotype and USNM 318341). In specimens with heavy speckling, pattern wraps around onto lateral portions of neck, extending to approximately one-half the height of the tympanum.

Variation.—Our sample includes one male, three females and a sexually undetermined juvenile. USNM 31834 and CAS 191800 both were gravid at the time of preservation, each containing two thinly-shelled eggs. USNM 318341 may have been gravid when preserved (remnants of what appear to be eggs remain), but some breakdown of the ovaries has occurred. Table 1 contains morphological measurements of the five specimens of *S. knollmanae* and characters and measurements differing from holotype description follow below.

Variation in head scalation is as follows: rostral 1.5–2.2 ($\bar{X}$ = 1.8 ± 0.3 *SD*; n = 4) mm wide; frontonasal 1.5–1.8 (1.7 ± 0.1; n = 4) mm wide and 1.0–1.1 (1.1 ± 0.1; n = 4) mm long; frontoparietal 2.5–2.9 (2.7 ± 0.2; n = 4) mm wide and 1.7–2.1 (1.9 ± 0.1; n = 4) long; frontal 0.9–1.9 (1.5 ± 0.4; n = 4) mm wide and 1.5–3.0 (2.4 ± 0.67; n = 4) mm long; interparietal 1.1 to 1.4 (1.2 ± 0.1; n = 4) mm wide and 1.7 to 1.9 (1.8 ± 0.1) mm long. Prefrontals are in broad contact (three specimens) or separated by an azygous interprefrontal (one specimen), the latter somewhat wider anteriorly where contacts frontonasal; increasingly narrow caudally where its most caudal border extends slightly beyond margin delineated by contact between prefrontal and frontal. Supraciliaries 12–16 ($\bar{X}$ = 13.4 ± 1.5 *SD*; n = 5) on right and 12–15 (2.6 ± 1.3; n = 5) on left; lower ciliaries, 5–18 (16.2 ± 1.1; n =

Table 2.—Comparisons of selected measurements and scale counts for *Sphenomorphus knollmanae* and two closely related congeners. Presented below are standard univariate statistics (means ± one standard deviation, sexually mature specimens only) and results of Student-Newman-Keuls multiple range tests. Superscript letter by means indicates group assignment (means with same letter are not statistically different at the $P > 0.05$ level). See text for definitions of abbreviations used in this table.

		Character													
		SVL	TL	AGD	HLL	HL	HB	SL	ED	TD	PVS	MBS	SUL	IFL	4th Toe
S. knollmanae	$\bar{X}$	49.1^{a}	—	25.3^{a}	18.4^{a}	10.5^{b}	6.6^{a}	3.5^{a}	2.7^{a}	1.3^{b}	77.0^{b}	36.5^{b}	6.5	6.3	18.5^{b}
$n = 4$	*SD*	1.3	—	2.5	0.1	0.6	0.5	0.3	0.2	0.3	4.2	2.4	0.6	0.5	1.3
S. beyeri	$\bar{X}$	58.9^{a}	—	30.2^{a}	22.3^{a}	12.5^{ab}	8.2^{a}	4.2^{a}	2.7^{a}	1.5^{b}	91.3^{a}	39.5^{a}	6.5	6.4	20.3^{a}
$n = 14$	*SD*	6.1	—	3.6	2.0	1.1	0.9	0.4	0.3	0.2	1.7	1.2	0.8	1.3	0.8
S. diwata	$\bar{X}$	54.7^{a}	—	25.6^{a}	24.2^{a}	13.3^{a}	7.9^{a}	4.3^{a}	2.6^{a}	2.6^{a}	92.0^{a}	41.5^{a}	55.5	5.5	13.5^{c}
$n = 2$	*SD*	4.7	—	5.4	8.6	0.4	0.6	0.6	0.6	0.8	1.4	2.1	0.6	0.5	0.7

5) on right and 14–17 (16.0 ± 1.2; $n = 5$) on left; supralabials 6–7 (6.6 ± 0.5; $n = 5$); infralabials 6–7 (6.2 ± 0.4; $n = 5$) on right and 5–6 (5.8 ± 0.4; $n = 5$) on left.

In specimens with regenerated tails (USNM 318343 and CAS 191800), normal subcaudals replaced by a series of narrow scales that cover entire ventral surface of regenerated tail. Besides holotype, only CAS 191800 was weighed before preservation (3.4 g).

Ratios of morphological measurements for the series (holotype in parentheses) are as follows: SL/HL, $\bar{X} = 0.34 \pm 0.03$, range = 0.29–0.36 (0.35); SL/HB, $\bar{X} = 0.55 \pm 0.03$, range = 0.50–0.58 (0.55); HB/HL, $\bar{X} = 0.61 \pm 0.03$, range = 0.60–0.64 (0.64); HB/SVL, $\bar{X} = 0.13 \pm 0.01$, range = 0.12–0.15 (0.15); HL/SVL, $\bar{X} = 0.21 \pm 0.01$, range = 0.20–0.23 (0.23); ED/SL, $\bar{X} = 0.77 \pm 0.06$, range = 0.71–0.84 (0.77); ED/HB, $\bar{X} = 0.42 \pm 0.01$, range = 0.41–0.44 (0.41); AGD/SVL, $\bar{X} = 0.52 \pm 0.04$, range = 0.47–0.57 (0.47); HLL/SVL, $\bar{X} = 0.36 \pm 0.02$, range = 0.34–0.38 (0.37).

Comparisons.—Table 2 compares *S. knollmanae* with Group I *Sphenomorphus* species. Excepting its low number of paravertebrals, *S. knollmanae* adheres to the gestalt of Group I *Sphenomorphus* members (Brown & Alcala 1980); accordingly, the new species appears closely related to *S. beyeri* and *S. diwata*. Besides size and characters listed in Table 2 of this study, *S. knollmanae* differs from the former by coloration and disposition of color pattern (Brown et al. 1995). It differs from the latter by characters in Table 2 and also in that it invariably has only 4 supraoculars (vs. 5–6 in *S. diwata*) and fused frontoparietals (vs. 2 in *S. diwata*; Brown & Rabor 1967, Brown & Alcala 1980). As in *S. beyeri* (Brown et al. 1995) contact, or lack thereof, between the prefrontal scales is not fixed in this species as it is in *S. diwata* (Brown & Alcala 1980). The azygous interprefrontal scale exhibited by USNM 318344 also is apparent in some specimens of *S. beyeri* (Brown et al. 1995), but not in any known specimens of *S. diwata* (Brown & Rabor 1967, Brown & Alcala 1980).

The low number of paravertebrals in *S. knollmanae* assigns this species to Group III of Brown & Alcala's (1980) key; accordingly, comparisons with *S. leucospilos* and *S. laterimaculatus,* as well as *S. decipiens,* are warranted. Differences between *S. knollmanae. S. leucospilos,* and *S. decipiens* are as follows: *Sphenomorphus knollmanae* distinct by its 73–83 paravertebrals (vs. 63–68 in *S. leucospilos* and 57–66 in *S. decipiens*), 34–39 scales around midbody (vs. 32 in *S. leucospilos* and 32–38 in *S. decipiens*), and 17–20 fourth toe lamellae (vs. 14–18 in *S. decipiens*). *Sphenomorphus decipiens* also has a smaller overall body size

(SVL = 31–45 mm; Brown & Alcala 1980) than *S. knollmanae.* Differences in color pattern and body proportions between these three species also are apparent (Brown & Alcala 1980).

Body measurements and scale counts of the single known *S. laterimaculatus* specimen are very close to the range of variation of both *S. leucospilos* and *S. knollmanae* (see Brown et al. 1995). While the range of paravertebrals and midbody scales in *S. knollmanae* do not overlap with *S. laterimaculatus* (73–83 vs. 72 and 34–39 vs. 40 respectively), the small number of known *S. laterimaculatus* specimens (*n* = 1) precludes classification based solely on these characters. However, others are apparent: Brown & Alcala (1980) describe the frontoparietal of *S. laterimaculatus* as "long and pointed, almost as long as frontoparietals and interparietal together" (1980:178), a description which does not accord with the relative size of these scales in *S. knollmanae,* especially since the frontal of *S. laterimaculatus* touches three supraoculars, whereas the frontals of *S. knollmanae* only contact two supraoculars. In addition, the holotype of *S. laterimaculatus* has eight infralabials and all specimens of *S. knollmanae* have six or seven. There are six or seven first finger subdigital lamellae in *S. laterimaculatus* and five to six in *S. knollmanae.* Coloration and body proportion differences between these species are also apparent (see Brown & Alcala 1980).

Discussion

At the present time, the new species is only known from the type locality on Mt. Isarog (fig. 1 in Goodman & Gonzales 1990). Detailed habitat descriptions (see Brown 1919, and Whitmore 1984 for review of forest classifications), habitat photographs, and a map of the type locality for *S. knollmanae* are included in Goodman & Gonzales (1990).

Very little is known about the habitat and ecology of *S. knollmanae* and its closely-related congeners, *S. beyeri, S. diwata, S. laterimaculatus, S. decipiens,* and *S. leucospilos.* Excepting *S. decipiens* and *S. diwata,* all are known only from the Luzon faunal region; excepting *S. decipiens,* all are known only from small series. Taylor (1922) reported that the *S. beyeri* holotype from Mt. Banahao was collected on a rock ledge at 1500 m, but we collected most of our specimens from the Zambales Mountains by splitting open rotten logs, in pitfall traps, or under leaf litter—at high elevations (1265–1610 m; Brown et al. 1995). Brown & Alcala (1980) reported that *S. diwata* were found under leaf litter between 1600 and 1700 m on Mt. Hilong-hilong, northern Mindanao (see Brown & Rabor 1967). *Sphenomorphus decipiens* is also semi-fossorial at low to medium elevations (100–1200 m; Brown & Alcala 1980). The known specimens of *S. knollmanae* were taken from similar semi-fossorial environments on the forest floor on Mt. Isarog. All were captured by L. H. Heaney, A. Alcala, and coworkers (under leaf litter, in loose topsoil, occasionally beside rotten logs), while digging for worms to be used as bait for mammal traps. No habitat data are available for *S. laterimaculatus* and *S. leucospilos* (Brown & Alcala 1980).

Studies of high elevation scincids and their habitats have been sorely lacking, with the exception of a few instances (Brown & Alcala 1961a, Custudio 1986). The effects of altitudinal gradients on species richness, abundance, diversity, and distributional patterns have been addressed to a greater extent in birds (Goodman & Gonzales 1990) and mammals (Heaney et al. 1989, Rickart et al. 1991). Efforts to provide a preliminary report of altitudinal effects on scincid lizard distribution in the Philippines currently are under way. While mountain tops have been neglected by many collectors and surveyors in the past, a recent renewal of interest in their unique flora and fauna has produced discoveries (e.g., Gonzales & Kennedy 1990, Lazell 1992, Ross & Gonzales 1992) and rediscoveries (e.g., Ross & Lazell 1990; Brown et al. 1995; Crombie, pers. comm.) of many taxa endemic to the Philippines.

The works of Goodman & Gonzales (1990) and Oliver et al. (1992) have both stressed the importance of continued study of montane regions in order to fuel conservation efforts aimed at preserving these fragile centers of endemism and diversity (see Balate et al. 1992, for a bibliography of conservation in the Philippines). We support their invocations to public awareness with respect to this central issue of Philippine conservation given that we repeatedly have witnessed and participated in discoveries of endemic animals new to science which inhabit extremely limited distributions at high elevations in disappearing fragments of pristine habitat. The loss of such habitat can and often does have effects detrimental to populations of amphibians and reptiles restricted to the immediate area (pers. obs.).

Finally, while we do not wish to engage in speculation (sensu Lazell 1992) of exactly what species may await biologists in similar environments on Philippine mountains, we do agree with Ross & Gonzales (1992) that the northern Philippines (especially the Luzon faunal zone) is zoogeographically complex and contains more centers of endemism than previously thought. Our recent studies suggest that the higher volcanic peaks of southern Luzon (Mt.'s Bulusan, Mayon, Labo, Banahao, Isarog, Samat, Natib, Cuadrado, Angilo and Maquiling) all warrant intensive, long-term survey efforts of the kind that have produced (and continue to produce) many new discoveries on their neighbors.

Comparative material examined.—*Sphenomorphus beyeri* holotype, CAS 61183; *S. beyeri,* PNM 2300-2307, CMNH 3652-3655, 3657-3659, USNM 337768. *S. diwata* holotype (CAS 2478), *S. diwata* (CAS 133514 and 133515).

Acknowledgments

Collecting permits were facilitated by the Protected Areas and Wildlife Bureau of the Philippine Department of the Environment and Natural Resources, especially by A. Alcala, and C. Catibog-Sinha. The Philippine Bureau of Forestry Development and the Bicol University College of Fisheries, Tabaco, Albay assisted during the collection of these and other specimens during L. R. Heaney's group's field work on Mt. Isarog. R. I. Crombie of the United States National Museum (USNM) facilitated loans and provided many helpful comments and suggestions throughout this and related research. W. C. Brown and J. Vindum facilitated loans of specimens in the California Academy of Science (CAS) collections and A. Alcala and L. R. Heaney generously provided access to the specimens they collected on Mt. Isarog with R. de Leon, S. M. Goodman, E. A. Rickart and R. C. B. Utzurrum. RMB thanks the Miami University Zoology Department for its encouragement and JWF acknowledges the continued support of Thomas More College. Comments on preliminary drafts of the manuscript were provided by W. C. Brown, R. I. Crombie, R. F. Inger, S. M. Moody, S. Simon, and one anonymous reviewer. We owe a debt of gratitude to Pedro C. Gonzales (PNM) and Robert S. Kennedy (CMNH) for their continued support of our work with Philippine herpetofauna.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(1):29–44. 1995.

Revision of the South American freshwater fish genus *Sternarchorhamphus* Eigenmann, 1905 (Ostariophysi: Gymnotiformes: Apteronotidae), with notes on its relationships

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Abstract.—A revision of the apteronotid genus *Sternarchorhamphus* Eigenmann is presented. *Sternarchorhamphus muelleri* (Steindachner) from the Amazonas and Orinoco river systems, is redescribed and a lectotype is designated. *Sternarchorhamphus hahni* Meinken, a nominal species previously assigned to this genus, is transferred to another gymnotiform genus on the basis of evidence presented herein. As a consequence, *Sternarchorhamphus* is now considered monotypic. A brief discussion of Mago-Leccia's apteronotid subfamily Sternarchorhynchinae is provided and its monophyly is tentatively accepted. Relationships of *Sternarchorhamphus muelleri* within the Sternarchorhynchinae remain obscure, due to an absence of information on the phyletic history of closely related species, such as *Orthosternarchus tamandua* (Boulenger) and *Ubidia magdalenensis* Miles. A discussion on the taxonomic status of nominal species previously assigned to *Sternarchorhamphus* is provided.

Resumo.—Uma revisão do gênero de Gymnotiformes *Sternarchorhamphus* Eigenmann (família Apteronotidae) é apresentada. *Sternarchorhamphus muelleri* (Steindachner), das bacias dos rios Amazonas e Orinoco, é redescrita, e lectótipo é designado para esta espécie. Uma espécie nominal previamente referida a *Sternarchorhamphus, S. hahni* Meinken, é removida deste gênero; como conseqüência, *Sternarchorhamphus* é agora considerado gênero monotípico. Uma breve discussão sobre a subfamília de Apteronotidae proposta por Mago-Leccia, Sternarchorhynchinae, é apresentada, e sua monofilia é tentativamente aceita. A posição filogenética de *Sternarchorhamphus* dentro da subfamília permanece obscura, o que se deve, em parte, à ausência de informações sobre espécies relacionadas a *S. muelleri,* tais como *Orthosternarchus tamandua* (Boulenger) e *Ubidia magdalenensis* Miles. É feita uma discussão sobre o status taxonômico de espécies nominais previamente incluídas em *Sternarchorhamphus.*

The Neotropical gymnotiform genus *Sternarchorhamphus* Eigenmann (*in* Eigenmann & Ward 1905) was established to include three nominal species with elongate snouts, originally described in *Sternarchus* Bloch & Schneider (currently a junior synonym of *Apteronotus* Lacépède; e.g., Fowler 1951), namely: *Sternarchus* (*Rhamphosternarchus*) *macrostomus* Günther, 1870 (from Jeberos [=Xeberos], Río Marañon basin, Peru), *Sternarchus* (*Rhamphosternarchus*) *muelleri* Steindachner, 1881 (type species of *Sternarchorhamphus*; from the Rio Amazonas, at Pará State, Brazil), and *Sternarchus tamandua* Boulenger, 1898 (from the Rio Juruá, a tributary of the Rio Amazonas in Brazil). Eigenmann (*in* Eigenmann & Ward 1905:166), however, noted that this latter species was probably a member of "a genus distinct from *Sternarchorhamphus* as here understood" and, in fact, it was subsequently used by Ellis (1913) to establish the monotypic apteronotid genus *Orthosternarchus.*

The first appearance of the name *Sternarchorhamphus* was in a key to genera of Gymnotiformes ("Gymnotidae" of earlier authors) presented by Eigenmann & Ward (1905). An unequivocal citation present in that publication (p. 165) makes Eigenmann the sole author of the genus, according to Article 50a of the International Code of Zoological Nomenclature (1985). In that key, the new taxon was first included in the "Sternarchinae" (=Apteronotidae), and distinguished from *Sternarchorhynchus* Castelnau on the basis of its "snout straight, the gape moderate," rather than "snout strongly decurved, mouth minute." Additionally, it was stated that *Sternarchorhamphus* seemed to be "intermediate between *Sternarchus* and *Sternarchorhynchus,* having the long snout of the latter and mouth size approaching the former" (Eigenmann & Ward 1905:165), a position also held by Ihering (1907).

Some years later, Meinken (1937) described *Sternarchorhamphus hahni* on the basis of a single specimen from the Rio Paraná drainage in Argentina. That was the first record of the genus outside of the Amazon basin. As discussed below, however, the examination of the holotype of *S. hahni* showed that it does not belong to the Apteronotidae.

Mago-Leccia (1976) first noted the presence of *Sternarchorhamphus* in the Río Orinoco system. He also proposed a phylogenetic scheme for Venezuelan gymnotiform genera where *Sternarchorhamphus* and *Sternarchorhynchus* were considered sister-groups within the Apteronotidae (Mago-Leccia 1976, fig. 99). Along with *Orthosternarchus* Ellis and *Ubidia* Miles, those two genera were assigned to the Sternarchorhynchinae (not of Hoedeman 1962), a proposed apteronotid subfamily whose members were recognized by their "very elongate snout and reduced mouth gape" (Mago-Leccia 1976:206; see also Mago-Leccia 1978:14 and Mago-Leccia 1994:13).

Campos-da-Paz (1992) had recently expressed some doubts about the monophyly of the *Sternarchorhamphus* plus *Sternarchorhynchus* clade, but tentatively recognized Mago-Leccia's subfamily Sternarchorhynchinae.

In a recent investigation, Triques (1993) did not find characters supporting a close relationship between *Sternarchorhamphus* and *Sternarchorhynchus.* Instead, he proposed *Sternarchorhamphus* as the sister-group to a subunit of the Apteronotidae including the short-snouted genera *Adontosternarchus* Ellis, plus *Sternarchella* Eigenmann and *Porotergus* Ellis (Triques 1993: 123, fig. 24).

Mago-Leecia (1994) recently included two species in *Sternarchorhamphus: S. muelleri* and *S. hahni.* He stated in a footnote (p. 36), however, that this latter species could belong to a different gymnotiform genus, but without additional discussion. *Sternarchorhamphus macrostomus* was used by him to establish a new monotypic apteronotid genus, *Platyurosternarchus* Mago-Leccia, whose relationships are currently unknown. The Sternarchorhynchinae appear only as part of a classificatory system proposed by Mago-Leccia (1978) (Mago-Leccia 1994:13).

The present study is a revision of *Sternarchorhamphus* Eigenmann. A detailed morphological description and osteological analysis of the type species, *S. muelleri,* is presented, along with data on geographic distribution based on recent collections from the Amazon and Orinoco drainages. Reexamination of the holotype of *S. hahni* resulted in a transfer of this taxon to another gymnotiform genus.

Methods.—Most measurements were taken according to Mago-Leccia (1978) and were made point-to-point with dial calipers and ruler on the left side of specimens whenever possible. Measurements that require further explanation are the following: LEA (Mago-Leccia et al. 1985) is the distance from the tip of snout to posterior end of anal-fin base; interorbital width is the space between the dorsal margins of the eyes; head depth was taken at the occiput; and tail depth was measured at posterior end of the anal fin. "HL" denotes head length.

In the counts of pectoral-fin rays, the anterior unbranched rays are indicated by lower-case roman numerals, and branched rays are indicated by arabic numerals. The term "branched rays" refers to all rays posterior to the anterior unbranched rays, even if the posterior terminal ray is unbranched at its base or distal segment. All specimens with indications of regeneration and/or injuries at the posterior region of body were excluded from measurements of total length (TL) and tail length (CL), and counts of caudal-fin rays. Morphometric and meristic data for the paralectotype of *Sternarchorhamphus muelleri* are given between brackets.

Osteological illustrations were prepared with the aid of a camera lucida, from a specimen cleared and counterstained for bone and cartilage with Alizarin red and Alcian blue respectively, according to the procedure of Taylor & Van Dyke (1985). Vertebral counts were made on this specimen and from radiographs of additional specimens, and follow Mago-Leccia et al. (1985). Bone terminology follows Mago-Leccia et al. (1985), except that the terms mesethmoid (e.g., Fink & Fink 1981) and anguloarticular (see Nelson 1973) were used instead of ethmoid and angular, respectively. In the list of material examined, "c&s" indicates a cleared and stained specimen.

Specimens examined for the present study are deposited in the following institutions: American Museum of Natural History, New York (AMNH), Academy of Natural Sciences of Philadelphia, Philadelphia (ANSP), Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA); Museu Nacional, Rio de Janeiro (MNRJ), Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP), Naturhistorisches Museum, Wien (NMW), National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM), and Zoologisches Museum, Berlin (ZMB). In the "Material Examined" section, names of collectors are cited when known, and the term "EPA" refers to the "Expedição Permanente da Amazônia," a Brazilian field expedition under the direction of P. Vanzolini (MZUSP) financed by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), São Paulo State Government.

Sternarchorhamphus Eigenmann, 1905

Sternarchorhamphus Eigenmann *in* Eigenmann & Ward 1905:160, 165–166, pl. VIII, fig. 7, partim, type by original designation *Sternarchus* (*Rhamphosternarchus*) *muelleri* Steindachner, 1881.—Ihering 1907, in key to "Gymnotidae," key to species of Brazil.—Eigenmann 1910, list of species.—Regan 1911, listed.—Ellis 1912, in key to "Sternarchinae."—Ellis 1913, in key to "Sternarchinae," described, food items, mutilation and regeneration of caudal peduncle.—Jordan 1920, listed, Eigenmann & Ward considered as authors.—Eigenmann & Allen 1942, in key to "Apteronotinae," briefly described, list of species.—Miles 1945, compared to *Ubidia.*—Miles 1947, compared to *Ubidia.*—Fowler 1951, Brazil, list of species.—Travassos 1960, synonymy, inclusion of *S. hahni.*—Géry & Vu-Tân-Tuê 1964, briefly compared to *Gymnorhamphichthys* Ellis, present in key to Apteronotidae, upper Amazon.—Britski

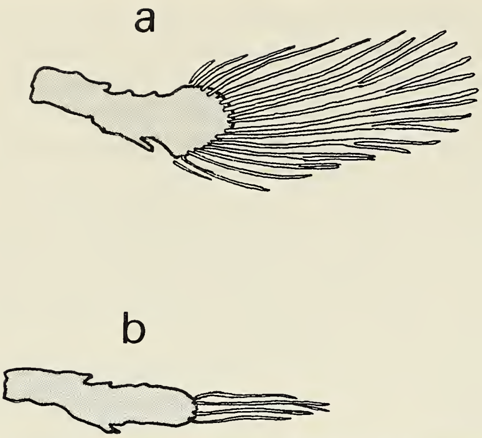

Fig. 1. Diagrammatic view of caudal-fin skeleton of apteronotid fishes. a. Widespread condition in the Apteronotidae (modified from Meunier & Kirschbaum, 1984:140, fig. 5a). b. Caudal-fin skeleton of *Sternarchorhamphus muelleri.*

1972, reported from Rio Paraná basin.—Mago-Leccia 1976, described from Venezuela, osteology, first record in the Río Orinoco basin, sister group of *Sternarchorhynchus,* assigned to the "Sternarchorhynchinae."—Mago-Leccia 1978, listed in the "Sternarchorhynchinae."—Bullock et al. 1979, listed.—Kramer 1990, discussion on electric organ discharge patterns.—Campos-da-Paz 1992, compared to *Sternarchorhynchus.*—Triques 1993, relationships, Rio Orinoco.—Mago-Leccia, 1994, diagnosis, brief description, notes on osteology, species.

Diagnosis.—According to recent studies on interrelationships of gymnotiform genera (Mago-Leccia 1976, Triques 1993; see also "Note on Relationships," below), the following characters are derived for *Sternarchorhamphus,* among closely related apteronotids: caudal-fin rays reduced in number (two to five rays; Fig. 1); presence up to five irregular rows of diminutive dentary teeth (most easily observed on the anterior portion of this bone in adults); presence of a mesocoracoid; and snout slightly turned dorsally.

The following combination of characters, either primitive or of uncertain polarity, distinguishes *Sternarchorhamphus* from all other known apteronotids: snout elongated and laterally compressed; upper jaw produced and pointed, lower jaw somewhat included; teeth minute, present on both jaws at all ages; mouth small to moderate, 11.2–16.5% [16.5%] in HL; eyes small, 2.5–4.4% [3.6%] in HL; lateral ethmoids present; scales rare or absent on antero-dorsal, and dorsal regions of body; dorsal fleshy filament originating on anterior third of total length and extending to vertical through posterior end of anal fin.

Etymology.—From *Sternarchus,* an earlier nominal genus of the Apteronotidae and currently junior synonym of *Apteronotus,* and the Greek *rhamphos,* for beak. Gender masculine.

Distribution.—Most examined specimens of *Sternarchorhamphus* were collected at localities near the main channels of the Rio Amazonas and Río Orinoco, and their large tributaries. Additional specimens came from the vicinities of Belém (Pará State, Brazil), Amapá (Amapá State, Brazil), and the Río Ucayali basin (Peru; Fig. 2). Mago-Leccia (1976) was the first to record *Sternarchorhamphus* from Venezuela, studying specimens from Río Portuguesa and Río Apurito. Recent collections from the Río Orinoco originated in the deep river channel (examined specimens from the Orinoco Delta and middle Orinoco, collected by the crew of R/V *Eastward,* 1978–1979, deposited at AMNH, ANSP, and USNM). Ellis (1913) and Santos et al. (1984) examined specimens from the Rio Tocantins basin.

Note on relationships.—Published phylogenetic hypotheses of the Apteronotidae do not include more than six of the ten currently accepted genera (e.g., Mago-Leccia 1976, Triques 1993) and, therefore, a comprehensive cladogram for the family is still unavailable (efforts on this subject are in progress elsewhere; J. Albert, and M. Triques, pers. comm.). It is beyond the scope

Fig. 2. Geographic distribution of *Sternarchorhamphus muelleri.* Some symbols represent more than one collection locality and/or lot of specimens.

of this study to present a detailed discussion on the intrafamilial relationships of the Apteronotidae. Furthermore, specimens of the apteronotids *Orthosternarchus tamandua* (Boulenger, 1898) and *Ubidia magdalenensis* Miles (1945) are extremely rare in collections, making it impossible to examine their internal anatomy and precluding a rigorous test of Sternarchorhynchinae monophyly (*O. tamandua* MZUSP 2647 [1 ex.] and *U. magdalenensis* USNM 123795 [1 ex.; paratype] were examined for external features).

The characters used by Mago-Leccia to define the Sternarchorhynchinae (1976), "reduced mouth gape" and "elongate snout," and to include *Sternarchorhampus* in it, are rather vague; their status as secondary homologues (=synapomorphies; see Pinna 1991) depends not much from their overall similarity, but rather on a well-corroborated hypothesis of relationships of closely related groups. An attempt to give these characters a more objective approach is presented below.

Sternarchorhynchines all have the mouth gape length less than 38% of the snout length. In remaining apteronotids, most gymnotiforms (except rhamphichthyids), and most closely related non-gymnotiform ostariophysans (Characiformes and Siluriformes; see Fink & Fink 1981), this value is consistently greater than 55%. When mouth gape length is compared to postorbital length, the value is always less than 31% in sternarchorhynchines, and greater than 40% in the proposed non-rhamphichthyid outgroups.

In most apteronotids, remaining gymnotiforms (but, again, not rhamphichthyids), and most closely related non-gymnotiform ostariophysans, snout length represents less than 40% in head length. In *Orthosternarchus, Sternarchorhamphus* and *Sternarchorhynchus* this value is always greater than 50%; *Ubidia,* however, is a unique case. Although it also has a conspicuously elongate snout, the eye in this genus is located well forward in the head (an autapomorphic feature; see Mago-Leccia 1994:159, fig. 56B), resulting in the snout length/head length ratio decreasing to around 40%. Comparing snout length to postorbital length results in values of more than 90% for sternarchorhynchines (except *Ubidia* which, because of eye position, has the snout 70% of postorbital length) and less than 80% in remaining non-rhamphichthyid groups cited.

Currently available evidence indicates that the Rhamphichthyidae is distantly related to the Sternarchorhynchinae (Mago-Leccia 1976, 1978; Triques 1993), and the "reduced mouth gape" and an "elongate snout" can be hypothesized as being independently acquired in these taxa.

Some authors have called attention (e.g., Schaefer 1987) and discussed (e.g., Pimentel & Riggins 1987) the questionable general utility, in phylogenetic analyses, of proportional differences observed between morphological characters. It should be noted, however, that the above discussion is based on previous phylogenetic hypotheses concerning external (Fink & Fink 1981) and internal (Mago-Leccia 1976, 1978; Triques 1993) gymnotiform relationships. Furthermore, the utilization of morphometry in the present case is an attempt to make the terms "reduced" (the mouth) and "elongate" (the snout) as objective as possible (this kind of strategy is commonly observed in literature; e.g., Weitzman & Fink 1985 [fig. 79, characters 18, 32, and 40]). Additional justification for utilization of morphometry was found in Chappill (1989:231), who stated that "[q]uantitative characters should generally only be used [i.e., in phylogenetic analyses] when the choice is between examining them or abandoning the analysis entirely for want of sufficient characters." In some cases, however, there is evidence that morphometry can explicitly be used for phylogenetic purposes (e.g., Pinna 1989:24 [character 2], Costa 1990 [fig. 32, characters 13, 34, 39, 46, 80 and 89], Schaefer 1991 [fig. 15, character 13], and Vari 1991 [fig. 11, characters 17 and 42]).

In conclusion, the monophyly of the Sternarchorhynchinae, including *Sternarchorhamphus,* is tentatively accepted. The position of this genus within the subfamily, however, remains uncertain until additional material of related genera is available, which will allow a more detailed analysis of this question.

Sternarchorhamphus muelleri (Steindachner, 1881)

Figs. 1–5, Table 1

Sternarchus (*Rhamphosternarchus*) *Mülleri* Steindachner 1881:99, original description, Pará State, Brazil.—Steindachner 1882:15, pl. V, fig. 4, described, no exact locality, Rio Amazonas at Pará State, Brazil.

Sternarchorhynchus mülleri (not *S. mulleri* Castelnau 1855).—Eigenmann & Eigenmann 1891:62, listed, Pará.—Eigenmann 1894:625, listed, Pará.

Sternarchorhamphus mülleri.—Eigenmann & Ward 1905:165–166, pl.VIII, fig. 7, assigned as type species of *Sternarchorhamphus,* original designation, Pará.—Eigenmann 1910:449, listed, Pará to Peru.—Ellis 1913:142–143, 174, 182–183, figs. 10 and 23–25, described, food habits, regeneration of caudal peduncle, Alcobaça (="Alcoboca"), Rio Tocantins, Pará.—Meinken 1937:79, compared to *Sternarchorhamphus hahni.*—Fowler 1939:276, Contamana, Peru.—Eigenmann & Allen 1942:320, listed, lower Amazon to the Ucayali.—Fowler 1945:180, fig. 65, Peru (Contamana) and Amazonas.—Miles 1947:184, compared to *Ubidia magdalenensis.*

Sternarchorhamphus muelleri.—Ihering 1907:277, Amazonas, Pará.—Mago-Leccia 1976:244–249, fig. 78, described from Río Orinoco, Venezuela.—Ortega & Vari

1986:12, Peru.—Campos-da-Paz 1992: 24, 134, briefly compared to *Sternarchorhynchus.*—Mago-Leccia, 1994:35, 36, 71, 107, 156, 203, fig. 52, brief description, notes on osteology, listed.

Sternarchorhamphus mulleri.—Starks 1913: 23, described, variation of anus position, Pará.—Santos et al. 1984:18, 78, figure, in list of species from lower Rio Tocantins, common names, Brazil.—Triques 1993:91, listed, discussion of relationships to other gymnotiforms.

Sternarchus mulleri.—Jordan 1920:512, cited as type species of *Sternarchorhamphus.*

Sternachorhamphus [misspelling] *müelleri.*—Magalhães 1931:178, cited.

Sternarchus mülleri.—Travassos 1960:24, cited as type species of *Sternarchorhamphus.*

Sternarchoramphus [misspelling] *mulleri.*—Begossi & Braga 1992:107, tb.2, and 11, fig. 5, common name in Rio Tocantins, listed as fish avoided as food.

Material examined.—Brazil: NMW 65328:1, lectotype (photograph; new designation), 260.5 mm LEA, no exact collection site, Rio Amazonas at Pará State, F. Steindachner donation, accession file number "1874.I.299 & 299a"; NMW 65328:2, paralectotype, 249.0 mm LEA, same data of lectotype; INPA 4850, 7 specimens, Camaleão, Ilha da Marchantaria, Rio Solimões, Amazonas State, 3 Feb 1982, G. M. Soares; INPA 4852, 5 specimens, Camaleão, Ilha da Marchantaria, Rio Solimões, Amazonas State, 1 Jun 1981, G. M. Soares; MNRJ 1221, 1 specimen, no collection data; MNRJ 1222, 2 specimens, no collection data; MNRJ 9022, 2 specimens, 'Ver-o-Peso' market, Belém, Pará State, 10 Feb 1958, L. Travassos & F. Pires leg.; MNRJ 12182, 1 specimen, Amapá, Amapá State, Apr 1981, G. W. Nunan et al.; MZUSP 6983, 7 specimens, Rio Madeira, 25 km below Nova Olinda, Amazonas State, 27 Sep 1967, EPA; MZUSP 9580, 1 specimen, fish market at Manaus, Amazonas State, 17–19 Sep 1968, EPA leg.; MZUSP 23321, 1 specimen, mouth of Paraná do Catito, below mouth of Rio Juruá, Rio Solimões, Amazonas State, 4 Oct 1968, EPA; MZUSP 24675, 1 specimen, Santa Luzia, Rio Purus, Amazonas State, 11 Jan 1975, P. E. Vanzolini; USNM 52547, 2 specimens, Pará to Manaus, Rio Amazonas, 1901, J. B. Steere.

Peru: ANSP 95834, 2 specimens, Río Ucayali at Cantamana, Jul–Aug 1937, W. C. Morrow; ANSP 120348, 2 specimens, Pucallpa, on Río Ucayali, 18–19 Jun 1969, E. J. Huggins.

Venezuela: ANSP 149460, 3 specimens, shallow river, N side of river across from Isla Tres Caños, Delta Amacuro, 13 Nov 1979, R/V *Eastward* (H. Lopez, M. Corcoran); ANSP 149457, 1 specimen, Río Orinoco, below Barrancas, ca. km 140, depth 26 m, Delta Amacuro, 17 Feb 1978, R/V *Eastward* (Lundberg & Baskin); ANSP 160250, 6 specimens, Río Guariquito at confluence of Río Orinoco, Estado Bolivar, 25 Nov 1985, B. Chernoff et al.; ANSP 162297, 2 specimens, Río Orinoco, near mouth of Río Caura, Estado Bolivar, 22 Nov 1985, G. J. Lundberg et al.; ANSP 166792, 1 specimen, Caicara, L. Bartolico, Estado Bolivar, Río Orinoco basin, 20 May 1987, M. Rodriguez & R. Richardson; ANSP 166793, 1 specimen, Caicara, Castillero, Estado Bolivar, Río Orinoco basin, 19 Apr 1988, M. A. Rodriguez & A. Martinez; USNM 226339, 1 specimen, Río Orinoco, deep river channel, Brazo Imataca, 82 n. m. upstream from sea buoy, Territorio Federal Delta Amacuro, 22 Feb 1978, D. Taphorn; USNM 226491, 2 specimens, Río Orinoco, deep river channel, north side of Isla Tortola, 123 n. m. from sea buoy, Delta Amacuro Fed. Territory, 19 Feb 1978, J. N. Baskin; USNM 226495, 3 specimens, Río Orinoco, Brazo Imataca, south from Isla Remolino, ca. km 82.9 from sea buoy, Delta Amacuro Fed. Territory, 22 Feb 1978, Baskin/Lundberg; USNM 228805, 6 specimens (1 C&S), across from Palua, ca. 182

Table 1.—Morphometric data for the paralectotype (NMW 65328:2) and additional non-type material of *Sternarchorhamphus muelleri.* TL, LEA, HL, and CL are expressed in mm; measurement 1 is expressed as % of TL; measurements 2 to 7 are expressed as % of LEA; 8 to 21 as % of HL; 22 as % of CL. *SD,* standard deviation; and *n,* number of examined specimens.

	Paralectotype	Range	$\bar{X}$ *SD*	*n*
TL	292.0	261.0–446.0	— —	15
LEA	249.0	188.0–375.0	— —	17
HL	30.0	20.5–63.3	— —	28
CL	43.0	35.0–77.0	— —	15
1) Standard length	85.2	81.4–88.2	83.9 ± 1.7	15
2) Anal-fin length	90.4	89.1–93.0	91.2 ± 1.1	15
3) Body depth	10.1	8.7–12.2	10.2 ± 0.8	18
4) Head length	12.1	11.4–14.5	12.4 ± 0.9	18
5) Pre-anal distance	9.3	8.0–10.8	9.1 ± 0.7	18
6) Pre-pectoral distance	12.7	11.3–15.4	12.7 ± 1.1	18
7) Tail length	17.2	16.7–22.7	19.5 ± 1.9	14
8) Snout length	49.5	45.9–52.9	49.3 ± 2.0	28
9) Eye diameter	3.6	2.5–4.4	3.3 ± 0.4	28
10) Mouth width	16.5	11.2–16.5	13.3 ± 1.4	25
11) Interorbital width	11.9	8.0–13.0	10.6 ± 1.4	28
12) Snout to occiput	90.1	83.5–91.7	87.4 ± 2.3	28
13) Postorbital distance	53.4	46.9–53.8	50.5 ± 1.9	28
14) Pectoral-fin length	45.2	43.5–59.0	50.9 ± 5.2	28
15) Pre-anal-fin length	75.9	68.8–79.8	72.9 ± 2.6	26
16) Snout to anus	58.7	48.5–60.2	54.8 ± 3.5	27
17) Anterior naris–posterior naris	5.6	3.3–5.6	4.3 ± 0.6	26
18) Posterior naris–eye	25.7	22.0–30.3	26.8 ± 2.1	26
19) Head depth	62.0	52.1–63.9	57.6 ± 3.8	26
20) Head width	24.1	22.2–29.9	25.1 ± 1.9	28
21) Branchial opening	19.4	15.6–19.4	17.2 ± 1.2	28
22) Tail depth	9.7	6.3–10.6	8.2 ± 1.3	14

n. m. from sea buoy, 9 Nov 1975, H. Lopez & O. Riviero; USNM 228806, 6 specimens, shallow river, downstream from sea buoy 82, near mouth of a small caño, Delta Amacuro Fed. Territory, 21 Nov 1979, H. Lopez et al.; USNM 228808, 1 specimen, shallow river, north shore, 49 n. m. from sea buoy, Delta Amacuro Fed. Territory, 20 Nov 1979, Lopez et al.

Diagnosis.—As for the genus.

Description.—Morphometric data for the paralectotype (NMW 65328:2) and additional specimens of *S. muelleri* are given in Table 1. The lectotype (NMW 65328:1) is shown in Fig. 3.

Body strongly compressed laterally, especially posterior to abdominal cavity, deepest in this region; dorsal profile from nearly straight to gently convex. Lateral line complete, extending to caudal peduncle, but not onto caudal fin in some specimens.

Head laterally compressed, more markedly so anteriorly, deepest at occiput and widest in opercular area; snout pointed and conical, slightly turned dorsally in most specimens; eyes reduced in size, completely covered with skin, located dorso-laterally on head; small (paired) sensory pore present, dorsal to eye and usually near vertical through anterior border of eyes.

Mouth small, sub-terminal (inferior in some specimens), its gape usually not reaching vertical through anterior border of anterior nare; upper jaw projected, lower jaw somewhat included. Single patch of numerous diminutive conical teeth present on pre-

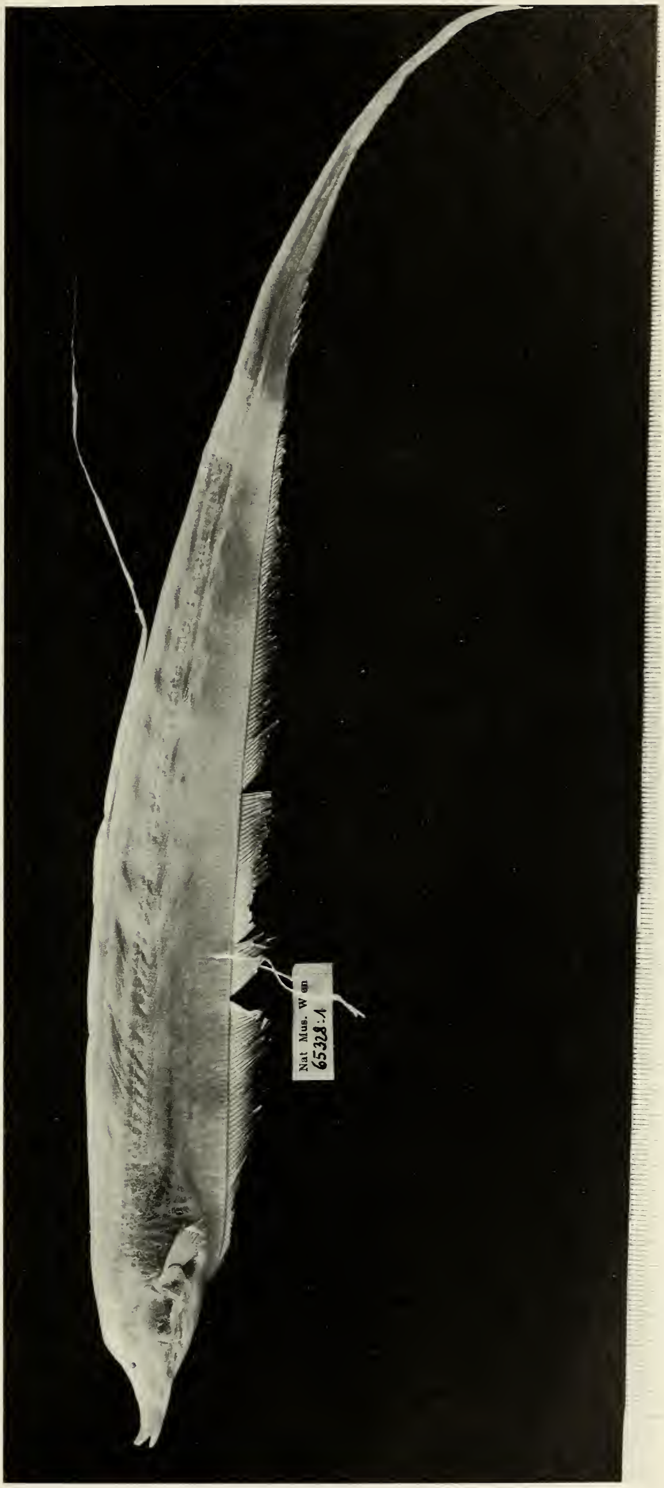

Fig. 3. *Sternarchorhamphus muelleri*, NMW 65328:1, 314.5 mm TL, 260.5 mm LEA, lectotype; Brazil, Rio Amazonas at Pará State, no exact collection site.

maxilla (25–40, $\bar{X} = 34.1$, $n = 7$ [approx. 35 in paralectotype]). Usually four of five irregular rows of similar teeth on dentary (25–45, $\bar{X} = 36.4$, $n = 7$ [approx. 25 in paralectotype]). Maxilla and mesopterygoid edentulous. Small rounded papillae covering part of the roof and floor of the oral cavity. Anterior nares tubular; posterior ones rounded, without a tube and remote from eyes.

Branchial opening reduced to a short slit immediately anterior to pectoral-fin origin; branchial membranes joined or partially joined to isthmus. Anterior chamber of gas bladder small, posterior elongate. Anus and urogenital papilla adjacent and located ventral to opercular region, shifting anteriorly with age.

Pectoral fins moderate, elongate and slightly pointed, with ii + 12–14 rays [ii + 13]. Anal fin with 230–262 rays [231], its origin near vertical through nape; first anterior anal-fin rays less developed (some undivided) and smaller than posterior ones.

Scales small, cycloid, absent or greatly reduced in number on anterior region of body and dorsally; lateral line perforated scales usually larger than those immediately dorsal and ventral to it. Scales above lateral line four to nine. Small scales, sometimes in single series, present on caudal fin in some specimens.

Dorsal filament (="dorsal thong"; a modified muscle according to Mago-Leccia 1994) originating on anterior third of total length, its tip reaching vertical through posterior end of anal fin. Tail (region from base of last anal-fin ray to tip of caudal fin) elongate, laterally compressed, ending in reduced caudal fin with two to five rays [four]; condition unique among Gymnotiformes. Caudal peduncle sometimes with discrete constriction at caudal-fin base.

Osteological features of *Sternarchorhamphus muelleri,* relevant at the generic level, are as follows: premaxilla broadest anteriorly, and extending posteriorly to near the maxilla; maxilla elongate and curved posteriorly, its anterior portion well-developed (Figs. 4 and 5); dentary large, extending posteriorly and covering anterior portion of retroarticular; Meckel's cartilage well-developed and elongate, partially associated with anguloarticular and dentary; coronomeckelian bone reduced in size, compared to adjacent bones; retroarticular well-developed, with pointed antero-ventral process; lateral ethmoids present; vomer elongate, its anterior portion "arrow-shaped" and contacting parasphenoid through small cartilaginous bridge; posterior end of vomer pointed; palatine cartilage present, well-developed anteriorly and contacting anterior portion of maxilla; mesopterygoid broad, edentulous, with poorly-developed ascending process; parasphenoid elongate, bifurcate anteriorly and posteriorly; infraorbital series represented only by canal-bearing portions of bones; mesethmoid elongate, rounded and reduced at its anterior portion; two cranial fontanels present and well-developed (interfrontal larger than interparietal); supraoccipital small, with reduced crest; posttemporal fossae absent; opercle ornamented with numerous small trabeculae; mesocoracoid present; scapular foramen absent; coracoid with well-developed postero-ventral process, but not reaching cleithral symphysis; posttemporal fused to supracleithrum; extrascapular present; two postcleithra; four pectoral radials; four branchiostegal rays, first and second almost filamentous, others large and laminar; urohyal broad and expanded posteriorly with reduced head, and approaching in size the basihyal and first ceratobranchial; gill rakers not ossified; four infrapharyngobranchials, fourth one cartilaginous; five epibranchials, fifth one cartilaginous; upper pharyngeal tooth plate with seven or eight teeth, connected to third epibranchial through a ligament; lower pharyngeal tooth plate with 12–13 teeth; Weberian apparatus without claustrum; 16–17 precaudal vertebrae (Weberian complex included); two "rib-like bones" (modified ribs?) present in posterior wall of abdominal cavity, anterior one enlarged, laterally compressed and turned an-

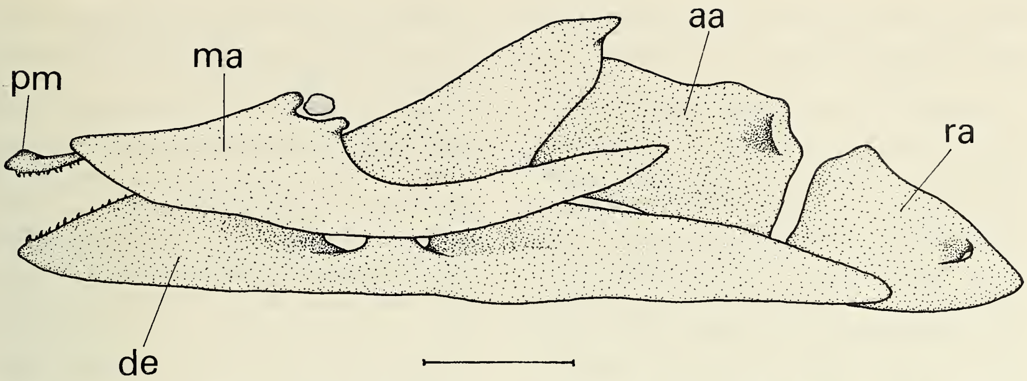

Fig. 4. Jaws of *S. muelleri*, USNM 228805, 188.8 mm LEA. Lateral view of left side. Scale bar = 1 mm. aa, anguloarticular; de, dentary; ma, maxilla; pm, premaxilla; ra, retroarticular.

teriorly; proximal pterygiophores of anal fin with expanded, pointed, symmetric projections anteriorly, directed dorsally on the anterior third of pterygiophore, well-developed posterior to abdominal region; 91–99 vertebrae to base of last anal-fin ray (Weberian complex included); well-developed intermuscular bones, especially conspicuous dorsally and ventrally to vertebral column, and posterior to abdominal region; caudal-fin skeleton consolidated into a single element of reduced size.

Color in alcohol.—Body light yellowish brown, covered with diminutive irregular dark spots (chromatophores), most on dorsal portion of head and snout, and on back. The overall coloration can vary from pallid to melanistic. Pectoral fins hyaline at base, and usually dark distally (chromatophores on fin membranes); anal fin of some specimens with continuous black margin along entire length, with melanophores also present over fin membranes; specimens from the Río Orinoco, however, can be nearly completely pallid (J. Lundberg, pers. comm.). Caudal fin hyaline.

Food habits.—Stomach-contents of *Sternarchorhamphus* showed fragments of partially digested insect larvae (tentatively identified as Diptera), along with some unidentified Annelida. These findings agree with those by Ellis (1913:174), who had also

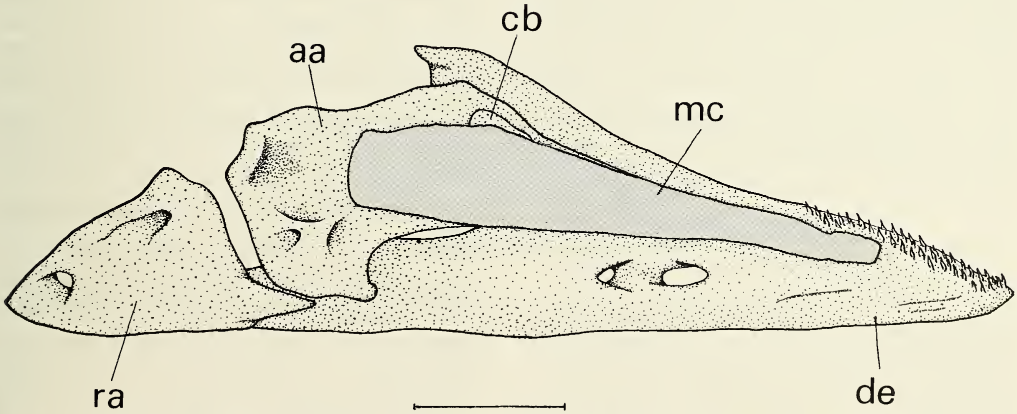

Fig. 5. Lower jaw of *S. muelleri*, USNM 228805, 188.8 mm LEA. Medial view of left side. Scale bar = 1 mm. aa, anguloarticular; cb, coronomeckelian bone; de, dentary; mc, Meckel's cartilage; ra, retroarticular.

noted a single unidentified Entomostraca specimen and additional insect larvae, other than Diptera.

Remarks.—Santos et al. (1984) listed the names "ituí" (a common name for most apteronotid fishes in Brazil) and "tuvira" (also used for other Gymnotiformes, except the Electrophoridae) for *S. muelleri* in the lower Rio Tocantins region. The same authors also observed that this species is the only apteronotid with some commercial value as a food fish in that area. Begossi & Braga (1992), curiously, listed *S. muelleri* as a fish avoided as food by local fishermen at Rio Tocantins (in States of Maranhão and Tocantins), and recorded the common name "lampréia" to this species (that name is also assigned for other non-apteronotid gymnotiform fishes occurring in that area).

Langner & Scheich (1978) and Kramer (1990) discussed the electric organ discharges (EODs) of some gymnotiforms, including specimens they identified as *Sternarchorhamphus,* which showed a fundamental frequency of EOD between 1300 and 1700 Hz. A figure presented by Langner & Scheich (1978:236, fig. 1), and later reproduced by Kramer (1990:198, fig. 4.57), however, does not show *Sternarchorhamphus,* but *Sternarchorhynchus.*

Etymology.—Steindachner proposed the name *Mülleri* (the original spelling in his 1881 paper) for the new species in honor of Johannes Müller, a famous German ichthyologist of the 19th century. Several different spelling forms for this species are currently widespread in literature (see synonymy, above). According to the International Code of Zoological Nomenclature (1985; Article 32d), however, the correct form is *muelleri.*

Taxonomic status of *Sternarchus* (*Rhamphosternarchus*) *macrostomus* Günther, *Sternarchus tamandua* Boulenger, and *Sternarchorhamphus hahni* Meinken

Günther (1870) described *Sternarchus* (*Rhamphosternarchus*) *macrostomus* ("*macrostoma*" in the original spelling; not *Sternarchus macrostomus* Fowler [1943]) on the basis of a single specimen from Jeberos (=Xeberos), Río Marañon drainage, Peru. This nominal species was subsequently assigned to *Sternarchorhynchus* by Eigenmann & Eigenmann (1891; "Upper Amazon"). Eigenmann (in Eigenmann & Ward 1905) included *S. macrostomus* in *Sternarchorhamphus,* without any detailed explanation. Ellis (1913) did not examine specimens of *S. macrostomus* and simply quoted Günther's original description, following Eigenmann's placement of the species. This view remained unaltered since then, until the recent work of Mago-Leccia (1994), who used the species to establish the monotypic apteronotid genus *Platyurosternarchus.*

Platyurosternarchus first appeared in a key to apteronotid genera (Mago-Leccia 1994: 26). Later, in the same study, that author stated that the genus was "proposed in order to locate properly the species *Sternarchus macrostomus,*" that the new genus is "clearly different from *Sternarchorhamphus*" (p. 37), and provided a photograph of the head of a specimen from the Orinoco basin (p. 160, fig. 57A). A list of distinctive features (including uniquely derived characters, such as the overall morphology of caudal fin) was also given by Mago-Leccia, who definitely demonstrated that *P. macrostomus* and *S. muelleri* are different species (but note also characters already pointed out by Günther 1870). Relationships of *Platyurosternarchus,* however, were not discussed in that work, and the closest relatives of that genus remain uncertain. A preliminary view of this problem suggests that *Platyurosternarchus* and *Sternarchorhamphus* belong to different subsets within the family Apteronotidae and are not sister groups. As in *S. muelleri,* the snout in *P. macrostomus* is elongate (around 50% in head length), but the latter species does not have the reduced mouth gape length characteristic of sternarchorhynchines (approximately 65% in snout length, and 75% in postorbital length vs. less than 35% in snout length, and less than 31% in postorbital length, respectively). The possibility of *Platyurosternarchus macrostomus* constitutes the sister-group of the Sternarchorhynchinae cannot be dismissed at this time, but further detailed investigation is needed (see discussion on the Sternarchorhynchinae, above).

Sternarchus tamandua was described by Boulenger (1898) on the basis of a single specimen, with an injured tail, from Rio Juruá (Brazil). The species was transferred to *Sternarchorhamphus* by Eigenmann (in Eigenmann & Ward 1905), who was followed by Ihering (1907) and Eigenmann (1910). Later, the species was used by Ellis (1913) to establish the monotypic apteronotid genus *Orthosternarchus.* The name of this genus, however, appeared first in key to genera to "Gymnotidae" (=Gymnotiformes) from British Guiana provided by Ellis (1912; type-species' name was not mentioned), and that should be considered its original description. Curiously, not a single specimen of *Orthosternarchus* was recorded from Guiana until the present date. Little has been published on this poorly known species since then, mainly because of its scarcity in collections. Detailed information on its internal morphology and osteology is unavailable. The overall form of the snout is an autapomorphic feature, clearly suggesting that *O. tamandua* is not conspecific with *S. muelleri* or any known apteronotid (see, for example, Ellis 1913: 144, fig. 11, Mago-Leccia 1994:147, fig. 41). Since this genus is currently assigned to the Sternarchorhynchinae, the possibility of *Orthosternarchus* and *Sternarchorhamphus* are its sister-groups must be left open until enough material is available to allow this kind of investigation. If a sister-group relationship between these two genera can be demonstrated, then an interesting taxonomic question will arise, since their included species were once referred to a single genus, *Sternarchorhamphus.* Current available evidence is scarce and cannot definitively show a close relationship between *O. tamandua* and *S. muelleri,* so these species are here kept in their own separate genera.

A study on the single known specimen of *Sternarchorhamphus hahni* Meinken (holotype, ZMB 31367), collected near Corrientes, Rio Paraná basin in Argentina, revealed that it lacks the diagnostic features of the Apteronotidae (e.g., caudal fin internally supported by a single bony element; a dorsal fleshy filament) and should rather be referred to *Rhamphichthys* Müller & Troschel, 1846 (Rhamphichthyidae). In addition to several features observed only in rhamphichthyids and closely related groups among gymnotiforms (Hypopomidae; see Mago-Leccia 1978, and Triques 1993; e.g., no teeth on both jaws; anterior nares not tubular and located close to upper lip), *S. hahni* has 323 anal-fin rays (330 recorded by Meiken 1937; vs. a maximum of 290 anal-fin rays in related groups), a condition apparently uniquely derived for *Rhamphichthys* (or a subset of it) among closely related taxa. Mago-Leccia (1976, 1994) previously posed some doubts on the taxonomic status of *S. hahni* but, because of lack of access to type material, did not discuss the question in greater detail (a more detailed approach on this subject is currently being published elsewhere; Campos-da-Paz & Paepke 1994).

In conclusion, it seems reasonable not to include the nominal species *S. hahni* Meiken and *S. macrostomus* (Günther) in *Sternarchorhamphus* which, otherwise, would make it non-monophyletic. *Sternarchus tamandu* Boulenger remains in *Orthosternarchus* Ellis until a detailed phylogenetic study on the Sternarchorhynchinae reveals its position regarding that genus. The solution presented herein is to consider *Sternarchorhamphus* a monotypic subunit of the Apteronotidae, comprising only *S. muelleri* (Steindachner). As discussed above, however, its phylogenetic relationships to other sternarchorhynchine apteronotid genera remains uncertain, depending on more complete and conclusive investigations than those presented so far.

Acknowledgments

For conversations and discussions on systematics and taxonomy of gymnotiform fishes, I am grateful to J. Albert, H. A. Britski, W. J. E. M. Costa, C. Cox-Fernandes, J. G. Lundberg, N. A. Menezes, H.-J. Paepke, M. C. C. de Pinna, J. P. Sullivan, S. Toledo and M. L. Triques. I am deeply indebted to the following individuals and institutions for their hospitality, access to collections and/or to specimens under their care, logistic and equipment support, loan of specimens and all kinds of additional assistance: N. Feinberg, G. J. Nelson and M. S. T. Piza (AMNH); E. B. Böhlke, P. A. Buckup, W. G. Saul, and S. A. Schaefer (ANSP); M. C. C. de Pinna (Field Museum of Natural History, Chicago); M. Jégu (INPA); C. A. Bizerril, U. Caramaschi, D. F. Moraes, Jr., I. B. Moreira, G. W. Nunan and J. C. de Oliveira (MNRJ); F. A. Bockmann, H. A. Britski, J. L. Figueiredo, N. A. Menezes, O. T. Oyakawa, L. M. S. Porto, and M. L. Triques (MZUSP); B. Herzig (NMW); J. G. Lundberg (University of Arizona, Tucson); E. P. Caramaschi, W. J. E. M. Costa, and R. Sachsse (Universidade Federal do Rio de Janeiro); S. Jewett, R. P. Vari, and S. Weitzman (USNM); and H.-J. Paepke (ZMB). Earlier versions of manuscript benefited from comments and suggestions by J. Albert, H. A. Britski, W. J. E. M. Costa, J. G. Lundberg, N. A. Menezes, T. A. Munroe, M. C. C. de Pinna, and R. P. Vari. A photograph of the lectotype of *S. muelleri* was taken by Mrs. A. Schumacher (NMW), and kindly provided by B. Herzig (NMW).

The author was financially supported by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), São Paulo State Government, Brazil. The following institutions also funded visits to study part of their gymnotiform collections: Academy of Natural Sciences of Philadelphia (Philadelphia), American Museum of Natural History (New York), and National Museum of Natural History, Smithsonian Institution (Washington, D.C.).

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(1):45–49. 1995.

A new species of *Neoperla* (Insecta: Pleocoptera: Perlidae) from Mississippi

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Abstract.—*Neoperla coxi,* a new species, is described from male, female, egg and nymphal stages, and a holotype male is designated. Males differ from all known Nearctic *Neoperla* in having most of the aedeagal tube spinulose. The new species is apparently endemic to southwest Mississippi.

During a recent survey to determine the status of *Alloperla natchez* Surdick & Stark, 1980, and *Haploperla chukcho* (Surdick & Stark 1980), two chloroperlid stoneflies endemic to southwest Mississippi, specimens of an undescribed *Neoperla* were collected near the type localities of these species. A few additional specimens were found among unidentified material in my collection and from P. K. Lago of the University of Mississippi, and a larger series was obtained from the Mississippi Entomological Museum (MEM), Mississippi State University. The material from the MEM was collected by malaise and blacklight traps at three sites in the Homochitto National Forest with the support of National Science Foundation grant DEB-9200856 awarded to Richard Brown.

Recent study of extensive *Neoperla* collections from throughout Mississippi and Alabama (Stark & Harris 1986, Stark & Lentz 1988.) suggests the new species is endemic to the Homochitto National Forest and surrounding areas of southwest Mississippi and perhaps Louisiana.

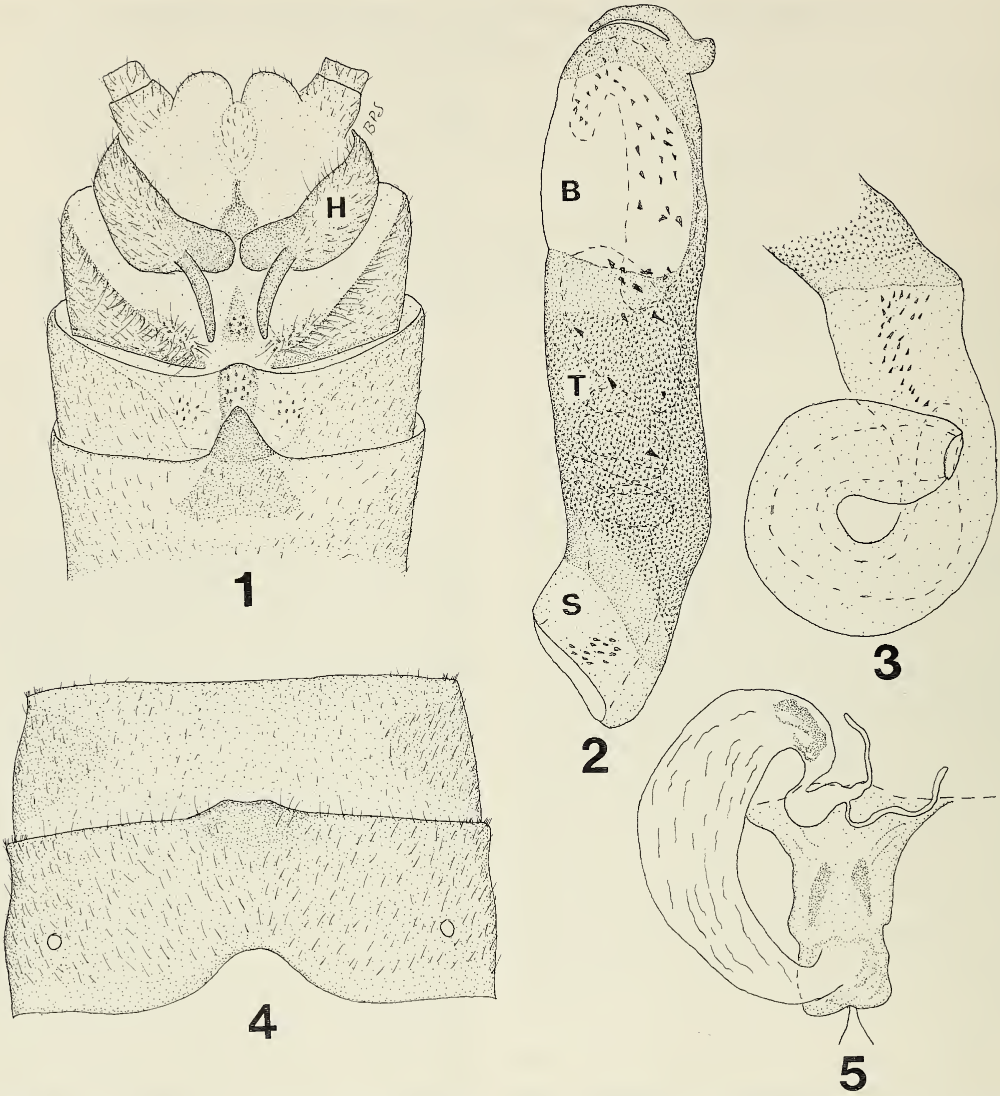
The holotype is placed in the National Museum of Natural History (USNM) on indefinite loan from the Mississippi Entomological Museum. Paratypes are in the collections of the author (BPS), the University of Mississippi (UM) and the Mississippi Entomological Museum. Terminology follows Stark & Lentz (1988).

Neoperla coxi, new species
Figs. 1–8

Male.—Forewing length 8–10 mm. General color yellow patterned with brown. Wings amber brown with darker veins; costa and subcosta pale. Legs yellow except for diffuse dorsal brown spot near apex of femora and a narrow longitudinal brown band extending from femur for ⅔ of outer tibial margin. Cerci pale. Process of tergum 7 triangular, upturned in lateral aspect and armed ventrally with 4–5 prominent sensilla basiconica. Mesal sclerite of tergum 8 with lateral margins parallel for most of length. Hemiterga slightly tapered apically, finger-like process of hemitergum slender and bent slightly ventrolaterad (Fig. 1). Tube of aedeagus slightly sinuate, 3.1 times as long as bulb; conspicuous spicules cover most of tube (Fig. 2). Sac sparsely armed in basal half by a pair of basolateral patches of slender spines (Figs. 2–3); apical armature of scattered, thickened spines (Fig. 2), mid section unarmed (Figs. 2–3).

Female.—Forewing length 11–13 mm. Posterior margin of sternum 8 produced into a small rounded to slightly bilobed tab (Fig. 4). Spermathecal stalk membranous except for small apical section lined with fine brown setae (Fig. 5); stalk grotesquely inflated in some specimens.

Egg.—Length 0.31 mm; width 0.19 mm. Sessile collar surrounded by a single irreg-



Figs. 1–5. *Neoperla coxi* male and female genitalia. 1, Male terminalia; 2, Aedeagal tube, lateral; 3, Aedeagus, sac partially extruded, apical armature not shown; 4, Female sterna 8 and 9; 5, Vagina and spermathecal stalk, dorsal. T = tube; S = sac; B = bulb; H = hemitergum.

ular row of reticulation. Striae relatively straight, narrowed at each end and separated by wide sulci. Sulci with 4–5 irregular aeropyle rows. Micropyles in sulci near equator (Figs. 7–8).

Mature nymph.—Body length 7–9 mm. General color yellow patterned with brown. Anterior of frons covered with a broad transverse brown pigment band; posterior margin of band sinuate, anterior margin straight. Ocellar area covered with a small diffuse brown spot. Pronotal disk ringed by a sub-marginal pigment band. Each abdominal tergum with a narrow transverse pigment band (Fig. 6).

Etymology.—I am pleased to name this species for my friend and colleague, Prentiss G. Cox, in recognition of his interest and support of research at Mississippi College.

Types.—Holotype ♂ and 104 ♂ and 48 ♀

paratypes from Middleton Creek, Franklin County, Mississippi, T5N R4E Sec 31S, 1 Jun 1992, T. Schiefer, R. Fontenot (USNM, MEM). Additional paratypes, all from Mississippi: Claiborne Co: Little Sand Creek, Rocky Springs, 14 May 1977, B. Stark, 1 ♀ reared (BPS). Sand Creek tributary, 0.5 mi W Hunt Road, 18 May 1978, B. Stark, 1 ♀ (BPS). Same location, 3 Jun 1986, B. Stark, J. Ballard, 1 ♀ (BPS). Copiah Co: Brushy Creek, Hwy 27, 0.5 mi E Hopewell, 20 May 1978, B. Stark, 1 ♂, 1 ♀ reared (BPS). Franklin Co: Clear Springs Lake, 4.5 mi SW Meadville, 30 May 1988, P. K. Lago, 1 ♂ (UM). Middleton Creek, T5N R4E Sec 31S, 9–15 Jun 1992, T. Schiefer, R. Fontenot, 6 ♂ (MEM). Same data except 29 Jun 1992, 4 ♂ (MEM). Same data except 30 Jun–6 Jul 1992, 1 ♂ (MEM). McGehee Creek tributary, T6N R4E Sec 26SW, 1 Jun 1992, T. Schiefer, R. Fontenot, 88 ♂, 35 ♀ (MEM). Porter Creek, T5N R4E Sec 8NW, 1 Jun 1992, T. Schiefer, R. Fontenot, 6 ♂, 3 ♀ (MEM). Hinds Co: Sand Creek, Hunt Road, 24 Apr 1992, B. Stark, G. Gee, D. Kelly, 2 ♂ (BPS).

Discussion.—This description of *N. coxi* brings to 14 the number of Nearctic *Neoperla* species. Using keys in Stark & Lentz (1988), males of *N. coxi* are identified as *N. stewarti* Stark & Baumann, 1978, or *N. osage* Stark & Lentz, 1988, and females are identified as *N. stewarti. N. coxi* males differ from all known Nearctic species in having most of the aedeagal tube spinulose (Fig. 2) and they also differ from both *N. osage* and *N. stewarti* in lacking prominent aedeagal armature in the basal half of the sac (Figs. 2–3). Separation of unassociated females of *N. coxi* from *N. stewarti* is more difficult, but the subgenital plate is slightly longer and the spermathecal stalk lining is less developed in *N. coxi;* females of other Nearctic *Neoperla* differ from *N. coxi* in having most of the spermathecal stalk lined with brown setae. Nymphs are virtually identical in color pattern to *N. robisoni* Poulton & Stewart, 1986 (Ernst et al. 1986, Poulton & Stewart 1991), with perhaps a less extensive ocellar pigment spot in *N. coxi.* The egg collar and posterior pole of *N. coxi* bear less prominent reticulations than do the eggs of *N. stewarti.*

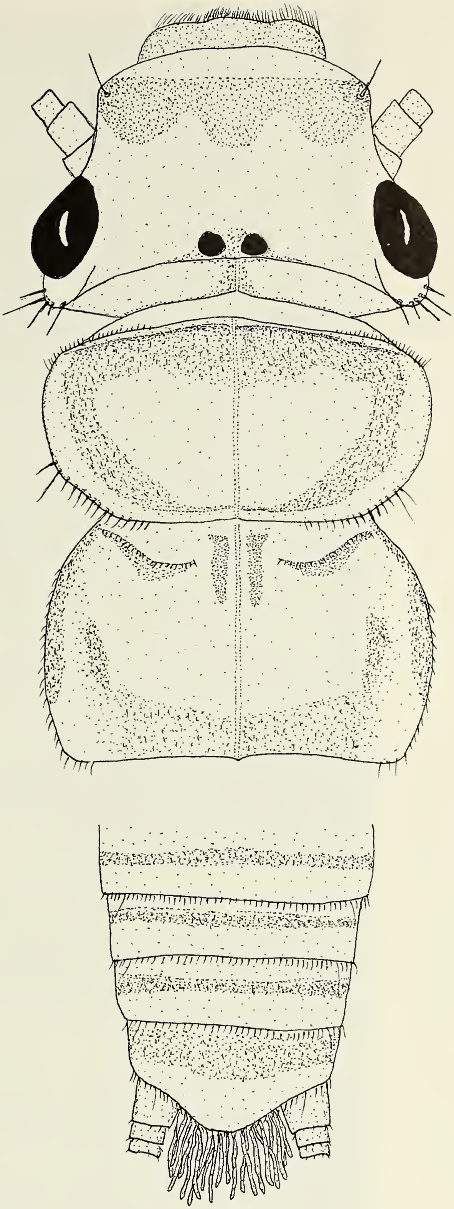

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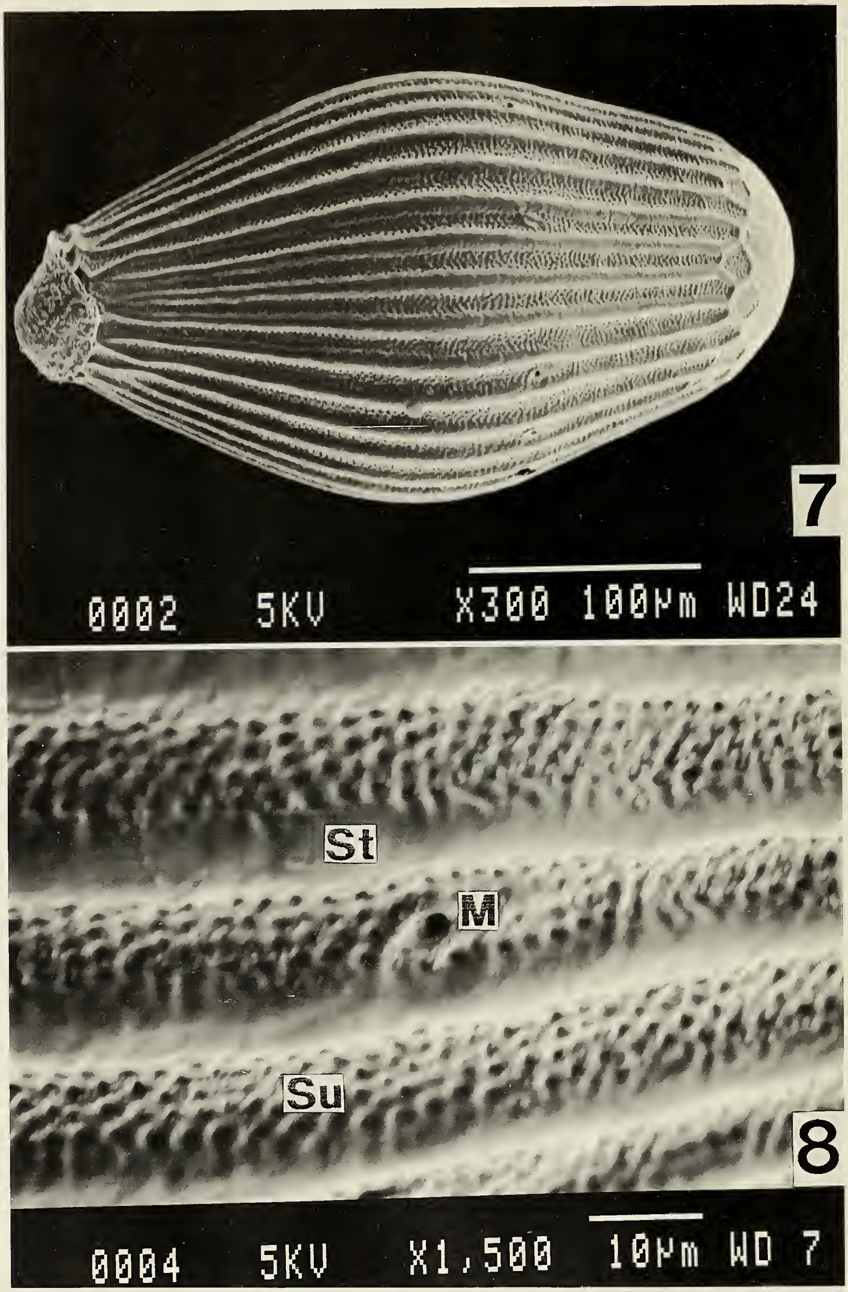
Fig. 6. *Neoperla coxi* nymphal habitus.

Six *Neoperla* species are now known from Mississippi but only *N. robisoni* and *N. carlsoni* Stark & Baumann, 1978, have been



Figs. 7–8. *Neoperla coxi* eggs. 7, Entire egg, lateral; 8, Detail of surface. St = striae, Su = sulci, M = micropyle.

collected from the same streams with *N. coxi.* At the Middleton Creek site in Franklin County, personnel of the Mississippi Entomological Museum operated a malaise trap continuously from 2 June through 31 August of 1992, and blacklight collections were made 1 June, 29 June and 31 August. Early collections through 8 June contained exclusively *N. coxi; N. robisoni* males first appeared by 9 June and males of the 2 species were collected together through 6 July. Thereafter, no males of *N. coxi* were taken but a single female was present in a mid-August malaise trap. *N. robisoni* males were collected through July and August and by late August, the first *N. carlsoni* specimens were taken. Although elsewhere in Mississippi, *N. carlsoni* has been collected as early as 22 June, at the Middleton Creek site a temporal emergence sequence which begins with *N. coxi* and ends with *N. carlsoni* may occur.

Acknowledgments

I thank R. L. Brown and T. Schiefer (Mississippi State University) and P. K. Lago (University of Mississippi) for the loans of specimens. K. St. John (University of Mississippi School of Dentistry) helped in the preparation of photomicrographs.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(1):50–53. 1995.

Macrobrachium catonium, a new troglobitic shrimp from the Cayo District of Belize (Crustacea: Decapoda: Palaemonidae)

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Abstract.—A new troglobitic shrimp, *Macrobrachium catonium,* is described from the Vaca Plateau, Cayo District of Belize. It is the third albinistic member of the genus known to occur along the Gulf of Mexico-Caribbean versant of Middle America. It may be distinguished from the Oxacan *M. villalobosi* Hobbs by the eye which is more pigmented and lacks an apical cleft, and by the shorter, often slightly upturned rostrum which does not reach the distal extremity of the antennal scale. It differs from the Tabascan *M. acherontium* in possessing a more attenuate (less vaulted) rostrum, and from both in that usually there are more than two ventral rostral teeth, and fewer subapical spines on the appendix masculina.

The new shrimp described herein is the third albinistic member of the genus *Macrobrachium* known to occur in caves on the Gulf of Mexico-Caribbean versant of Middle America (Botosaneanu 1986). *Macrobrachium villalobosi* Hobbs (1973) has been reported from a single locality, Cueva del Nacimiento del Río San Antonio, 10 km SSW of Acatán, Oaxaca, Mexico, and *M. acherontium* Holthuis (1977) from two caves in Tabasco, Mexico. Specimens of the new troglobite have been collected in two caves located approximately 46 km apart on the Vaca Plateau in the Cayo District of Belize close to Guatemala.

Macrobrachium catonium, new species

Description.—Rostrum (Fig. 1a, d) moderately high, weakly arched, and slightly deflected or upturned anteriorly, tip not reaching distal extremity of antennal scale; dorsal margin with 6 to 9 teeth, as many as 3 bispinous (8 in holotype of which 3 bispinous), and 1 or 2 epigastric; ventral margin with 2 to 5 teeth.

Carapace (Fig. 1a) with antennal spine arising slightly posterior to ventral part of orbital margin and hepatic spine almost directly ventral to first epigastric tooth. Branchiocardiac groove prominent.

Abdomen (Fig. 1a) smooth, pleura of fifth abdominal somite with acute posteroventral angle, more anterior pleura rounded posteroventrally. Sixth somite 1.5 times as long as fifth, and telson 1.2 times longer than sixth; dorsal surface of telson (Fig. 1j, o) with anterior pair of spines situated at base of posterior third and posterior pair at about base of posterior sixth, slightly posterior to midway between anterior pair and median apex of telson; posterior margin of telson sharply contracted, forming broadly acute tip, and bearing 2 pairs of spines ventral to margin, more mesial pair decidedly overreaching apex of telson, lateral pair falling short of apex; (holotype with row of 8 plumose setae between mesial pair of spines and single simple submarginal seta dorsally).

Eyes (Fig. 1a, d) moderately large, rounded distally and with apical black to purplish pigment spot; cornea over pigmented area lacking facets.

Antennule (Fig. 1a, d) with proximal podomere of peduncle longer than combined length of distal 2 podomeres, these subequal in length, and distal podomere falling short of base of lateral spine on antennal scale; distolateral spine on basal podomere reaching slightly beyond midlength of penultimate podomere; holotype with lateral long flagellum about 5 times length of postorbital length of carapace, mesial flagellum about 3 times as long. Antenna (Fig. 1a, d, l) with peduncle as illustrated, basal segment with ventrolateral spine, flagellum about 7.3 times as long as postorbital carapace length. Antennal scale 2.5 times as long as broad, with lateral margin almost straight.

Gnathal appendages (Fig. 1b, e, h, i, k, m) as figured. Third maxilliped reaching slightly beyond midlength of antennal scale.

First pereiopod (Fig. 1a) overreaching antennal scale by length of dactyl, latter subequal in length to mesial margin of palm of chela; carpus about twice length of chela and slightly shorter than merus. Second pereiopod (Fig. 1a, n) overreaching antennal scale by only slightly more than length of chela; latter with fingers slightly longer than smooth palm; opposable margin of fixed finger with 1 very small corneous tubercle near base, otherwise fingers lacking tubercles, but both fingers with scattered fine setae and subapical clusters of curved stiff ones; carpus 1.2 times as long as either propodus or merus, and merus 1.4 times longer than ischium. Third pereiopod overreaching antennal scale by propodus and ⅓ length of carpus; latter almost half as long as merus, and merus 2.5 times as long as ischium. Fourth pereiopod overreaching antennal scale by dactyl and slightly less than half length of propodus; propodus approximately 2.7 times length of dactyl; carpus about half as long as merus, and latter almost 2.5 times as long as ischium. Fifth pereiopod overreaching antennal scale by dactyl and ¼ length of propodus; propodus almost 5 times length of dactyl and 1.7 times length of carpus, latter little less than ⅔ length of merus; merus 2.6 times length of ischium.

First pleopod (Fig. 1c) with exopodite 2.2 times as long as endopodite. Second pleopod (Fig. 1f) with exopodite 1.2 times length of endopodite and latter with appendix masculina (Fig. 1f, g) reaching distinctly beyond its midlength. Lateral ramus of uropod (Fig. 1o) with straight lateral margin bearing fixed spine and longer, slenderer, movable one at its mesial base.

Branchial formula typical of that of many, if not most, other members of *Macrobrachium*: 5 pleurobranchs corresponding to pereiopods, 2 arthrobranchs at base of third maxilliped, podobranch on coxa of second maxilliped, and epipodites on second maxilla and first maxilliped.

Size.—Carapace length of male holotype 9.9 mm; that of 12 females, none of which ovigerous, ranging from 8.8 to 14.4 mm.

Color.—Lacking pigment except for eye spot which purplish to black.

Type locality.—Lake in Actun Chapat (cave), Cayo District, Belize. This cave is located on the northern end of the Vaca Plateau and although it has not been fully explored it is estimated to be about 2 km in length. Shrimp were found in the lake passage, apparently a perched overflow route with a series of small lakes extending more than 150 m. The shrimp were numerous on the silt-covered substrate of the lakes which were as deep as 6 m. The troglobitic crab, *Typhlopseudothelphusa acanthochela* Hobbs, 1986, occurred in small numbers and the catfish with reduced eyes, *Rhamdia laticauda typhla* Greenfield, Greenfield, & Woods, were fairly abundant. Bats were roosting over the lakes and probably were insectivorous *Natalus* sp. and *Mormoops* sp. and frugivorous *Corollia* sp. and *Glosso-*

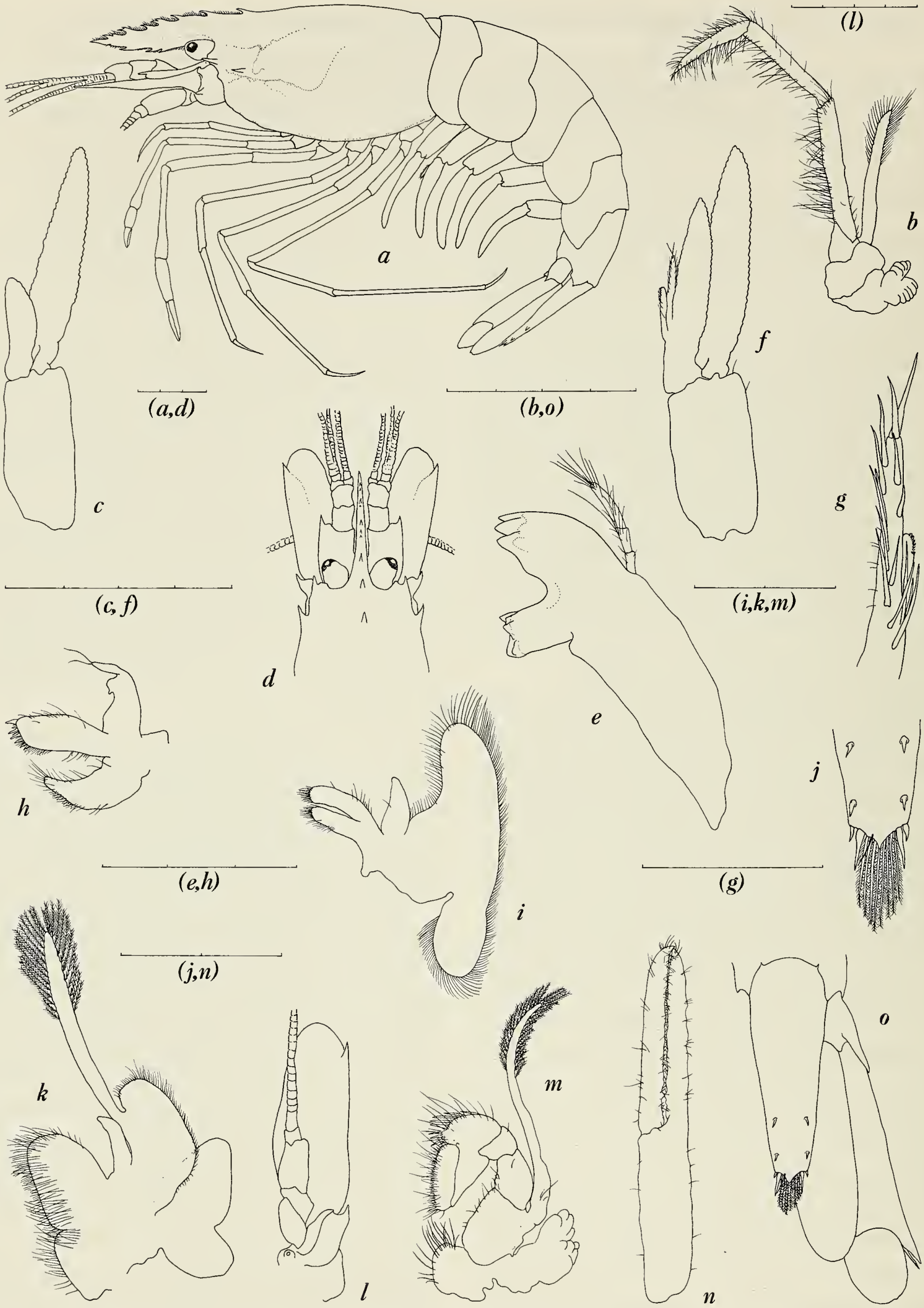

Fig. 1. *Macrobrachium catonium,* new species (all appendages from left side of holotype except c and h from female paratype from type locality): a, Lateral view; b, Third maxilliped; c, f, First pleopods; d, Dorsal view of anterior region of carapace, including cephalic appendages; e, Mandible; g, Appendices masculina and interna; h, First maxilla; i, Second maxilla; j, Dorsal view of caudal end of telson; k, First maxilliped; l, Ventral view of basal part of antenna; m, Second maxilliped; n, Chela of second pereiopod; o, Dorsal view of telson and right uropod. (Scales in mm.)

phaga sp. Temperature of the lake water in December 1991 was 25°C.

Specimens examined.—In addition to 1 ♂ and 9 ♀ from the type locality (Actun Chapat, 5 Dec 1992, R. Foster & W. R. Elliott, coll.), specimens were examined from Tunkul Cave, Chiquibal System, Cayo District, Belize, 1 ♀, 24 Mar 1986, D. Coons, coll. and from "Chiquibal System," Cayo District, Belize, 2 ♀, 8 Mar 1986, D. Coons, coll. (This cave is located approximately 46 km south of Actun Chapat on the south end of the Vaca Plateau near Guatemala.)

Disposition of types.—The holotype (USNM 260328) and 10 of the paratypic females are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. A paratypic female is in the collection of the Texas Memorial Museum, Austin, and another in the Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands.

Relationships.—*Macrobrachium catonium* is closely related to the two Mexican troglobitic shrimps assigned to the genus, *M. villalobosi* and *M. acherontium.* The three are markedly similar suggesting common ancestry. The apically notched eyes and long (reaching to or beyond the distal end of the antennal scale), slender, straight rostrum of *M. villalobosi* sets it apart from the other two, and the comparatively slender (nearly straight rather than with a strongly convex ventral margin) rostrum with usually more than two ventral teeth in *M. catonium* distinguishes it from *M. acherontium.* In addition, there are fewer subapical setae on the appendix masculina of *M. catonium* than in the other two species. Holthuis (1977: 191) reported the presence of 5 pleurobranchs but no other gills, exopods, or epipods in *M. acherontium* whereas *M. catonium* possesses 2 arthrobranchs at the base of the third maxilliped, and epipodites on the second and first maxillipeds.

Etymology.—*Catonium* (L.), the lower world, noting the subterranean habitat of this shrimp.

Acknowledgments

Thanks are extended to T. Miller for locating and sending us the misplaced shrimp collected from the Chiquibul Cave system in 1986, and to D. Coons who collected three of the specimens. We are also grateful to R. Foster and W. R. Elliott who collected the shrimp from the type locality, and to the latter who provided us with the information recorded in the description of the type locality. For their critical review of the manuscript appreciation is extended to C. W. Hart, Jr., B. F. Kensley, and A. B. Williams.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(1):54–60. 1995.

Procambarus (*Ortmannicus*) *nueces* (Decapoda: Cambaridae), a new crayfish from the Nueces River Basin, Texas

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Abstract.—*Procambarus* (*Ortmannicus*) *nueces* is described from a small, sluggish tributary to the Nueces River in Atascoso County, Texas. It may be distinguished from its closest relative, *P.* (*O.*) *zonangulus* Hobbs & Hobbs, by the less attenuated distal part of the male first pleopod which lacks a cephalomesial shoulder and bears a more robust mesial process.

Four specimens of this new crayfish, including a first form male and three juveniles, were collected for the Smithsonian Institution by Bruce B. Collette and Oliver S. Flint from the type locality on 10 September 1960. While its distinct features were recognized several years ago and futile searches made in several collections for additional specimens, we were reluctant to describe this new species until additional material became available. Not until July 1993, when the second author, assisted by Howard and Stephen Kronk, collected in the area where the original lot had been taken, were two additional specimens secured, both procured with the aid of a seine in the same segment of stream in which Collette and Flint collected almost 39 years earlier. Although other aquatic habitats in the area were sampled in July and a search was made for burrows, no other crayfish were found. We offer the following description of this new species that is based on six specimens (3 adults and 3 juveniles) from the type locality.

Procambarus (*Ortmannicus*) *nueces*, new species
Fig. 1, Table 1

Diagnosis.—Body pigmented, eyes well developed. Rostrum of adults with well defined marginal spines but lacking median carina. Carapace with single moderately strong cervical spines. Areola 14.7 to 17.3 times as long as wide and constituting 32.0 to 36.4% of total length of carapace and 44.0 to 47.9% of postorbital length. Suborbital angle very small to virtually obsolete; postorbital ridge with small, corneous cephalic tubercle; hepatic area weakly tuberculate; branchiostegal spine well developed. Antennal scale almost twice as long as broad, widest slightly proximal to midlength. Ischia of third and fourth pereiopods with simple hooks overreaching basioischial articulation and lacking opposing tubercles on corresponding basis; coxa of fourth pereiopod with strong bulbiform boss, that of fifth much smaller and flattened. First pleopods of first form male reaching coxa of third pereiopods, symmetrical but not conspicuously tapering distally; cephalomesial margin lacking even rudiment of hump or shoulder. Terminal elements consisting of: (1) short, tapering mesial process directed caudodistally and inclined laterally, and (2) cephalic process obscuring much of central projection in cephalic aspect, corneous, subacute, tapering from broad base, inclined mesially and gently curved caudally, its apex lying slightly mesial to central projection; caudal element consisting of corneous, tapering acute caudal process lying against caudal surface of central projection and inconspicuous, non-corneous, setiferous caudal knob at lateral base of cephalic process; and corneous central projection, largest of terminal elements, inclined mesially and tapering to apex which directed caudodistally and slightly laterally. Annulus ventralis about 1.7 times as wide as long, dextral half elevated little more than sinistral; sinus originating on median line, disappearing under dextral wall and emerging on caudal flank of dextrally directed tongue, slightly posterior to midlength of annulus, where crossing median line and, in gentle arc, coursing caudally to margin of annulus. Sternum cephalic to annulus deeply cleft and bearing few prominent tubercles. Unadorned postannulur sclerite more than half as broad and as long as annulus. First pleopod present in female.

Holotypic male, form I.—Cephalothorax (Fig. 1a, l) subcylindrical in section, only slightly broader than high. Abdomen narrower than thorax (20.1 and 24.1 mm). Greatest width of carapace greater than height at caudodorsal margin of cervical groove. Cephalic section of carapace twice as long as areola, length of latter 33.1% of entire length of carapace (44.9% of postorbital carapace length). Surface of carapace punctate dorsally, granulate to tuberculate laterally. Rostrum not noticeably deflected ventrally, with basally subparallel margins gently converging to level of distal margin of penultimate podomere of antennular peduncle where diverging and forming well developed marginal spines marking base of acumen, latter reaching distal extremity of ultimate podomere of antennular peduncle; dorsal surface concave with many small setiferous punctations particularly in basal half. Subrostral ridges evident in dorsal aspect for very short distance at caudal margin of orbit. Postorbital ridges well developed, grooved dorsolaterally and bearing well developed spiniform tubercles at cephalic extremities. Suborbital angle very weak, virtually obsolete. Branchiostegal spines comparatively well developed. Single cervical spine on both sides of carapace rather small but well defined and acute.

Abdomen (Fig. 1j) slightly shorter than carapace. Pleura of third through fifth segments subtruncate to rounded with caudoventral extremities subangular. Cephalic section of telson (Fig. 1e) with 2 spines in each caudolateral corner, mesial one on each side movable; caudal margin of caudal section with shallow median excavation at end of dorsomedian groove extending length of section. Cephalic lobe of epistome (Fig. 1o) subcylindrical with elevated (ventrally) irregular margins and bearing acute anteromedian projection; central area subplane except for anteromedian groove; distinct anteromedian fovea and median longitudinal groove present on main body. Ventral surface of proximal podomere of antennular peduncle with strong spine slightly proximal to midlength. Antennal peduncle with small spiniform tubercles on basis and ischium; flagella reaching midlength of telson. Antennal scale (Fig. 1h) 2.2 times as long as broad, widest slightly proximal to midlength; greatest width of lamella more than twice width of thickened lateral part.

Third maxilliped extending cephalically to level of ultimate podomere of antennular peduncle; ischium not produced distolaterally, its ventral surface densely studded with plumose setae.

Right chela (Fig. 1m) subovate in cross section, not strongly depressed. Mesial surface of palm with row of 6 tubercles subtended dorsolaterally by additional row of 6 and few scattered ones and ventrally by row of 4. Entire palm tuberculate but ventrolateral surface more weakly so. Dorsal and ventral longitudinal ridges weak on both fingers. Opposable surface of fixed finger with dorsal row of 20 tubercles and lower one of 8; dorsal row, with fifth from base largest, extending from base of finger slightly beyond level of locking tubercle (more distal ones too small to be included in illustration); ventral row much shorter, extending along middle third of finger and consisting of locking tubercle, which much larger than others and, not visible in dorsal aspect, 7 proximal and 3 distal to it; band of minute denticles present ventral to dorsal row of tubercles and suddenly broadening at level of locking tubercle, covering entire opposable surface distally to base of corneous tip; except for few small tubercles on proximodorsal and proximoventral surfaces, finger otherwise with setiferous punctations. Opposable margin of dactyl with dorsal row of 24 small to minute, rounded tubercles along proximal ⅔ of finger and ventral row of 13 along second fourth of finger from base; band of minute denticles situated between tubercles of dorsal row proximally, broadening at level of proximal end of ventral row and covering opposable margin to base of corneous tip of finger; mesial surface with row of 6 tubercles along proximal third flanked by few others proximally but, except for few additional tiny tubercles proximally, finger with setiferous punctations. Both fingers with punctations forming rows flanking inconspicuous longitudinal ridges and those with longer setae projecting toward opposable member. Carpus of chela longer than broad, bearing prominent oblique furrow dorsally; tuberculate mesially and on mesial half of dorsal surface; ventral surface with usual 2 distal tubercles, otherwise sparsely punctate. Merus tuberculate dorsally, distomesially, and ventrally; 2 premarginal tubercles larger than others on dorsodistal surface; ventral surface with mesial row of 16 tubercles and less clearly defined lateral one of 10. Ischium with ventromesial row of 5 tubercles.

Hooks on ischia of third and fourth pereiopods (Fig. 1f) simple, both overreaching basioischial articulation and neither opposed by tubercle on corresponding basis. Coxa of fourth pereiopod with prominent bulbiform boss; that of fifth with much smaller compressed one. Sternum between third, fourth, and fifth pereiopods comparatively deep with mat of plumose setae extending mesially from ventrolateral margins.

First pleopods (Fig. 1b, c, d, g, n) as described in "Diagnosis." Uropod (Fig. 1e) with both lobes of basal podomere bearing small acute spine, both rami with distolateral spines, and distomedian spine on mesial ramus situated distinctly proximal to boadly rounded distal margin.

Allotypic female.—Differing from holotype, except in secondary sexual characters, as follows: 2 marginal spines on sinistral side of rostrum; acumen slightly overreaching antennular peduncle; cephalic section of telson with 3 spines in each caudolateral corner, more mesial pairs on each side movable, mesialmost spines minute; cephalic lobe of epistome more concave; antennal flagellum reaching tergum of sixth abdominal segment; 5 tubercles present in row ventral to mesial row on palm of chela (Fig. 1p); opposable margin of fixed finger with single dorsal row of 10 small tubercles along basal half, locking tubercle (only member of ventral row present) situated near midlength of finger and minute denticles on both fingers confined to single row; opposable margin of dactyl with dorsal row of 12 small tubercles extending from base of finger to level of locking tubercle on fixed finger, ventral row represented by only 2 tubercles on proximal third of finger; merus with 14 tubercles in ventromesial row and 11 in ventrolateral row (rows not distinct in part, so numbers approximate); ventromesial surface of ischium with row of 4 tubercles.

Annulus ventralis and adjacent sternal elements as described in "Diagnosis."

Color notes.—Dorsum of carapace mostly pale tan but rostrum darker and with reddish suffusion; rostral and postorbital ridges bluish gray, latter flanked ventrolaterally by reddish splotch; mandibular adductor areas covered by reticulate dark brown pattern; dorsolateral part of branchiostegites with conspicuous black stripe extending from brownish-to-almost-black cervical groove to caudal margin of carapace; remainder of lateral surface of carapace pale gray with darker gray mottlings; cervical spine white and caudal flange of carapace edged in dark

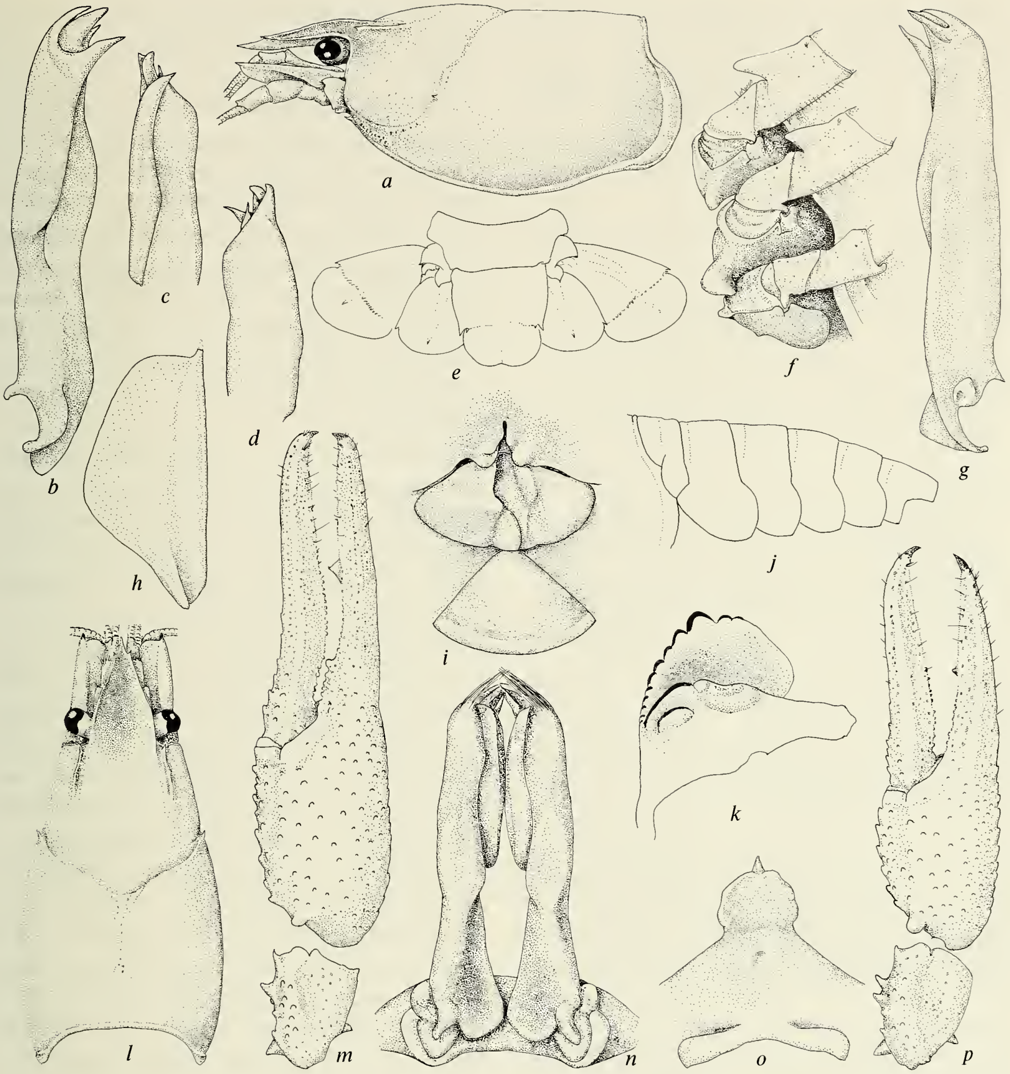

Fig. 1. *Procambarus* (*Ortmannicus*) *nueces,* new species (all from holotype except i, p from allotype): a, Lateral view of carapace; b, Mesial view of first pleopod; c, Caudal view of same; d, Cephalic view of same; e, Dorsal view of sixth abdominal segment, telson, and uropods; f, Basal podomeres of third, fourth, and fifth pereiopods; g, Lateral view of first pleopod; h, Antennal scale; i, Annulus ventralis and flanking sternal elements; j, Lateral view of abdomen; k, Caudal view of mandible; l, Dorsal view of carapace; m, Dorsal view of distal podomeres of cheliped; n, Caudal view of first pleopods; o, Epistome; p, Dorsal view of distal podomeres of cheliped.

gray. Abdomen with broad dorsomedian black stripe extending from carapace through anterior third of sixth abdominal segment, most of which pinkish tan; stripe interrupted by narrow transverse bands of pinkish tan along caudal margins of terga; black stripe flanked laterally by narrower pinkish tan stripe, and it, in turn, separated from mostly reddish pleura by concave splotches of gray-merging-to-black on bases of pleura, dark color continuing along caudodorsal margins of pleura; telson and uropods, particularly lateral ramus of latter, reddish brown. Antennae and antennules

Table 1.—Measurements (mm) of *Procambarus* (*O.*) *neuces,* new species.

	Holotype	Allotype	Paratype
Carapace			
Entire length	48.4	54.0	40.3
Postorbital length	35.6	39.3	40.3
Width	24.1	26.1	20.1
Height	22.0	24.0	19.0
Areola			
Width	1.0	1.0	1.0
Length	16.0	17.3	14.7
Rostrum			
Width	7.9	9.0	7.0
Length	14.5	17.7	11.0
Right chela			
Length, palm mesial margin	16.1	10.8	12.6
Palm width	13.6	11.2	10.4
Length, lateral margin	50.9	34.3	41.5*
Dactyl length	30.5	21.1	25.1
Abdomen			
Width	20.1	24.0	17.2
Length	47.0	53.0	41.0

* Approximate, tip broken.

greenish cream; antennal scales also pale laterally, lamella suffused with pink. Cheliped with distal part of merus and dorsal and distomesial parts of carpus olive tan, remainder of these and more proximal podomeres pinkish cream; palm of chela pinkish cream dorsally with olive to dark greenish brown tubercles, deeper pink ventrally; fingers with greenish suffusion proximodorsally, and dactyl also proximomesially, fading quickly distally to very pale cream. Remaining pereiopods with merus and carpus greenish dorsally, otherwise, cream to pinkish cream.

Size.—See Table 1 for measurements of the only three adult individuals available.

Type locality.—Sluggish stream tributary of the Nueces River 4.3 miles (6.9 km) south of Jourdanton at junction of State Routes 97 and 173, Atascosa County, Texas. About 5 m at its widest point, the stream was extremely turbid when visited 24 July 1993 and very little flow was noted. The channel was slightly sinuous and tree limbs and other vegetative debris impeded the flow in various sections. The substrate consisted of sand, gravel, and in the pooled areas that were as deep as 1.5 m, the bottom was covered with silt. Sedges and grasses as well as composite plants dominated the riparian vegetation on the upstream (east) side of the bridge along St. Rte. 97 and the water received direct sunlight for much of the daylight hours.

Disposition of types.—The holotypic male, form I, and allotype (USNM 260326 and 260327) are deposited in the National Museum of Natural History, Smithsonian Institution, as are the paratypes consisting of 1 ♂I, 1 juv ♂, and 2 juv ♀.

Relationships.—*Procambarus* (*O.*) *nueces,* new species, belonging to a closely allied group of species often treated as the *blandingi* "group" of the subgenus (see Ortmann 1905:100, Hobbs 1962:286), has its closest affinities with *P.* (*O.*) *zonangulus* Hobbs & Hobbs, 1990. Within this assemblage are the following currently recognized species: *P.* (*O.*) *blandingii* (Harlan 1830), *P.* (*O.*) *acutus* (Girard 1852), *P.* (*O.*) *acutissimus* (Girard 1852), *P.* (*O.*) *lecontei* (Hagen 1870), *P.* (*O.*) *hayi* (Faxon 1884), *P.* (*O.*) *viaeviridis* (Faxon 1914), *P.* (*O.*) *cuevachicae* Hobbs, 1941, *P.* (*O.*) *caballeroi* Villalobos, 1944, *P.* (*O.*) *verrucosus* Hobbs, 1952, *P.* (*O.*) *lophotus* Hobbs & Walton, 1960, *P.* (*O.*) *texanus* Hobbs, 1971, *P.* (*O.*) *geminus* Hobbs, 1975, *P.* (*O.*) *zonangulus,* and *P.* (*O.*) *nechesae* Hobbs, 1990. Four of these crayfishes typically have symmetrical first pleopods: *P.* (*O.*) *viaeviridis, P.* (*O.*) *texanus, P.* (*O.*) *zonangulus,* and *P.* (*O.*) *nueces;* at least one population of *P.* (*O.*) *cuevachicae* has nearly symmetrical ones. The new species differs from *viaeviridis,* which is the most marginal member of the group, in many conspicuous respects: among them, *P.* (*O.*) *nueces* has well developed marginal spines on the rostrum; the setiferous caudal knob of the first pleopod is laterally rather than cephalically situated, is not conspicuously produced, and the setae partly obscure other terminal elements; and the central area of the annulus ventralis is not deeply excavate. Distinguishing it from *P.* (*O.*) *cuevachicae* are a more strongly tapering, subacute, less compressed cephalic process and a less twisted central projection of the first pleopod in first form males, and a straight, not reflexed, hook on the ischium of the fourth pereiopod that is not opposed by a tubercle on the corresponding basis. From *texanus* it differs in that the cephalic process and central projection are bent caudally at distinctly less than a right angle to the shaft of the appendage, and there is not even a hint of a shoulder on the appendage proximal to the terminal elements; the cephalic lobe of the epistome is subcircular instead of subtriangular in outline; in the female there are fewer tubercles adorning the sternum anterior to the annulus, and the postannular sclerite is about ⅔ as long as broad and is as long as the annulus ventralis. The new crayfish differs from *P.* (*O.*) *zonangulus* in that the first pleopod is not distinctly tapering distally and it lacks any trace of a shoulder on the cephalic or cephalomesial surface proximal to the terminal elements; the mesial process is less attenuate and comparatively stockier; in the female there are markedly fewer tubercles on the sternum anterior to the annulus, and the length of the postannular sclerite is as great as that of the annulus along its median longitudinal axis.

Acknowledgments

We are grateful to B. B. Collette and O. S. Flint for securing the first specimens of this new crayfish of which we are aware and to H. and S. Kronk for their assistance in obtaining additional specimens. For their critical reading of the manuscript we extend thanks to J. F. Fitzpatrick, Jr., of the University of South Alabama, and C. W. Hart, Jr., and R. B. Manning, of the National Museum of Natural History.

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On a new *Somanniathelphusa* Bott, 1968, from Vietnam (Crustacea: Decapoda: Brachyura: Parathelphusidae)

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Abstract.—A new species of parathelphusid freshwater crab, *Somanniathelphusa pax,* is described from Hanoi, Vietnam. The new species seems to be most closely allied to species from southern China, but differs in the form of the carapace, male abdomen and male gonopods.

Specimens of a freshwater crab recently obtained from a market in Hanoi, Vietnam, proved to belong to an undescribed species of *Somanniathelphusa* Bott, 1968 (family Parathelphusidae Alcock, 1910). The genus *Somanniathelphusa* s. str. as now recognized (Bott 1970, Ng 1988, Ng & Naiyanetr 1993, Naiyanetr 1994), contains six described species: *S. brevipodum* Dai, Song, He, Cao, Xu & Zhong, 1975 [China], *S. chongi* (Wu, 1935) [China], *S. falx* Ng & Dudgeon, 1992 [China], *S. sinensis* (H. Milne Edwards, 1853) (type species) [China], *S. taiwanensis* Bott, 1968 [Taiwan], and *S. zanklon* Ng & Dudgeon, 1992 [Hong Kong]. Naiyanetr (1994) recently reviewed the genus *Somanniathelphusa* and showed that it should be split into four genera: *Somanniathelphusa* s. str., *Sayamia* Naiyanetr, 1994, *Esanthelphusa* Naiyanetr, 1994, and *Chulathelphusa* Naiyanetr, 1994.

The freshwater crab fauna of Vietnam is poorly known. Many of the Indo-Chinese species described by H. Milne Edwards (1853), A. Milne Edwards (1869), De Man (1904) and Rathbun (1904, 1905), did not have precise collection localities. With regards to the parathelphusids belonging or allied to *Somanniathelphusa, Potamon* (*Parathelphusa*) *prolatus* was described from "Mois Chero" in northern Cochinchina (Rathbun 1902:186), a location which is now supposed to be part of northern Vietnam (Türkay & Naiyanetr 1987:392). *Potamon* (*Parathelphusa*) *prolatus,* incorrectly synonymized with *Sayamia dugasti* (Rathbun 1902) by Bott (1970:112), is a valid species and should be transferred to *Esanthelphusa* (P. Naiyanetr, pers. comm.). *Chulathelphusa neisi* was described from somewhere in Cochinchina (Rathbun 1902:186), which may be somewhere in or near Vietnam. Balss (1914:408) reported *Somanniathelphusa sinensis* from Tonkin in Vietnam, but Ng & Dudgeon (1992:757) noted that this record is doubtful and his specimens must be reexamined.

The present paper describes the new species, *Somanniathelphusa pax.* The abbreviations G1 and G2 are for the male first and second pleopods respectively. Measurements are given in millimeters, in the sequence carapace width by carapace length. Specimens examined are deposited in the Zoological Reference Collection (ZRC), Department of Zoology, National University of Singapore.

Systematic Account

Family Parathelphusidae Alcock, 1910

Genus *Somanniathelphusa* Bott, 1968

Fig. 1. *Somanniathelphusa pax,* new species. Holotype male, carapace 41.9 by 32.8 mm (ZRC). Dorsal view.

Somanniathelphusa pax, new species
Figs. 1–3

Material examined.—Holotype male (carapace 41.9 by 32.8 mm) (ZRC), Hanoi, Vietnam, from Dong Xuan market, leg. T. Kosuge, 19 Oct 1993. Paratype female (carapace 34.8 by 26.6 mm) (ZRC), same data as holotype. 2 males (larger, carapace 30.9 by 24.8 mm), 2 females (larger, carapace 31.2 by 25.0 mm) (ZRC), market in Hanoi, Vietnam, leg. A. U. Kara, September 1994.

Description of holotype male.—Carapace broader than long, surfaces smooth, transversely convex (Figs. 1, 2A). Epigastric cristae sharp, distinct, separated by deep longitudinal groove; postorbital cristae sharp, distinct, reaching to beginning of shallow cervical grooves, inner edge of crista reaching to slightly below inner edge of epigastric crista; beyond cervical grooves, cristae are rounded, curving gently to meet bases of first epibranchial teeth; median H-shaped depression distinct, relatively deep (Figs. 1, 2A, B). Frontal margin gently sinuous, confluent with sinuous, smooth supraorbital margin. External orbital angle triangular, inner margin distinctly shorter than outer, outer margin gently convex to straight. Anterolateral margin with 3 strongly developed, sharp epibranchial teeth, first triangular, last spiniform, first and second teeth directed forwards, last tooth directed obliquely outwards (Fig. 2A, B).

Ischium of third maxilliped rectangular, much longer than wide, with deep submedian, longitudinal sulcus; basis separated from ischium by distinct suture; merus squarish, medially depressed; exopod long, reaching to middle of margin of merus, with pronounced subdistal tooth on inner margin and long flagellum (Fig. 2C).

Chelipeds strongly asymmetrical, left larger; outer surfaces of both chelae smooth (Figs. 1, 2F). Merus with small but distinct subterminal spine on dorsal margin. Carpus with strong, sharp spine on inner distal margin; inner margin granulated (Fig. 1). Fin-

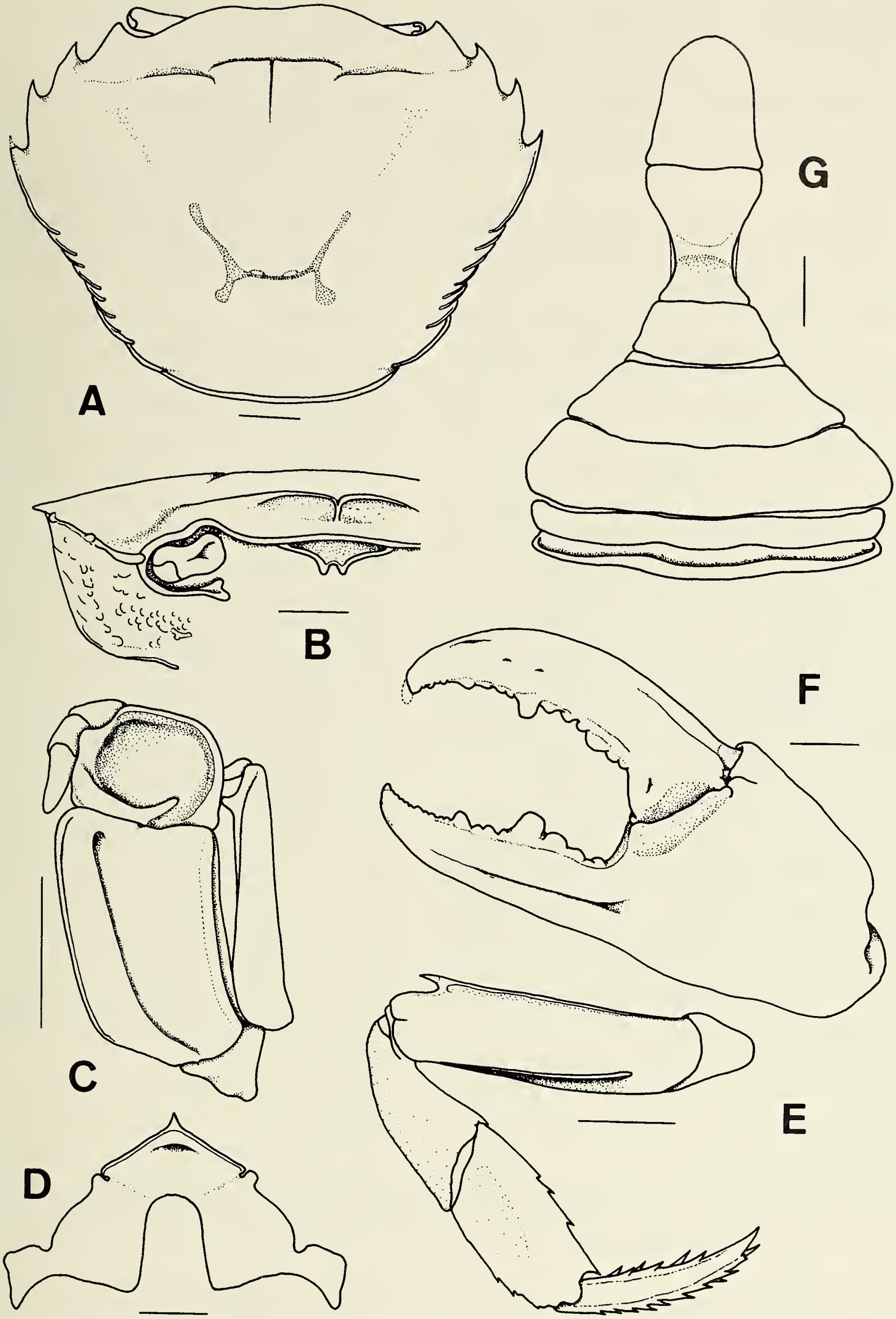

Fig. 2. *Somanniathelphusa pax,* new species. Holotype male, carapace 41.9 by 32.8 mm (ZRC). A, carapace; B, frontal view; C, left third maxilliped (hairs omitted); D, anterior sternites; E, last left ambulatory leg; F, enlarged (left) chela; G, abdomen. Scales = 5.0 mm.

gers of both chelae longer than palm, fingers of smaller chela not distinctly gaping when closed, with numerous denticles along cutting edges; fingers of larger chela strongly gaping when closed, cutting edges lined with several large and numerous smaller teeth (Fig. 2F).

Second pair of ambulatory legs longest. Merus with very strong, distinct dorsal subterminal spine (Fig. 2E).

Male abdominal cavity reaches an imaginary line joining anterior edges of bases of chelipeds (Fig. 2D). Suture between sternites 2 and 3 only present medially, lateral parts obscured; suture between sternites 3 and 4 very shallow, indistinct (Fig. 2D). Male abdomen distinctly T-shaped, telson broadly triangular, lateral margins gently concave, gradually converging towards rounded tip; segment 6 subequal in length to telson, strongly constricted at subproximal part, with low but distinct submedian tranverse ridge, length 1.2 times greatest width, distal width 1.3 times proximal width; segments 3–5 progressively more trapezoidal, segments 1 and 2 narrow (Fig. 2G).

G1 terminal and subterminal segments not demarcated (Fig. 3A–C); distal part slender, distal half gradually curving laterally outwards, tip bent laterally; basal part very broad, outer margin distinctly convex when viewed ventrally (Fig. 3D–F). G2 with very short distal segment, 0.07 times length of elongated basal segment (Fig. 3G).

Paratype female.—The paratype female is fully mature. One of its chelae is distinctly larger than the other, but the degree of enlargement of the major chela is not as pronounced as in the holotype male. The branchial regions of the female are distinctly inflated and appear swollen, much more than in the holotype male. In some of the large species of *Somanniathelphusa* (e.g., *S. bangkokensis* and *S. sexpunctata*), larger specimens generally appear to be less inflated than smaller ones. The holotype male of *S. pax* is distinctly larger than the female (carapace 41.9 by 32.8 mm against 34.8 by 26.6 mm). The paratype female agrees with the holotype male in all other non-sexual characters. The non-type specimens show some variation in the form of the frontal margin, from sinuous to almost straight.

Color.—Young males and females are beige to dull brown on all dorsal surfaces, the ventral surfaces being dirty white. Large males vary from brown to purple on the dorsal surfaces.

Discussion.—In characters such as cristae of the carapace, shape of the male abdomen and gonopods, *S. pax* clearly belongs to *Somanniathelphusa* (sensu Naiyanetr 1994) which occurs in China and Taiwan (Dai et al. 1975, Bott 1970, Ng & Dudgeon 1992). The carapace of *S. pax* is more rectangular compared to species like *S. sinensis* and *S. zanklon* which are more oval. The male abdominal segment 6 of *S. pax* is similar in shape to that of *S. sinensis, S. zanklon* and *S. falx,* but its telson is less triangular, with the distal part broader. Compared to *S. chongi,* the male abdominal segment 6 of *S. pax* is also proportionately less elongate (length to maximum width ratio 1.2 against 1.4). The deep and distinct longitudinal groove on the pollex of the enlarged male chela is diagnostic for *S. pax.* The G1s of *S. pax* however, differs markedly from all known congeners in having the tip bent laterally. In congeners, the tip is either straight, slightly folded laterally or hooked downwards (fide Wu 1935, Dai et al. 1975, Ng & Dudgeon 1992).

As for allied genera and species known from Vietnam, *S. pax* differs from *Esanthelphusa prolatus* in that the anterolateral margin of *E. prolatus* is more convex, with the smaller epibranchial teeth directed forwards (margin less convex in *S. pax,* with the epibranchial teeth relatively larger and the last tooth directed obliquely outwards), the outer surface of the pollex of the enlarged male chela is smooth, without a longitudinal groove (longitudinal groove distinct in *S. pax*) and the male abdominal segment 6 is relatively shorter (length to

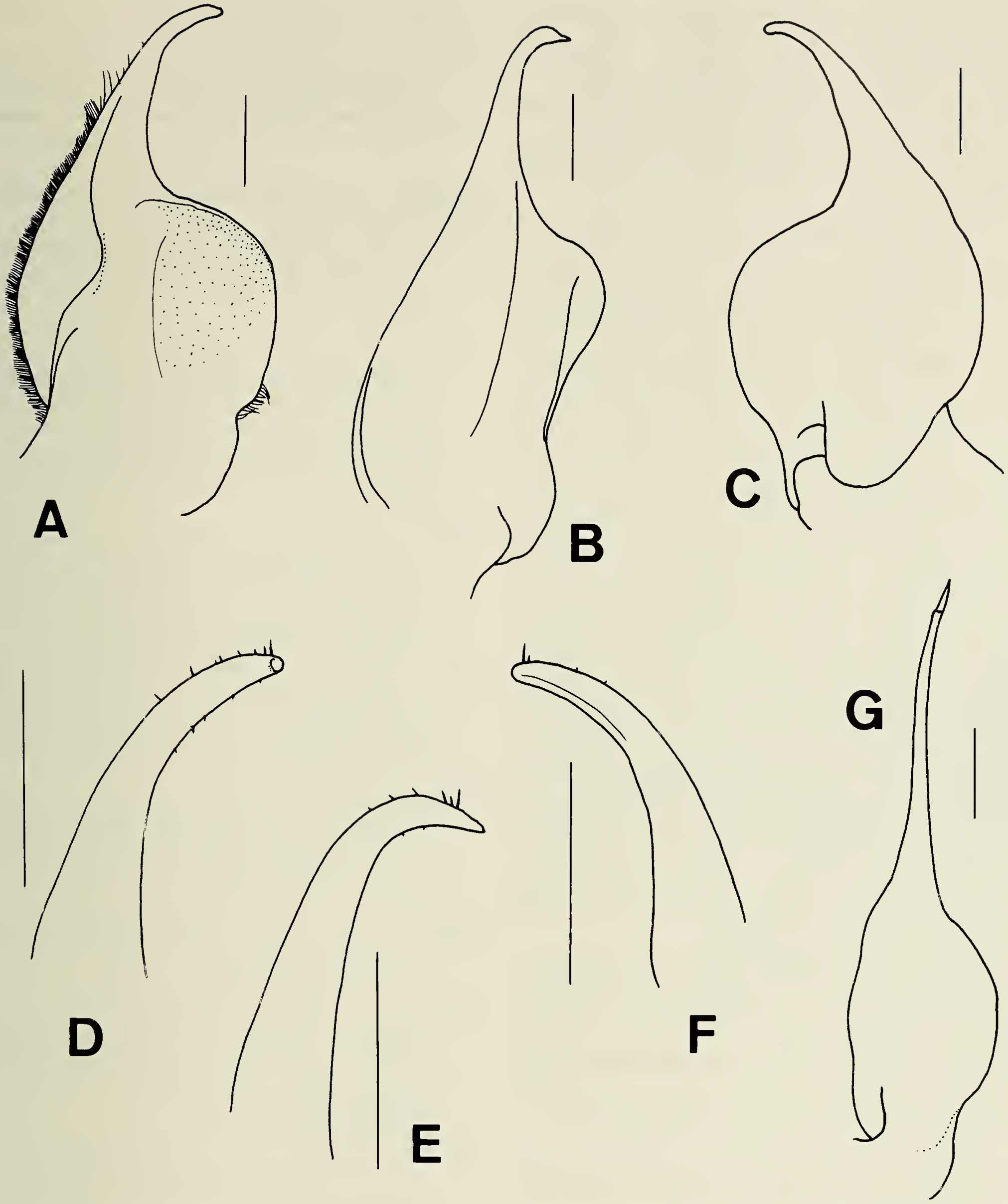

Fig. 3. *Somanniathelphusa pax,* new species. Holotype male, carapace 41.9 by 32.8 mm (ZRC). A–C, left G1; D–F, distal part of left G1; G, left G2. A, D, ventral views; C, F, dorsal views; B, E, ventro-marginal views. Scales = 1.0 mm.

maximum width ratio 0.9 against 1.2) with the distal width much wider than the proximal width (distal to proximal width ratio 1.6 in *E. prolatus,* 1.3 in *S. pax*) (fide Rathbun 1905:245, fig. 59, pl. XI fig. 4). The G1 of *E. prolatus* s. str. is not known.

The dorsal surface of the carapace of *Chulathelphusa neisi* is not only distinctly less convex than all other *Somanniathelphusa pax,* the distal male abdominal segments are not slender and there is no distinct constriction on segment 6 (length to maximum width ratio 1.0; distal to proximal width ratio 1.1) (cf. Rathbun 1905:249, fig. 61, pl. XI fig. 5). The first author has examined the G1 of *C. neisi,* and it is straighter, with the distal parts not curved or hooked, and the terminal segment distinctly demarcated compared to *S. pax.*

The type specimens of *S. pax* were obtained by the second author from a market in Hanoi which had almost certainly come from rice-fields near the city. The first author subsequently received additional specimens (non-types) from Hanoi and the species is apparently frequently sold in markets. The very low prices and abundance of the crabs strongly suggest that they came from the neighborhood of Hanoi. The collection of rice-field crabs for food is a common practice in Indo-China. The first author has observed this often in Thailand, and in every instance, the crabs had been collected from slow-flowing streams or rice-fields on the outskirts of the town and sold as a cheap source of protein. In Thailand, crabs are kept dried (the individuals often caked in mud) and can be kept alive for long periods provided they are kept cool (see Ng & Naiyanetr 1993:43). They are eaten in a variety of ways, but are usually fried with spices until they are crispy.

The study of the freshwater crab fauna of Vietnam is still very much in the exploration and survey stage. The number of taxa known is likely to increase substantially in the coming years as the country becomes more open to the scientific community.

Etymology.—The species name is derived from the Latin for peace. Used as a noun in apposition.

Acknowledgments

The first author is grateful to Anna Ursula Kara for passing the Vietnamese crabs to him for study and Phaibul Naiyanetr for information on *E. prolatus.* The study has been partially supported by a research grant (RP 900360) to the first author from the National University of Singapore.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(1):68–75. 1995.

A new species of *Goreopagurus* McLaughlin (Decapoda: Anomura: Paguridae) from the Pacific, and a comparison with its Atlantic counterpart

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Abstract.—*Goreopagurus garthi,* a new species of hermit crab, is described and illustrated. This Pacific representative of the heretofore monotypic, Atlantic genus *Goreopagurus* has necessitated minor emendations to the generic diagnosis. The similarities and differences between the two species are discussed.

Goreopagurus was erected by McLaughlin (1988) for *Pagurus piercei* Wass, 1963, a very distinctive western Atlantic species, known at the time of its original description from a single male specimen. When additional collections were critically examined, it became apparent that Wass' (1963) assignment of this species to *Pagurus* was incorrect. A suite of characters including the presence of a pair of pleopods, modified as gonopods, in females and a very short sexual tube on the right fifth coxa in males, phyllobranchiate gills, and highly distinctive chelipeds set *Goreopagurus* apart from all other members of the Paguridae.

Before publication of McLaughlin's (1988) paper, one of us (JH) had found several specimens in the collections of the Allan Hancock Foundation that bore a marked resemblance to *P. piercei.* Originally reported as *Pagurus* sp. (2) (Haig et al. 1970), they were subsequently cataloged into the collection simply as "genus?, sp. H." We have now had the opportunity to reexamine these specimens and confirm that they belong to *Goreopagurus.* McLaughlin's (1988) diagnosis, based exclusively on *G. piercei,* was rather restrictive. The discovery of *Goreopagurus garthi,* new species, necessitates minor emendations to the generic diagnosis.

One male and one female paratype have been deposited in the collections of the National Museum of Natural History, Smithsonian Institution (USNM). The holotype and remaining paratypes currently in the Allan Hancock Foundation (AHF), will eventually be housed in the Crustacea collection of the Natural History Museum of Los Angeles County (LACM). Comparative material of *G. piercei* from *Oculina* samples taken from Jeff's Reef, Florida, have been provided by the Harbor Branch Oceanographic Museum (HBOM). The length of the shield (SL), as measured from the tip of the rostrum to the midpoint of the posterior margin of the shield, is an indicator of specimen size. The symbols ♂, ♀, and ♀♀ refer to male, female, and ovigerous female respectively.

Goreopagurus McLaughlin, 1988

Emended diagnosis.—Eleven pairs of phyllobranch gills. Ocular acicles triangular, with strong submarginal spine; separated basally by basal width or more of 1 acicle. Antennal peduncle with supernumerary segmentation. Maxillule with internal lobe moderately well developed, with 1 stiff bristle; external lobe produced, not recurved.

Third maxilliped with well developed crista dentata and prominent accessory tooth; merus with or without dorsodistal spine. Sternite of third maxillipeds with or without small spine on either side of midline.

Right cheliped with chela very elongate, narrow; articulation with carpus generally perpendicular. Carpus strongly produced ventrally, dorsomesial margin weakly to greatly expanded. Left cheliped appreciably shorter than right; chela narrow, weakly triangular in cross-section, articulation with carpus perpendicular. Sternite of third pereopods with anterior lobe semisubovate, subquadrate or subrectangular. Sternite of fifth pereopods with 2 ovate or subcircular lobes. Fourth pereopods with propodal rasp consisting of 1 row of corneous scales; dactyl with or without preungual process.

Mature males with coxae of fifth pereopods generally symmetrical; vas deferens of right produced as short sexual tube, often directed laterally or posteriorly and sometimes partially obscured by posterior tuft of setae; coxa of left often with vas deferens slightly produced; with 3 unpaired uniramous or weakly biramous pleopods. Females with paired gonopores; well developed, paired first pleopods modified as gonopods; 4 unpaired pleopods, second to fourth with both rami well developed, fifth with endopod rudimentary or absent.

Abdomen flexed. Uropods asymmetrical. Telson with transverse suture; posterior lobes symmetrical or somewhat asymmetrical, separated by small median cleft; terminal margins oblique or straight, each armed with few to several small spines; lateral margins frequently delimited by narrow chitinous plate.

Goreopagurus garthi, new species
Figs. 1, 2, 3A, 4A

Pagurus, undescribed species (2): Haig et al. 1970:20.

Holotype.—1 ♂ (SL 2.27 mm), 29 mi S. of Punta Abreojos, west coast of Baja California, Mexico, "Velero IV" sta 1710-49, 95–102 m, 7 Mar 1949, LACM 49-55.9 (AHF 4926).

Paratypes.—West coast of Baja California, Mexico: 1 ♂ (SL 1.70 mm), 8 mi W of Isla Cedros, *Velero III* sta 1253-41, 117–119 m, 26 Feb 1941, LACM 41-33.20 (AHF 4135).—2 ♀♀ (SL 2.21, 2.30 mm), 29 mi S. of Punta Abreojos, *Velero IV* sta 1710-49 95–102 m, 7 Mar 1949, LACM 49-55.8 (AHF 4927.—2 ♂ (SL 1.31, 1.55 mm), 1 ♀ (SL 1.25), 1 ♀♀ (SL 1.37 mm), 8 mi W of Punta Redonda, *Horizon* sta A-11 Magbay Expedition, 106–116 m, 29 Jan 1964, LACM 64-237.1 (AHF 6416), USNM 267574.—1 ♂ (SL 1.76 mm), San Jaime Bank off Cabo San Lucas, *Velero III* sta 618-37, 137 m, 3 Mar 1937, LACM 37-19.16 (AHF 3717).

Description.—Shield (Fig. 1A) broader than long; anterior margins between rostrum and lateral projections somewhat concave; anterolateral margins sloping; posterior margin truncate; surface with scattered stiff setae. Rostrum acutely or obtusely triangular, terminating sharply or bluntly, and usually with slight, rounded keel. Lateral projections obtusely triangular or broadly rounded, with small submarginal spine or spinule.

Ocular peduncles usually as long as shield, stout or slightly constricted medially, and with 2 or 3 tufts of stiff setae; corneae usually slightly dilated. Ocular acicles acutely triangular, with strong submarginal spine; separated basally by at least basal length of 1 acicle.

Antennular peduncles overreaching corneae by ⅓ to ¾ length of ultimate segment. Ultimate segment with 1 or 2 long, stiff setae at dorsolateral distal margin and few scattered setae. Penultimate segment with few scattered setae. Basal segment with slender spine on lateral margin medially or distally.

Antennal peduncles equaling or overreaching ocular peduncles by nearly half length of ultimate segment. Fifth and fourth segments with few scattered setae. Third

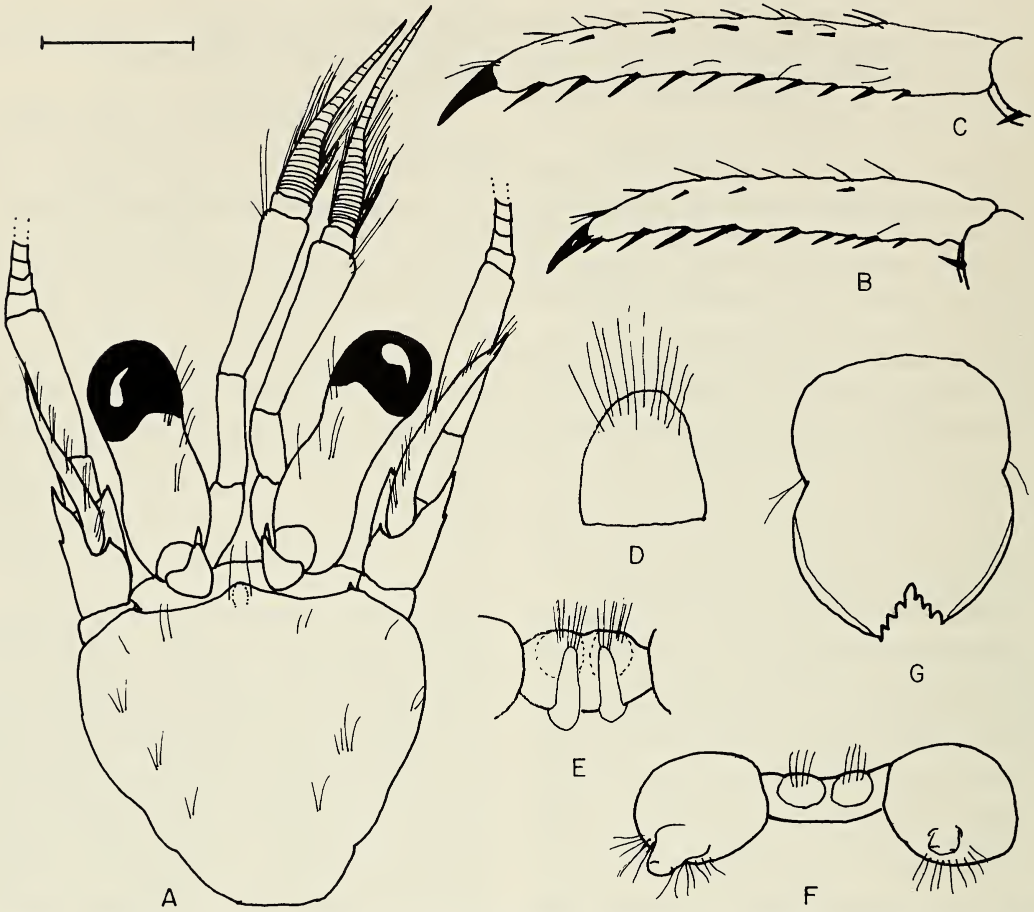

Fig. 1. *Goreopagurus garthi,* new species. A–D, G, Holotype, AHF 4926: A, shield and cephalic appendages; B, dactyl of second right pereopod (mesial view); C, dactyl of third right pereopod (mesial view); D, anterior lobe of sternite of third pereopods; E, sternite of fifth pereopods of female paratype (SL 2.3 mm), AHF 4927; F, coxae and sternite of fifth pereopod of male paratype, AHF 4135 (SL 1.7 mm); G, telson. Scale equal 1.0 mm (A–C), and 0.5 mm (D–F).

segment with strong, acute spine at ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in acute spine and usually with strong spine on lateral margin; dorsomesial distal angle with small spine. First segment unarmed. Antennal acicle long, reaching middle of ultimate peduncular segment, arcuate, terminating in small spine; mesial surface with row of tufts of stiff setae. Antennal flagella long; articles each usually with 1 or 2 short (≤length of 1 article) and 1 or 2 minute setae.

Third maxilliped with 1–3 tooth-like spines on basis; ischium with single accessory tooth on well developed crista dentata; merus with spine at dorsodistal margin. Sternite of third maxillipeds with tiny spinule on either side of midline.

Right cheliped (Figs. 2A, B; 3A, 4A) very elongate; palm, fixed finger and dactyl slender, somewhat dorsoventrally compressed. Dactyl ½ to ⅘ length of palm; cutting edge with 3 moderately prominent calcareous teeth in proximal ⅔, row of small corneous teeth in distal third, terminating in small corneous claw; dorsolateral margin with row of small spines or spinules or spinulose tubercles, increasing slightly in size distally, dorsal surface somewhat elevated in midline, unarmed or with single or double row of very small spinules. Palm slightly shorter than carpus; dorsomesial and dorsolateral margins each with row of very small spinules, increasing somewhat in size distally on fixed finger; dorsal surface often with row of very small spinules adjacent to dorsomesial margin, and additional scattered spinules, particularly numerous and more prominent on fixed finger; cutting edge of fixed finger with 2 moderately strong calcareous teeth in proximal half, row of small calcareous teeth in distal half, terminating in corneous claw, often worn. Carpus longer than merus, strongly produced ventrally; dorsomesial margin somewhat expanded in proximal half, armed with row of small spine, strongest proximally, dorsal surface with numerous short, transverse rows of small tubercles or spinules, dorsolateral margin usually not delimited but with transverse ridges extending onto mesial face dorsally; ventromesial and ventrolateral margins each with row of small spines or spinules, strongest on distal half of ventrolateral margin. Merus subtriangular; dorsal surface with few to numerous transverse ridges and stiff bristles; ventromesial and ventrolateral margins each with row of spines, strongest and more acute on ventrolaterally. Ischium with row of small spinules on ventromesial margin and short row of stiff bristles on lateral face ventrally.

Left cheliped (Fig. 2C, D) long and slender, but not reaching much beyond proximal margin of palm of right; dactyl and fixed finger weakly arched ventrally. Dactyl ¼ to ½ greater than length of palm; cutting edge with row of corneous teeth, terminating in small corneous claw; dorsal surface unarmed or with few tiny spinules proximally. Palm ½ to ⅔ length of carpus; dorsolateral margin with slight ridge, unarmed or with row of minute tubercles becoming slightly larger and somewhat more acute on fixed finger, dorsal surface strongly elevated in midline and armed with row of small spinules, becoming irregular on fixed finger, dorsal surface often with additional scattered minute spinules, particularly mesially and on fixed finger, dorsomesial margin not usually delimited, ventral surfaces with scattered tufts of long setae; cutting edge of fixed finger with row of very small calcareous teeth, interspersed distally by thin, corneous teeth. Carpus only slightly shorter to slightly longer than merus; dorsal surface somewhat flattened, dorsolateral margin with row of very small tubercles or spinules, dorsomesial margin with few tubercles or transverse ridges and stiff bristles extending onto mesial face dorsally, distal margin often with 1–3 small, blunt spinules; ventrolateral margin with row of small spines, ventromesial margin with few very small spinules. Merus subtriangular; dorsal surface with few short, transverse rows of stiff bristles; ventromesial margin with small spinules in proximal half and long stiff setae distally, ventrolateral margin with few spinules proximally and 2 or 3 acute spines distally. Ischium unarmed, but with several stiff bristles on lateral face ventrally.

Ambulatory legs (Figs. 1B, C; 2E–G) (third left pereopod missing in holotype), generally similar from left to right. Dactyls of second pereopods shorter than third, but both only slightly shorter to slightly longer than propodi; dorsal margins each with sparse row of stiff bristles, ventral margins each with row of 8–10 corneous spines, lateral faces unarmed, mesial faces each with row of corneous spinules dorsally, more numerous on third. Propodi 1 and ⅓ to 1 and ½ times length of carpi; each with 1 or 2 corneous spinules at ventrodistal angle and row of widely-spaced corneous spinules on ventral margin, dorsal surfaces each with row of stiff bristles. Carpi each with small spine at dorsodistal margin, few stiff setae arising from low protuberances on dorsal surface and 1 or 2 stiff setae on ventral mar-

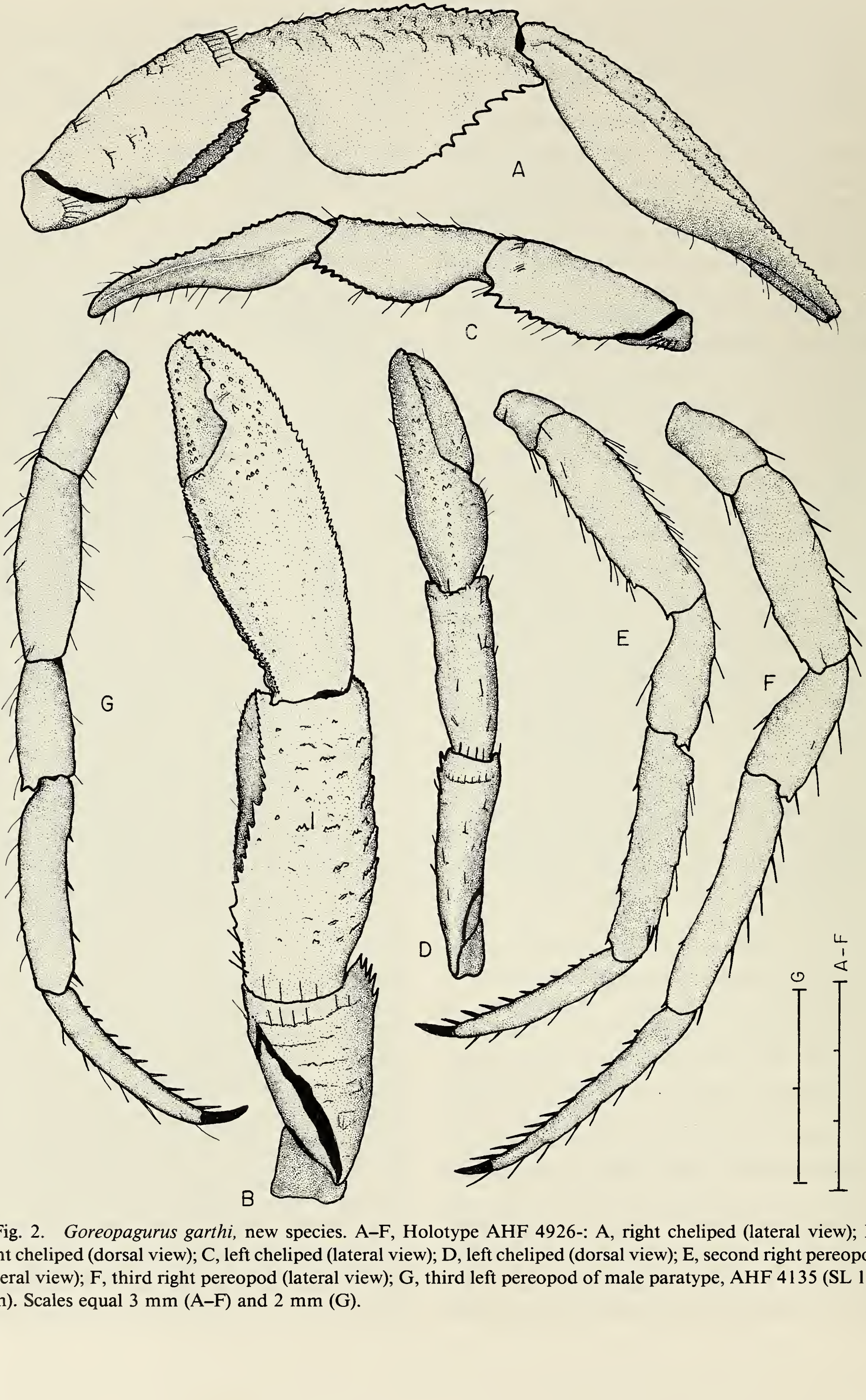

Fig. 2. *Goreopagurus garthi,* new species. A–F, Holotype AHF 4926-: A, right cheliped (lateral view); B, right cheliped (dorsal view); C, left cheliped (lateral view); D, left cheliped (dorsal view); E, second right pereopod (lateral view); F, third right pereopod (lateral view); G, third left pereopod of male paratype, AHF 4135 (SL 1.7 mm). Scales equal 3 mm (A–F) and 2 mm (G).

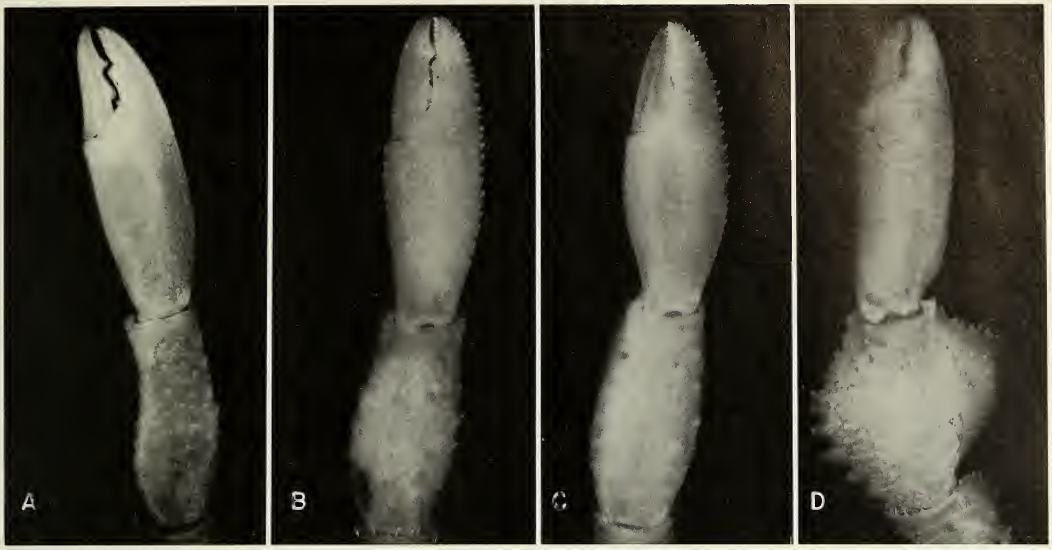

Fig. 3. Right cheliped (dorsal view): A, *Goreopagurus garthi,* new species, ovigerous female, AHF 4135 (SL = 2.3 mm); *Goreopagurus piercei* (Wass), B, ovigerous female, HBOM 089:06382 (SL = 1.8 mm); C, immature male, HBOM 089:06382 (SL = 1.4 mm); D, mature male, HBOM 089:06379 (SL = 1.6 mm). Magnifications equal: A, 10.4×; B, 19.0×; C, 19.8×; D, 11.0×.

gin medially. Meri with transverse, short ridges and stiff bristles or setae on dorsal surfaces, tufts of stiff setae and occasionally 2 or 3 often spinulose protuberances or small spinules on ventral surfaces, ventrolateral distal angles each with acute spine, appreciably smaller and sometimes absent on third pereopods. Ischia unarmed but with few stiff setae or bristles.

Sternite of third pereopods with semisubovate anterior lobe (Fig. 1D) provided with stiff bristles on anterior margin. Fourth pereopods with small preungual process at base of claw. Females with 2-segmented pleopods modified as gonopods (Fig. 1E) on first abdominal somite; fifth pleopod with endopod rudimentary. Males with quite short sexual tube (Fig. 1F) on coxa of right fifth pereopod (damaged in holotype), and with or without very short left sexual tube. Telson (Fig. 1G) with transverse suture; posterior lobes separated by shallow median cleft, terminal margins oblique, each with 3–5 small spines, outermost usually largest, lateral margins delimited by narrow chitinous band.

Etymology.—The specific name is given in honor of the late Dr. John S. Garth, in recognition of his many years of contributions to eastern Pacific carcinology.

Distribution.—At present known only from the outer coast of Baja California, Mexico, from Isla Cedros in the north to Cabo San Lucas in the south; 95–119 m.

Remarks.—*Goreopagurus garthi,* like *G. piercei,* is a very small species, with females mature (ovigerous) at shield lengths of only slightly more than 1 mm. However, clearly *G. garthi* is the larger of the two. McLaughlin (1988) reported a maximum shield length of 1.8 mm in 171 specimens of *G. piercei* examined, including the holotype. In our very small sample of *G. garthi,* shield lengths ranged from 1.2 to 2.3 mm. McLaughlin remarked that shield length in *G. piercei* was somewhat misleading, because of the tendency of the shield to increase in breadth with overall increase in animal size.

Fig. 4. Right cheliped (lateral view): A, *Goreopagurus garthi,* new species, male holotype, AHF 4926 (SL = 2.3 mm); *Goreopagurus piercei* (Wass), B, immature male, HBOM 089:06382 (SL = 1.4 mm); C, mature male, HBOM 089:06379 (SL = 1.8 mm). Magnifications equal: A, 12.6×; B, 16.7×; C, 10.8×.

Since we had no specimens with shield lengths less than 1.0 mm, we had not seen this trend in *G. garthi.* In both males and females, the shield was consistently broader than long.

McLaughlin noted marked sexual dimorphism in *G. piercei,* exhibited particularly by development of the carpus of the right cheliped in males. In mature females and small males (Fig. 3B, C) there was only a slight tendency for the dorsal surface of the carpus to be expanded mesially. In mature males, this expansion was pronounced (Fig. 3D). In contrast, males and females of *G. garthi* exhibited very similar, obvious, but relatively weak, expansion in the carpus of the right cheliped (Figs. 2B, 3A). The ventral inflation of the carpus is conspicuous in both species (Figs. 2A, 4A–C); however, in *G. piercei* it is much less accentuated in small males.

Development of the male sexual tubes was not as pronounced in *G. garthi* as in *G. piercei* (cf. McLaughlin 1988:fig. 2f). Given the overall larger size of the Pacific species, it is quite possible that the males of *G. garthi* that we have examined were not yet fully mature. The sexual tubes of the male from Isla Cedros (Fig. 1F) were the most developed of all the males in our samples. The right coxa of the holotype male was damaged, thus the development of the sexual tube could not be ascertained; however, there was only a vestige of a left sexual tube in this specimen. If these males of *G. garthi* were not sexually mature, it is possible that in mature males sexual dimorphism of the carpus of the right cheliped might be manifest in the Pacific species as well.

Whether or not marked sexual dimorphism in the carpus of the right cheliped proves to be an attribute of *Goreopagurus,* this is a very distinctive genus. The minor emendations made to the generic diagnosis pertain to such interspecifically variable characters as the presence or absence of spines on the dorsodistal margin of the merus and sternite of the third maxillipeds, and the shape of the sternite of the third pereopods. Although McLaughlin (1975) and

Lemaitre et al. (1982) found the median projection of the sternite of the third maxilliped to be a diagnostic character for the *provenzanoi* group of *Pagurus,* the presence or absence of a spine on either side of the midline is variable (e.g., McLaughlin & Gunn 1992). Squires (1964) and McLaughlin (1974) both found the shape of the sternite of the third pereopods a generally reliable character for separating closely related species; however, at the generic level it is not as dependable (e.g., McLaughlin & Haig 1989). The dactyls of the ambulatory legs were reported as relatively short in *G. piercei.* They are of generally similar length per animal size in *G. garthi.*

Acknowledgments

We acknowledge, with thanks, the assistance of Paula Mikkelsen, Harbor Branch Oceanographic Museum, in the loan of comparative material of *Goreopagurus piercei.* This is a scientific contribution from the Shannon Point Marine Center.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(1):76–83. 1995.

Epilobocera wetherbeei, a new species of freshwater crab (Decapoda: Brachyura: Pseudothelphusidae) from Hispaniola

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Abstract.—*Epilobocera wetherbeei,* a new species of pseudothelphusid crab, is described from the Dominican Republic. The species can be easily distinguished from other species of *Epilobocera* by its small size, absence of anterolateral spinulation and characters of the first male gonopods. SEM microphotographs of the first and second male gonopods of *E. wetherbeei, E. sinuatifrons, E. haytensis* and *E. gertraudae* are provided. The apex of the second male gonopod in all species of *Epilobocera* studied is hollow, transversely truncate, with a prominent internal rib provided with spines. These characters distinctly separate *Epilobocera* from species in the subfamily Pseudothelphusinae where the gonopodal apex is spoon-shaped and provided with long setae. The new observations are incorporated into amended diagnoses of the subfamilies Epilobocerinae and Pseudothelphusinae.

The genus *Epilobocera* Stimpson, 1860, comprises six species of freshwater crabs restricted to the Greater Antilles and some nearby islands: *E. sinuatifrons* A. Milne Edwards, 1866, inhabits Puerto Rico and Saint Croix Island; *E. haytensis* Rathbun, 1893, is confined to Hispaniola; Cuba has three species, *E. armata* Smith, 1870, *E. cubensis* Stimpson, 1860, and the troglobic *E. gertraudae* Pretzmann, 1965; *E. gilmani* (Smith 1870), possibly conspecific with *E. cubensis,* has been described from Isla de Pinos. One species, *E. granulata* Rathbun, 1893, was described from an immature male labeled "West Indies" and the first male gonopod was not illustrated. Chace & Hobbs (1969) stated that "the material is now virtually macerated" and suggested that "In view of the immaturity of these specimens and the lack of specific type-locality, the species may remain a species *inquirenda* indefinitely unless it can be shown to be a synonym of *E. armata.*" The genus has been the object of recent revisions by Chace & Hobbs (1969), Pretzmann (1972) and Rodríguez (1982).

Due to the accessibility and small area of the Greater Antilles, their freshwater fauna is fairly well known. For this reason it has been noteworthy to find a new species of freshwater crab in the material recently collected by Dr. David Wetherbee during his explorations of the Cordillera Central of Hispaniola.

Materials and Methods

The materials used for the description of *Epilobocera wetherbeei* were collected as two separate lots. The first lot included the male holotype and one juvenile specimen collected on 2 Oct 1990, and sent to the junior author in the National Museum of Natural

History, Smithsonian Institution, Washington (USNM). The specimens were received in semi-dry condition, and the coloration was carefully noted at the time of reception (see "Color"). The specimens were subsequently placed in alcohol and shipped to the senior author for further study. The second lot was collected on 12 Jul 1991, at the type locality, and was shipped to the senior author by Dr. Wetherbee. The lot included two males and five ripe or ovigerous females. These specimens were in poor condition and almost all pereiopods and some carapaces have become dislocated. The specimens are deposited at the USNM and the Reference Collection of the Instituto Venezolano de Investigaciones Científicas, Caracas (IVIC).

Other abbreviations used are cb for carapace breadth, and cl for carapace length.

For comparative purposes we have studied the first and second gonopods of other species of *Epilobocera* deposited in IVIC, namely *E. sinuatifrons,* 1 male, cl 55.6 mm, from El Yunque, Coca Falls, Luquillo, Puerto Rico, collected 5 Feb 1972; *E. haytensis,* 1 male cl 43.2 mm, from Barahona, Dominican Republic, collected 3 Feb 1967; *E. gertraudae,* 1 male cl 31.5 mm, from Cueva Superior Majaguas, Sierra de San Carlos, Pinar del Rio, Cuba, collected 2 Aug 1977.

The first and second gonopods of the holotype of *E. wetherbeei* and all the species recorded above were dried, coated with platinum, and photographed on a scanning electron microscope Hitachi S-500. Point-drying was not used due to the extreme brittleness of the material. For the gonopods of *E. armata* and *E. cubensis* we have relied on drawings and notes made on the material already reported by Rodríguez (1982).

Subfamily Epilobocerinae Smalley, 1964

Genus *Epilobocera* Stimpson, 1860

Epilobocera wetherbeei, new species

Figs. 1, 2A, B, 3A, 4A

Material.—Rio Magua, tributary of Rio Mao, Sierra Platicos, northern slopes of the Cordillera Central, near the water divide, Provincia Santiago, Dominican Republic, at waterfall, 2300 m alt., 2 Oct 1990, leg. David Wetherbee, 1 male holotype, cl 16.5 mm, cb 26.6 mm, 1 juvenile (USNM).—Same data, 12 Jul 1991, 1 male paratype, cl 15.0 mm, cb 23.5 mm (IVIC), 1 male, broken carapace, cl approximately 12.5 mm, cb approximately 20.1 mm; 4 ovigerous female paratypes, cl 14.7, 15.5, 16.1 and 16.8 mm, cb 24.6, 25.8, 25.7 and 28.1 mm, 1 adult female broken carapace cl 14.2 mm, cb approximately 24.0 mm (USNM).

Description.—Carapace wide (cb/cl = 1.61 in holotype), strongly convex on antero-posterior axis. Cervical groove absent, only in female cl 15.5 mm indicated by thin line on left side of carapace. Antero-lateral margin without conspicuous depression behind antero-external angle, entire or slightly festooned on anterior portion, with occasional small papillae in holotype and male paratype, smooth or with 12 to 16 poorly-defined papillae in females. Postfrontal lobes absent, their position indicated only by rounded scars; median groove thin and shallow, obsolescent. Front lacks upper border, but surface of carapace in this area rounded off to lower margin. Lower margin clearly visible in dorsal view, slightly arched; strongly sinuous in frontal view. Surface of carapace smooth and polished, with regions not marked. No tooth present at aperture of efferent branchial channel.

Largest cheliped elongated, ischium overreaching by ¾ of its length margin of carapace. Palm moderately inflated, lower margin of palm and fixed finger sinuous; fingers arched, widely gaping. Walking legs slender, ischium of third pair 4.7 as long as wide. Third maxilliped with merus wide, antero-lateral border evenly rounded; exopod devoid of flagellum, overreaching ischium of endognath, its tip rounded, provided with plumose setae.

First male gonopod long and slender. Margin (sensu Smalley 1964a) progressively twisted dextrally, its middle portion direct-

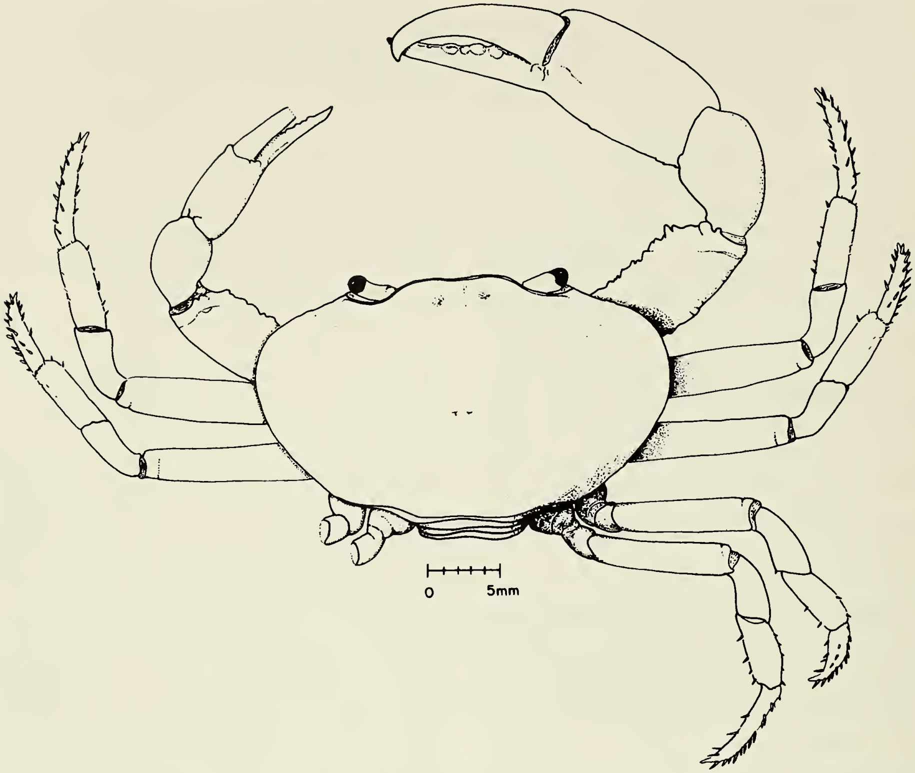

Fig. 1. *Epilobocera wetherbeei,* new species, holotype male, dorsal view of carapace and pereiopods.

ed mesially and its apical portion directed to cephalic side. Margin developed distally into strong recurved mesial lobe. Apex club shaped; bulging lateral process ("globulus" sensu Pretzmann 1972) with 7 strong hooked spines; finger-like caudal process ("nasus" sensu Pretzmann 1972) devoid of spines, apex with crenulations on inner side; mesial process ("caudaler Kamm" sensu Pretzmann 1972) consists of 5 spines disposed in comb-like structure directed externally; intermediate plate ("Querkamm" sensu Pretzmann 1972) with 5 slender spines; cephalic margin with few tiny proximal papillae, ending mesially in acute angle (broken in our SEM illustration of Fig. 3a). Second male gonopod straight, apex hollow, transversely truncate, prominent internal rib provided with spines.

Color.—According to field notes taken by the collector, the color in live specimens "varies from brown in some to orange. Orange specimens have maroon (reddish purple) walking legs and white claws." In the holotype specimen preserved in alcohol the color is as follows. Overall color carapace salmon pink. Walking legs lighter. Chelipeds still lighter, buff, articular membranes between merus and carpus, between carpus and propodus, and at base of dactyl, salmon pink and contrasting with buff of articles; membrane at either end of carpus darker than those at base of dactyl; membranes of major right chela darker than those of minor (left).

The fifth left leg is detached; articular membranes not colored on this or any other of the walking legs. Underside of the walking legs only slightly lighter in color than other sides.

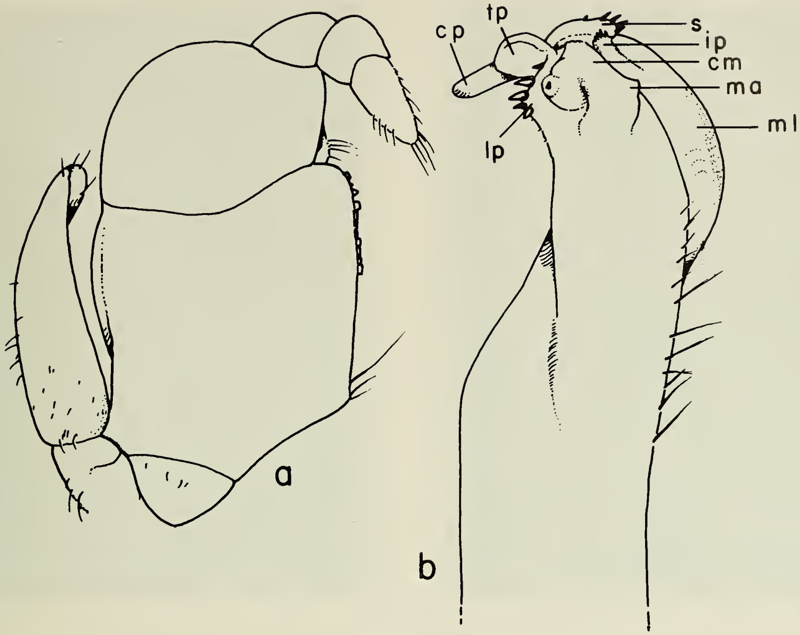

Fig. 2. *Epilobocera wetherbeei,* new species, holotype male: a, third maxilliped, right; b, apical portion of left first gonopod, cephalic view. ml, mesial lobe; lp, lateral process; cp, caudal process; s, spines of mesial process; ip, intermediate plate; cm, cephalic margin; ma, mesial angle of cephalic margin; tp, terminal process.

Underparts of body lighter than dorsum, but flush of salmon pink on sternal plate between chelipeds and third maxillipeds, with similar color on exposed articles of third maxilliped, pterygostomian and subhepatic regions. Abdomen not salmon pink, but of somewhat darker hue than adjacent sternites to each side.

Size.—The species is small for the members of the genus. Our largest male has a cl 26.6 mm, and females reach maturity at cl 24.6 mm.

Remarks.—The small size distinguishes this species from all others in the genus; in fact *Epilobocera sinuatifrons* and *E. haytensis,* are among the largest Pseudothelphusidae on record (cb 103.3 mm and 100.4 mm, Rodríguez 1982). The largest specimens recorded for *E. armata* and *E. cubensis* have a cb of 85.2 mm and 84 mm, respectively (Rodríguez 1982). The specimen of *E. gertraudae* examined by us has a cb of 53.8 mm. The absence of teeth on the antero-lateral margin and the smoothness of carapace characteristic of *E. wetherbeei* are only observed in *E. cubensis,* but while in this last species the margin has some rudimentary papillae, in *E. wetherbeei* it has none. The coloration observed in this species has not been reported for other *Epilobocera.*

The characteristic tooth present at the aperture of the efferent branchial channel in other species of *Epilobocera* (see Rodríguez 1982, fig. 3h–l), and which can be clearly seen through the channel aperture, is missing in this species.

The most important differences from other species are found in the apex of the first gonopods, as can be observed by the illustrations of the appendages of other species presented in figure 3 and the illustrations of the gonopods of *E. armata* and *E. cubensis* given by Chace & Hobbs (1969) and Rodríguez (1982). The strong mesial lobe of *E. wetherbeei* is found also in *E. gertraudae.*

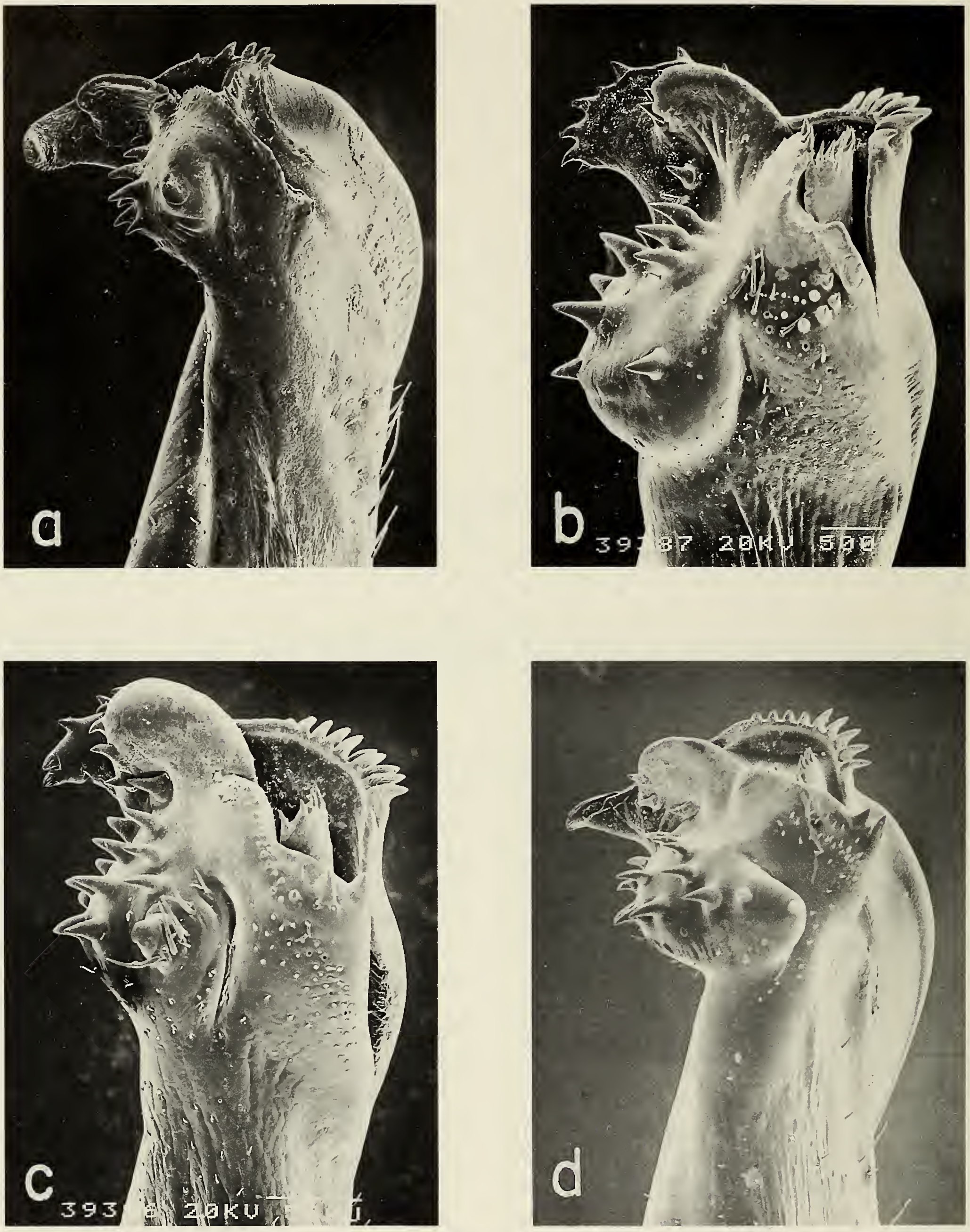

Fig. 3. Apical portion of left first gonopod: a, *Epilobocera wetherbeei,* new species, holotype; b, *E. sinuatifrons*; c, *E. haytensis*; d, *E. gertraudae.* d at same scale as c.

The number of strong spines on the bulging lateral process of the different species are: in *E. wetherbeei* 7, *E. sinuatifrons* 14–16, *E. haytensis* 12, *E. armata* 13–14, *E. cubensis* 8, and *gertraudae* 12. The finger-like caudal process is devoid of spines in *E. wetherbeei,* but armed with strong spines in *E. sinuatifrons* and *E. haytensis,* and with

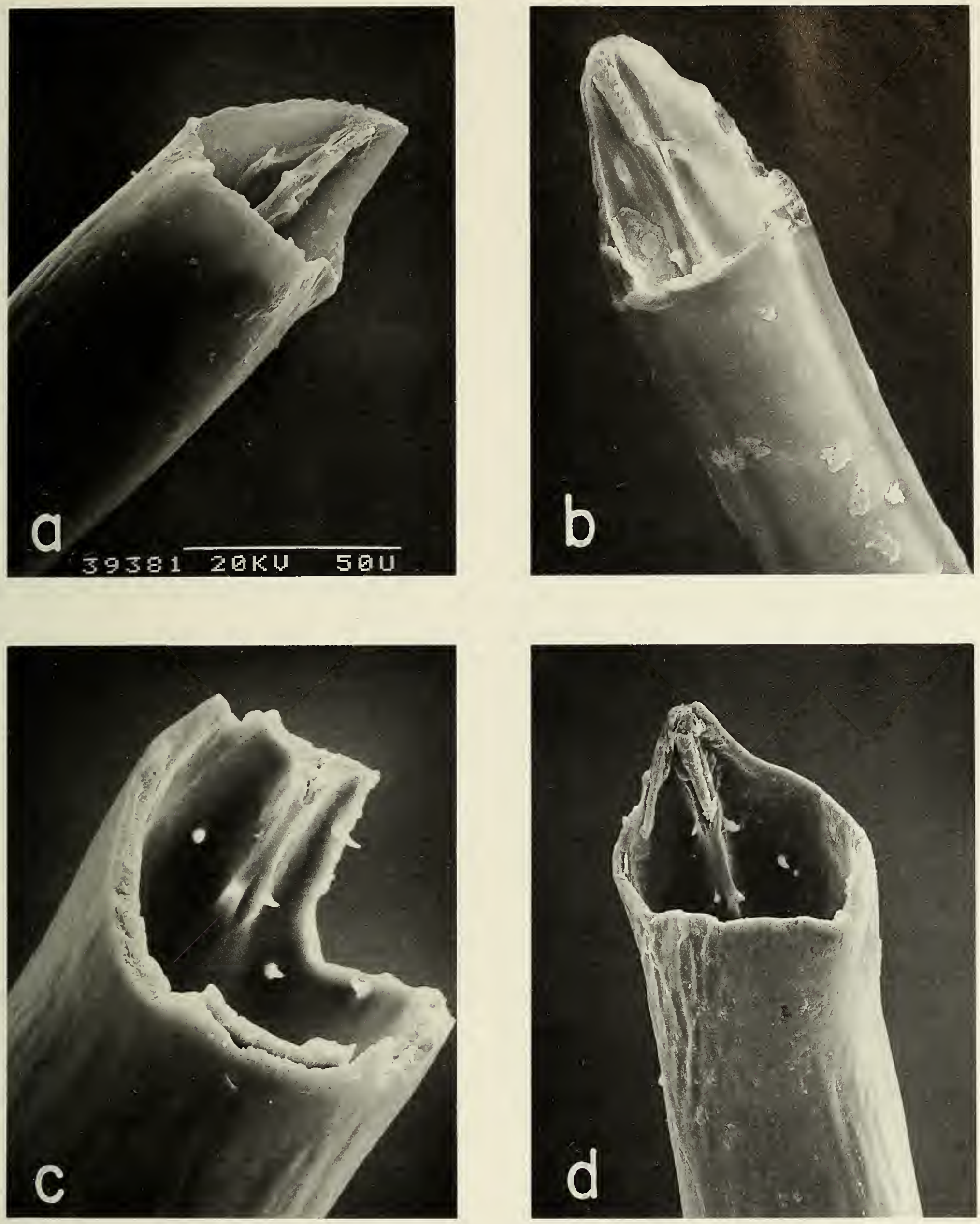

Fig. 4. Left second gonopod, detail of apex: a, *Epilobocera wetherbeei,* new species, holotype; b, *E. sinuatifrons*; c, *E. haytensis*; d, *E. gertraudae.* b, c, and d at same scale as a.

small spines in *E. armata, E. cubensis* and *E. gertraudae.* The number of spines on the mesial process in the different species are: in *E. wetherbeei* 5, *E. sinuatifrons* 7, *E. haytensis* 9, *E. armata* 9, *E. cubensis* 6, *E. gertraudae* 9. The terminal process has more than 3 spines in *E. sinuatifrons* and *E. haytensis*; in *E. armata, E. cubensis* and *E. gertraudae* there are only 2 or 3 spines on the cephalic side; in *E. wetherbeei* the process is devoid of spines. The intermediate plate has approximately the same form and number of spines in all the species. The cephalic margin in *E. wetherbeei* has a few tiny papillae proximally; in *E. haytensis* these papillae are stronger, disposed in a double row which extends through the length of the margin, in *E. armata, E. cubensis,* and *E. gertraudae* there are a few small spines; and in *E. sinuatifrons* this margin is produced into 6 long spines. The mesial angle of the cephalic margin is unarmed in *E. wetherbeei*; while it has two strong spines in all other species.

The apex of the second male gonopod in all species of *Epilobocera* is hollow, transversely truncate, with a prominent internal rib provided with spines. In some specimens can be observed a very thin membrane which prolongs the apex and which is lost during preparation of the appendage for scanning microscopy. The morphology of the apex of *Epilobocera* distinctly differs from all other species of Pseudothelphusidae where the gonopodal apex is spoon shaped and provided with long setae (Rodríguez & Suárez 1994). This character should be incorporated into the diagnoses of the subfamilies Epilobocerinae and Pseudothelphusinae, as follows.

Epilobocerinae Smalley, 1964b (caract. emend.): Pseudothelphusidae with apex of first gonopod bearing both a group of apical spines surrounding aperture of spermatic channel, and also large scattered spines; apex of second male gonopod hollow, transversely truncate, with prominent internal rib provided with spines.

Pseudothelphusinae Ortmann, 1893 (caract. emend.): Pseudothelphusidae with apex of first gonopod armed with a distinct group of apical spines surrounding aperture of spermatic channel; apex of second male gonopod spoon shaped and provided with long spines.

Etymology.—The species is named in honor of Dr. David K. Wetherbee, who collected the type material.

Common name.—The species is locally known as "Piñita."

Acknowledgments

We thank Dr. David K. Wetherbee for the opportunity to study this interesting species. SEM photographs were taken by Mr. Héctor Suárez.

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Alpheus angulatus, a new species of snapping shrimp from the Gulf of Mexico and northwestern Atlantic, with a redescription of *A. heterochaelis* Say, 1818 (Decapoda: Caridea: Alpheidae)

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Abstract.—Two species of the Edwardsii-group of snapping shrimp, *Alpheus heterochaelis* Say and *A. estuariensis* Christoffersen, have been recorded from coastal estuarine habitats of the Gulf of Mexico and Atlantic coasts of the United States. A new species, *A. angulatus,* has been discovered to inhabit these habitats across this range and is described and illustrated. The new species is morphologically similar to *A. armillatus,* the latter being a tropical species. A redescription with illustrations of *A. heterochaelis* is also provided herein.

The Edwardsii species group of *Alpheus* consists of at least 10 western Atlantic species (Chace 1972; Christoffersen 1979, 1984; Williams 1984; Abele & Kim 1986), of which *Alpheus heterochaelis* Say, 1818, is the most abundant and widely distributed. *Alpheus heterochaelis* was originally described from Amelia Island, Nassau County, Florida, and has been reported to range from the lower Chesapeake Bay to Aransas County, Texas, Cuba, Curaçao, Surinam, and possibly to São Paulo, Brazil (Chace 1972, Williams 1984).

A variety of studies have been done concerning the biology of *A. heterochaelis* (for example, Wilson 1903, Nolan & Salmon 1970, Knowlton 1973, Conover & Miller 1978, Mellon & Stephens 1978). Despite the abundance of studies on *A. heterochaelis,* the geographic limits and the systematic status of this species remain problematic. Based on apparent misidentifications of West Indian and Brazilian specimens, Chace (1972) questioned the occurrence of *A. heterochaelis* south of Surinam. Knowlton (1973) noted differences in egg size between laboratory reared *A. heterochaelis* from North Carolina and south Florida, and proposed that *A. heterochaelis* comprised two or more species. From a reevaluation of *Alpheus* inhabiting shallow-estuarine environments of the western Atlantic, Christoffersen (1984) suggested the existence of a species complex, and described a new species, *A. estuariensis* (holotype from the Rio Potengi estuary, Rio Grande do Norte, Brazil), ranging from the east coast of Florida into the Gulf of Mexico from Mississippi to Texas; Cuba; Dominican Republic; Trinidad; Curaçao; and from Ceará to Paraná, Brazil. Christoffersen (1984) further concluded that the *Alpheus* occurring in the northern Gulf of Mexico represents *A. estuariensis,* and described the range of *A. heterochaelis* to be from North Carolina to Paraíba, Brazil. However, using Christoffersen's (1984) key, specimens from Galveston were identified by the author as *A. heterochaelis.* Thus, plus a reexamination of museum specimens of *A. estuariensis* from the northern Gulf of Mexico suggest the existence of taxonomic ambiguity concerning the Edwardsii group of *Alpheus* from the coastal waters of the Gulf of Mexico and northwestern Atlantic.

An assessment of allozymic variation of specimens of *Alpheus* from Texas revealed the existence of two discrete and markedly different gene pools (McClure & Greenbaum 1994). Additional allozymic data (unpublished) indicate that these forms are sympatric throughout the northern Gulf of Mexico and Northwestern Atlantic coasts as far north as Beaufort, North Carolina. The present study was designed to provide morphological descriptions and identifications of the two electrophoretically identified species.

Materials and Methods

Snapping shrimps were collected at low tide by dip net in intertidal and shallow subtidal habitats consisting of sand or mud bottoms covered with oyster clumps or rocks. Shrimps were collected in coastal waters from south Texas to North Carolina (see Appendix for localities). Shrimps were stored at −80°C to fully preserve color patterns. Starch-gel electrophoresis (McClure & Greenbaum 1994) was used to sort the individuals into discrete electromorphic classes. Morphological characters were then assessed and compared with museum material and descriptions in the literature. Total Length (TL) of specimens is the combined measurements of the carapace, abdominal, and telson lengths.

Museum specimens of *A. heterochaelis, A. estuariensis, A. nuttingi,* and *A. armillatus* were obtained from the following institutions: Marine Research Division, Florida Department of Natural Resources, St. Petersburg, Florida (FBSC); Marine Environmental Sciences Consortium, Tuscaloosa, Alabama (MESC); Texas A&I University, Kingsville, Texas (TAI); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Muséum national D'Histoire naturelle, Paris, France (MNHN); Lamar University collection, Beaumont, Texas (LU). The original type material of *A. heterochaelis* and *A. armillatus* is not available; it is likely that the specimens have been lost. As the only detailed descriptions of *A. heterochaelis* are from the Carolinas (Christoffersen 1984), comparisons to this species were from material from the type locality and from the Carolinas. For *A. armillatus,* specimens from the type locality (Antilles) were used as a reference. Type material of the two species described here have been deposited in the USNM.

Alpheus angulatus, new species
Figs. 1, 2

Crangon armillatus.—Hay & Shore, 1918: 386, fig. 9. (not *Alpheus armillatus* Milne-Edwards, 1837).
Alpheus estuariensis.—Christoffersen, 1984: 191 (in part, see discussion).
Alpheus armillatus.—Chace, 1972:62 (in part, see discussion).

Holotype.—Male, 28 mm TL, on mud under rocks and rubble, South Padre Island, Texas, Laguna Madre just north of Brazos-Santiago Pass, coll. M. K. Wicksten, 4 Jul 1992, USNM 266804.

Material examined.—See Appendix.

Diagnosis.—Rostro-orbital depressions abrupt posteriorly. Ventral margin of carapace pronounced at an angle ventrally posterior to second pereopods. Minor claw of male not balaeniceps-shaped. Spine present on merus of first pereopod. Third and fourth pereopods with movable spine on ischium, lacking on fifth pereopod.

Description of holotype.—Rostrum reaching 0.5 length of first antennular segment; in form of raised crest extending beyond base of eyestalks and widening into flat triangular area (Fig. 1A). Ocular hoods prominent and unarmed, separated from rostrum by adrostral depressions abrupt posteriorly (Fig. 1A). Ocular hood width 0.27 times length of carapace. Carapace as figured (Fig. 1C), 0.35 times TL (range 0.31–0.40 for all specimens examined). Carapace smooth, posterior of carapace with cardiac notch;

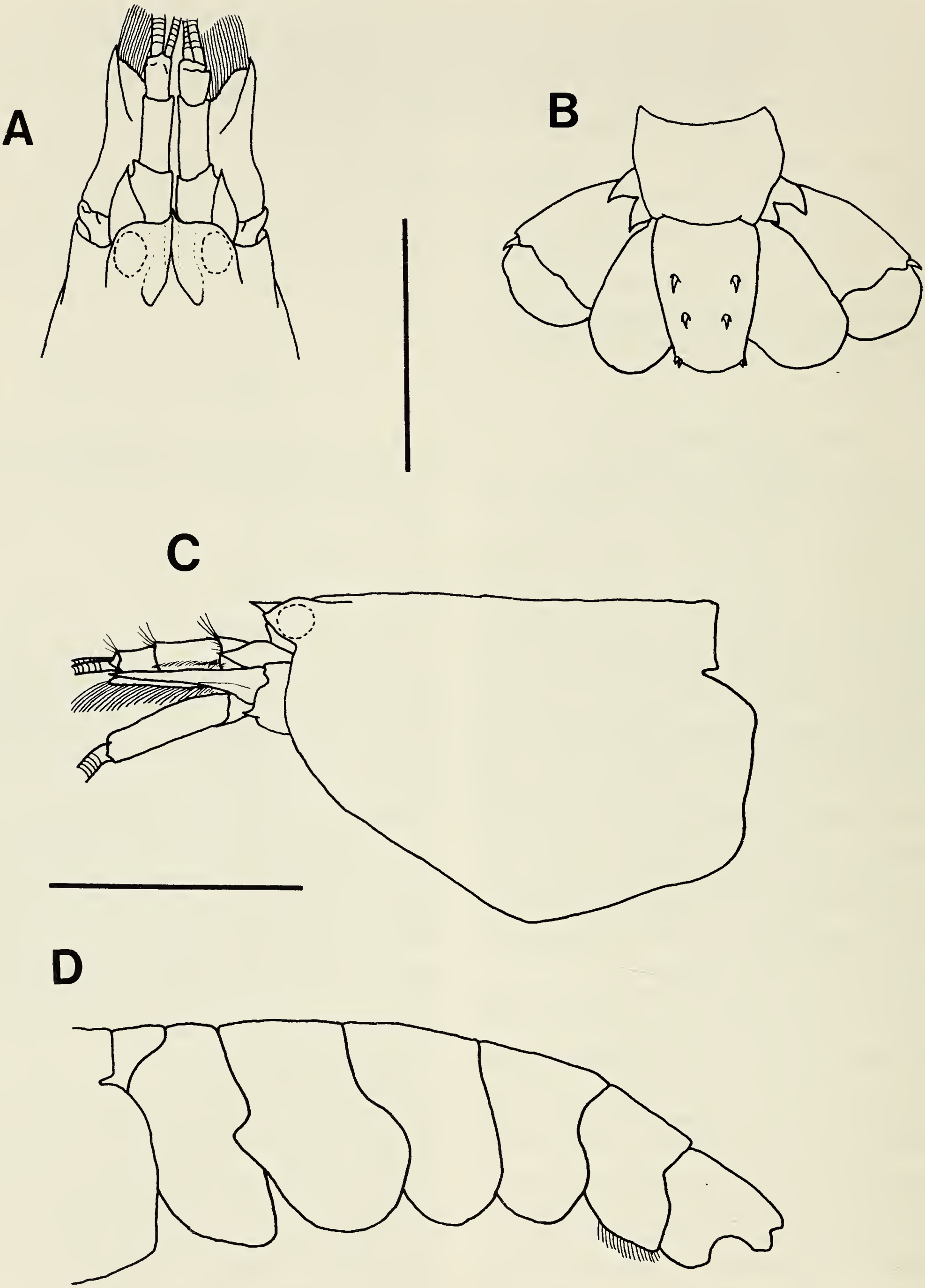

Fig. 1. *Alpheus angulatus,* new species. Adult male (holotype) from South Padre Island, Texas (TL = 28 mm). A, anterior carapace and antennae, dorsal; B, sixth abdominal somite, telson and uropods, dorsal; C, carapace and antennae, lateral; D, abdominal pleura, lateral. Bar indicates 5 mm.

ventral margin acute ventrally just posterior to articulation of second pereopod.

Abdomen as figured (Fig. 1D), 0.55 times total length (range 0.44–0.56). Pleura of abdominal somites 1 through 5 with ventral margins rounded. Sixth abdominal pleura with ventral margin acute posteroventrally. Telson (Fig. 1B) 0.11 times total length (range 0.09–0.14). Proximal telson width 0.67 of length, distal width about 0.5 of length; 2 pairs of dorsal spines, anteriormost pair positioned about 0.4 of telson length, posteriormost pair positioned at 0.67; posterior margin convex, with 2 pairs of lateral spines, space between spines with double row of setae.

Antennular peduncle with stylocerite dorsally flattened, terminating anteriorly at sharp point which reaches anterior margin of first antennular segment; second antennular segment longer than first and about 1.5 times as long as third (Fig. 1A, C).

Antennal spine reaching end of antennal peduncle, and just overreaching antennal scale; concave at middle and faintly convex at distal tip. Basal segment of antennal peduncle armed with spine ventrolaterally (Fig. 1A, C).

Mandible with 10 teeth. Third maxilliped reaching just beyond end of antennal peduncle; terminal article setose.

First pereopods (Fig. 2A, B, C) strongly chelate and unequal; merus armed with spine distoventrally. Major chela thick, setose distally; propodus length 0.51 times total body length (range 0.28–0.56); upper and lower margins deeply notched proximal to articulation of dactyl, upper notch width about 0.04 of propodus length, lower notch width about 0.11 of propodus length; maximum propodus height about 0.46 times length; dactyl length about 0.36 times propodus length; hand height with dactyl closed about 0.35 times propodus length; dactyl with entire upper and distal margins rounded, with setae arranged in tufts; opposable margin of dactyl with molar process tilted at angle to axis of dactyl; sculpture of propodus as figured (Fig. 2A, B), with upper and lower notches forming saddle-like depressions (extending about 0.07 and 0.11 times length of propodus, respectively) into the lateral surfaces of propodus; upper notch positioned about 0.5 the length of propodus, lower notch positioned about 0.61, having tuft of setae on proximal end of lower notch; angular area of upper mesial surface of fixed finger rounded, having granular texture and tufts of setae; distal end of propodus rounded, with tufts of setae. Minor chela robust and setose, with setal tufts increasing distally on both propodus and dactyl (Fig. 2C); not sexually dimorphic, lacking balaeniceps setose crest on dactyl; propodus 0.33 times total body length (range 0.15–0.37 for specimens examined); propodus height about 0.30 times length in both sexes; dactyl length about 0.5 times that of propodus length in both sexes.

Second pereopods slender and weakly chelate (Fig. 2D); carpus subdivided into 5 articles decreasing in length as follows (numbered from the proximal end); 1, 2, 5, 3 = 4. Third and fourth pereopods with ventral movable spine on ischium (Fig. 2E, F); dactyli simple; third pereopod propodus with 7 stout spines and 3 or 4 smaller alternating lateral spines, fourth with 8 stout spines and 5 or 6 alternating lateral spines. Fifth pereopod (Fig. 2G) with 8 or 9 spines on the propodus and several lateral bands of comb-like setae extending on distal half; ischium without spine. Second pleopod of male with appendix masculina shorter than appendix interna (Fig. 2H).

Coloration.—Overall dark olive green to brown, occasionally with blue tones around orbits, distal half of abdomen, and telson; body speckled with tiny brown or red-brown spots. Major chela dark olive green throughout mesial surface, unspeckled; upper and lower notches either colored as rest or major chela or lightened to pale yellow, rarely with blue; inner surface of major chela white or pale yellow, occasionally bluish; fingertips pale yellow or white. Minor chela dark olive

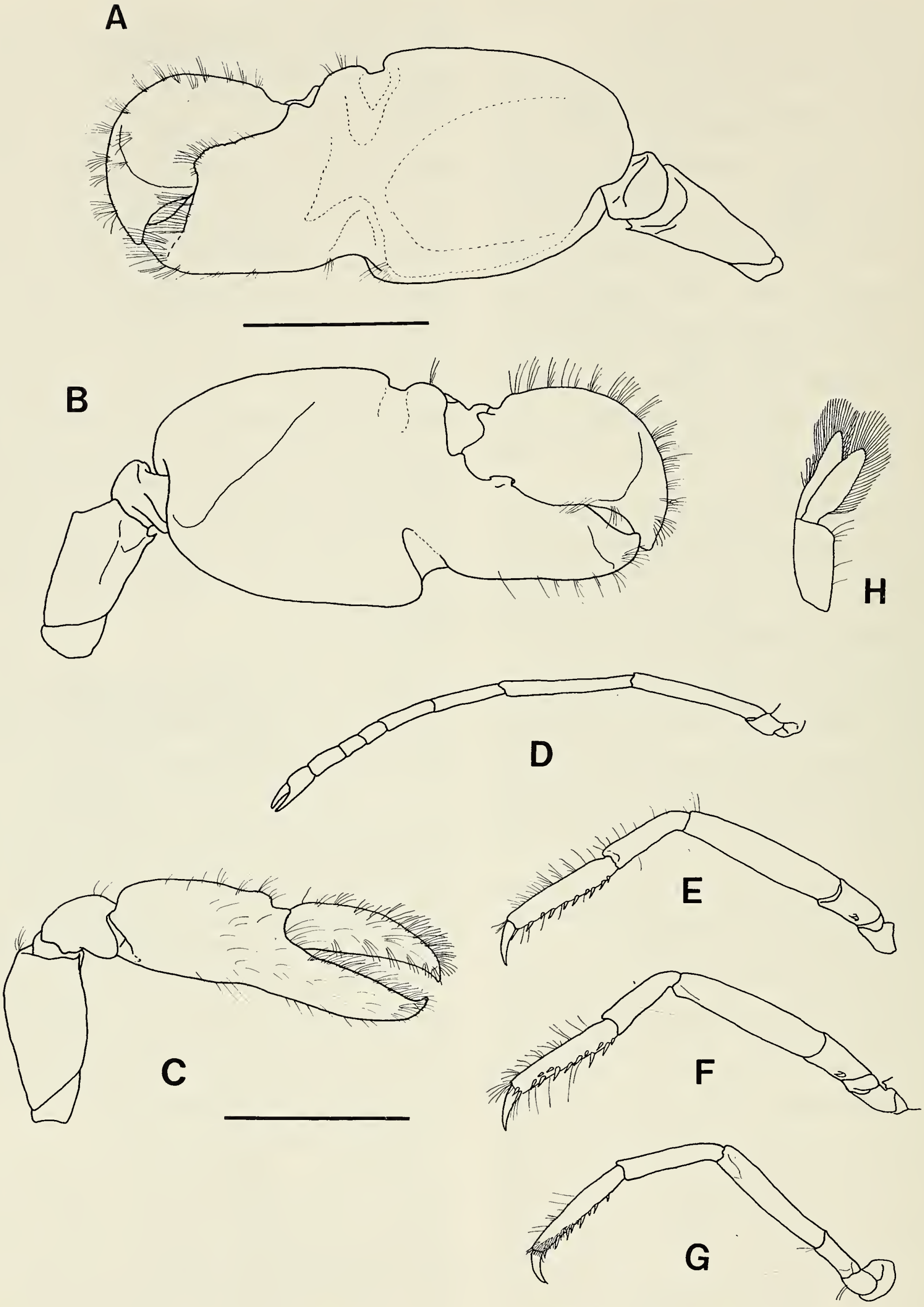

Fig. 2. *Alpheus angulatus,* new species. A, major first pereopod (right), dorsal; B, same, ventral; C, minor first pereopod (left); D, left second pereopod; E, left third pereopod; F, left fourth pereopod; G, left fifth pereopod; H, left second pleopod. Bar indicates 5 mm.

green. Second to fifth pereopods translucent to reddish, lightly speckled with reddish brown spots or mottled with red. Telson colored as abdomen, highly speckled with tiny brown or red-brown spots; uropods often bluish throughout, occasionally blue distally.

Size.—Total length for males ranging 17 to 38 mm, females 17 to 35 mm.

Etymology.—Specific name derived from the shape of the ventral margin of the carapace, which contains a pronounced angle posterior to the second pereopods.

Range.—The known range for this species is throughout the northern Gulf of Mexico and northwestern Atlantic as far north as Beaufort, North Carolina, and as far south as Quintana Roo, Mexico, and Haiti.

Habitat.—Intertidal and shallow waters in bays and other quiet waters consisting of mud bottoms with oyster clumps or rocks and rubble.

Alpheus heterochaelis Say, 1818
Figs. 3, 4

Alpheus heterochaelis Say, 1818:243.—Milne-Edwards, 1837:356.—Kingsley, 1878a:194, 1878b:329, 1879:417.—Brooks & Herrick, 1892:376, pl. 2.—Coutière, 1910:485.—Verrill, 1922:76, pl. 22, figs. 1, 2, 4a–c; pl. 24 figs. 7, 7a; pl. 30, figs. 1-1a, 1t, 2a–2e; pl. 33, figs. 1, 2.—Holthuis, 1959:102.—Williams, 1965:66, fig. 54, 1984:95, fig. 65.—Chace, 1972:67.—Coelho & Ramos, 1972:148.—Christoffersen, 1984:200, figs. 5–7.

Crangon heterochaelis.—Hay & Shore, 1918:386, fig. 8.—Schmitt 1935:144.

Holotype.—Not extant, Amelia Island, Nassau County, Florida.

Neotype.—1 male, 31 mm total length, Fort Saint George Inlet (8 miles south of Amelia Island), Duval County, Florida, intertidal habitat consisting of hard mud and clumps of oysters, coll. M. R. McClure and L. S. McClure, 25 May 1992, USNM 268646.

Material examined.—See Appendix.

Diagnosis.—Rostro-orbital depressions not abrupt posteriorly. Ventral margin of carapace evenly rounded, not pronounced at an angle ventrally posterior to second pereopods. Minor claw of male balaeniceps-shaped. Spine absent on merus of first pereopod. Third, fourth, and fifth pereopods with movable spine on ischium.

Description of neotype.—Rostrum carinate, reaching 0.5 length of first antennular segment, extending about as far as base of eyestalks. Ocular hoods prominent and unarmed, separated from rostrum by shallow adrostral depression. Ocular hood width 0.25 times length of carapace (Fig. 3A, C). Carapace as figured (Fig. 3C), 0.35 times TL (range 0.32–0.40 for all specimens examined). Carapace smooth, posterior with cardiac notch.

Abdomen as figured (Fig. 3D), 0.52 times total length (range 0.45–0.55). Pleura of abdominal somites 1 through 5 with ventral margins rounded. Sixth abdominal pleura with ventral margin acutely rounded posteroventrally. Telson (Fig. 3B) 0.12 times total length (range 0.09–0.14). Proximal telson width about 0.67 of length, distal width about 0.5 of length; 2 pairs of dorsal spines, anteriormost pair positioned about 0.5 of telson length, posteriormost pair positioned almost 0.75; posterior margin convex, with 2 pairs of lateral spines, space between spines with double row of setae (Fig. 3B).

Antennular peduncle with stylocerite dorsally flattened and terminating anteriorly at a sharp point which reaches anterior margin of first antennular segment; second antennular segment longer than first and about 1.4 times as long as third (Fig. 3A, C).

Antennal spine reaching end of antennal peduncle, and just overreaching antennal scale; spine faintly convex at distal tip, straight or slightly concave at middle. Basal segment of antennal peduncle armed ventrolaterally (Fig. 3A, C).

Mandible with 9 teeth. Third maxilliped

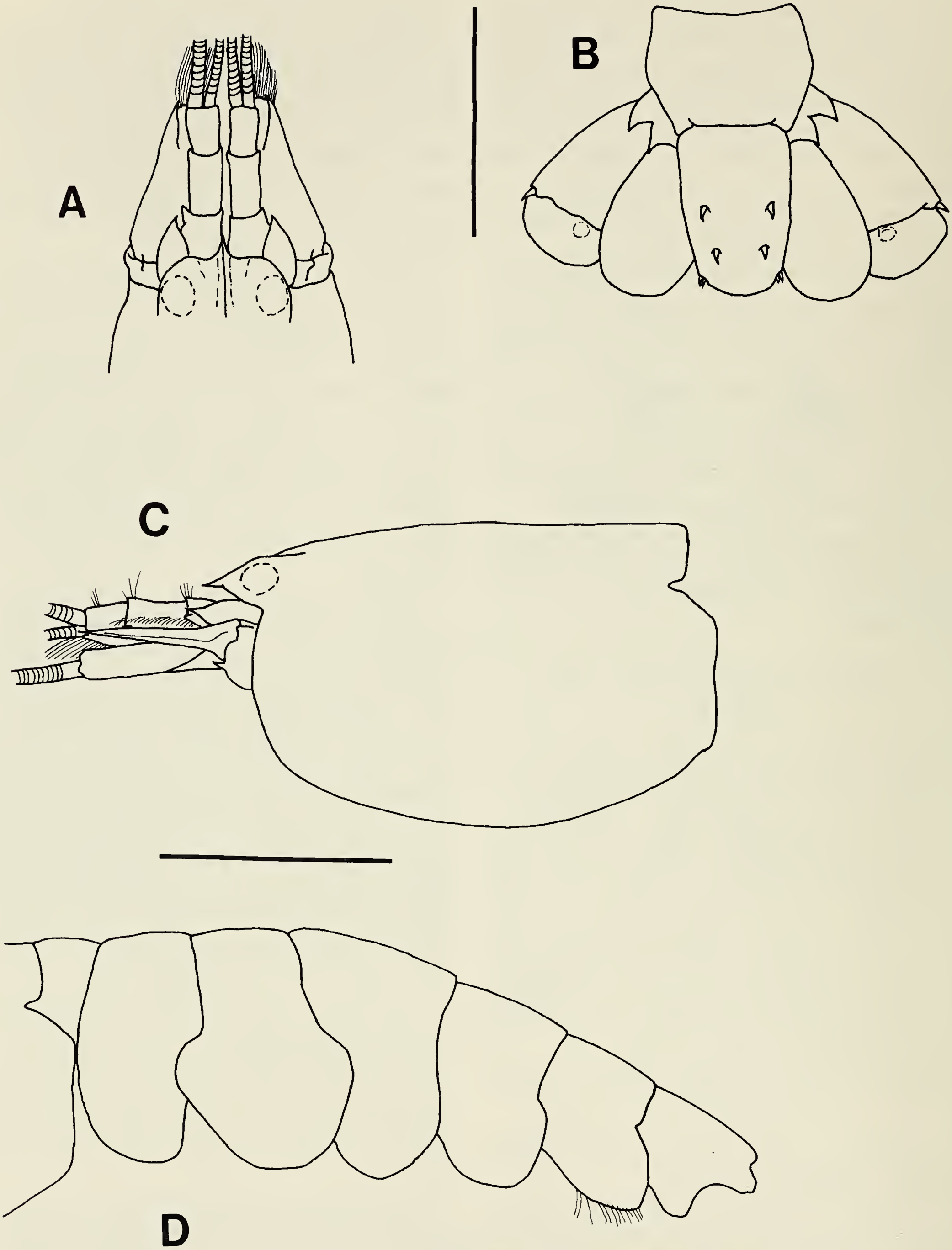

Fig. 3. *Alpheus heterochaelis* Say, 1818. A–L, Adult male (neotype) from Fort St. George Inlet, 8 miles south of Amelia Island, Florida (TL = 31 mm). A, anterior carapace and antennae, dorsal; B, sixth abdominal somite, telson and uropods, dorsal; C, carapace and antennae, lateral; D, abdominal pleura, lateral. Bar indicates 5 mm.

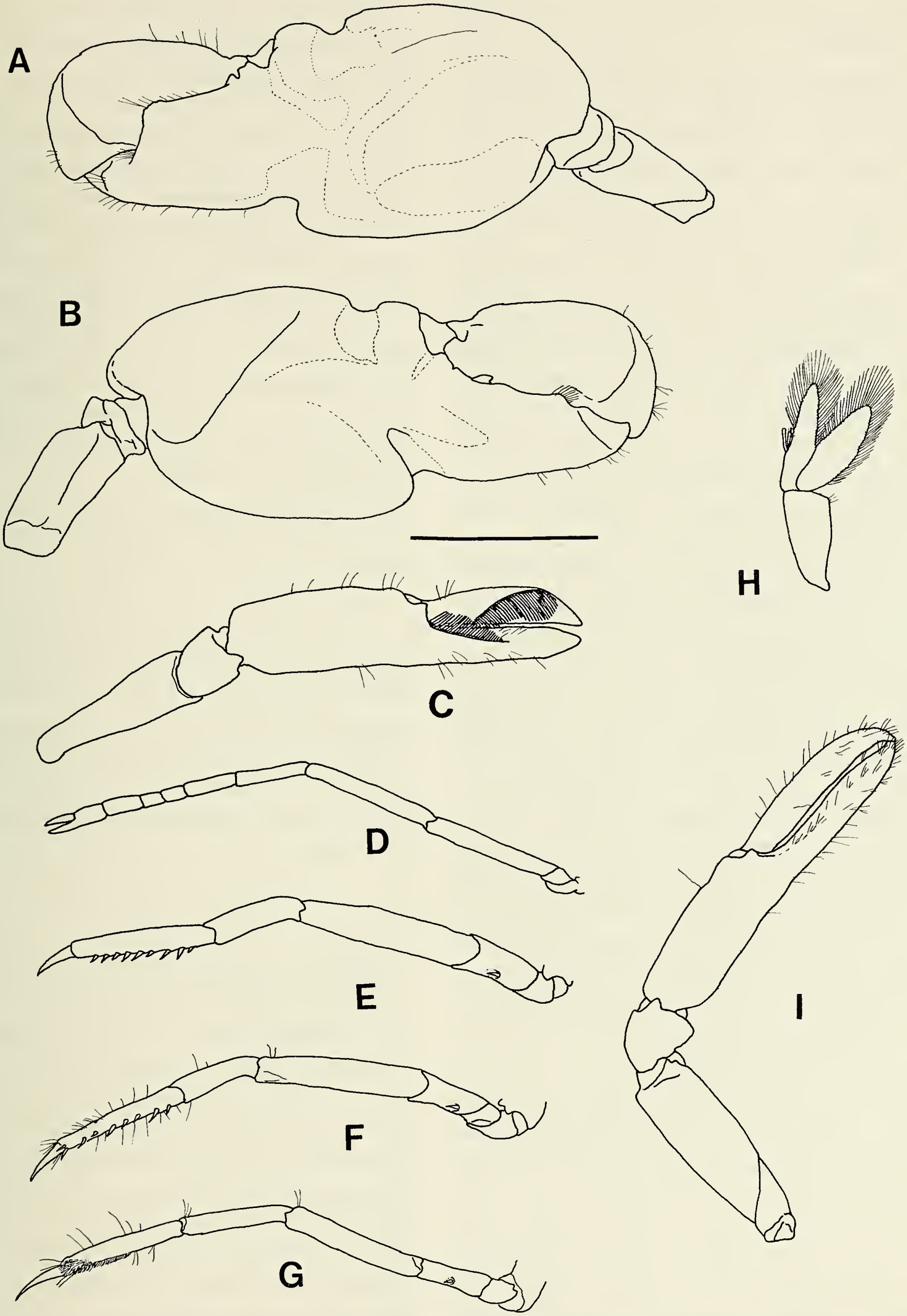

Fig. 4. *Alpheus heterochaelis.* A, major first pereopod (right), dorsal; B, same, ventral; C, minor first pereopod (left); D, left second pereopod; E, left third pereopod; F, left fourth pereopod; G, left fifth pereopod; H, left second pleopod; I, Adult female from Beaufort, NC, minor first (left) pereopod. Bar indicates 5 mm.

reaching end of antennal peduncle; terminal article setose.

First pereopods strongly chelate and unequal; merus unarmed distoventrally. Major chela (Fig. 4A, B) thick; propodus length 0.45 times total body length (range 0.29–0.61); upper and lower margins deeply notched proximal to articulation of dactyl, upper notch width about 0.07 of propodus length, lower notch width about 0.10 of propodus length; maximum propodus height about 0.45 times length; dactyl length about 0.35 times propodus length; hand height with dactyl closed about 0.32 times propodus length; dactyl with upper distal margin rounded, opposable margin with molar process tilted at angle to axis of dactyl; sculpture of propodus as figured, with upper and lower notches forming saddle-like depressions (extending 0.07 and 0.14 times length of propodus, respectively) into the lateral surfaces of propodus; upper notch positioned about 0.5 the length of propodus, lower notch positioned about 0.67; distal end of propodus rounded. Minor chela sexually dimorphic (Fig. 4C, I). Male minor chela balaeniceps-shaped, having setose crest on dactyl and accessory crest on opposable margin of the propodus; propodus 0.32 times total body length (range 0.22–0.40 for specimens examined); propodus height about 0.24 times length in males, 0.19 times length in females; dactyl length about 0.45 times that of propodus length in males, and about 0.5 in females.

Second pereopods (Fig. 4D) slender and weakly chelate; carpus subdivided into 5 articles decreasing in length as follows (numbered from the proximal end): 1, 2, 5, 3 = 4. Third to fifth pereopods (Fig. 4E, F, G) with ventral movable spine on ischium; dactyls simple; third pereopod propodus with 9 or 10 stout spines, fourth with 8 stout spines; fifth pereopod with 7 spines on propodus, with several lateral bands of comb-like setae extending on distal half. Second pleopod of male with appendix masculina shorter than appendix interna (Fig. 4H).

Coloration.—Overall olive green to brown, often with blue tones around orbits, distal half of abdomen, and telson; body speckled with tiny brown or red-brown spots. Major chela olive green with pale area at lower center of palm; raised areas of palm and opposable margin of fixed finger very dark green; upper and lower notches pale yellow to pale blue; inner surface of major chela white to pale blue; fingertips pale yellow or white. Minor chela olive green. Second to fifth pereopods translucent to pale blue, lightly speckled with reddish brown spots. Telson colored as abdomen; exopod of uropods blue on distal segment; endopod of uropods blue distally.

Size.—Neotype total length 31 mm. Total length for males ranging 16 to 45 mm, females ranging 18 to 57 mm.

Range.—Lower Chesapeake Bay southward and westward into the Gulf of Mexico; Cuba; Curaçao (Williams 1984); Bermuda (Verrill 1922); Surinam (Chace 1972); southward to Paraíba (Christoffersen 1984).

Habitat.—Intertidal and shallow waters in bays and other quiet waters consisting of mud bottoms with oyster clumps or rocks and rubble.

Discussion

Although *Alpheus angulatus* and *A. heterochaelis* are morphologically similar, they are not closely related. *Alpheus heterochaelis* and *A. angulatus* were referred to as *Alpheus* group A and group B, respectively in McClure & Greenbaum (1994), where the two species are shown to be highly divergent electrophoretically. *Alpheus heterochaelis* was the most common species that the author collected from Texas and from North Carolina. This species differs from the other Edwardsii-group *Alpheus* mentioned herein in that *A. heterochaelis* possesses a balaeniceps-type minor claw in males, and a movable spine on the ventral surface of the ischium of the fifth pereopod. *Alpheus heterochaelis* is further distinguished from *A.*

angulatus in that the rostro-orbital area in the former lacks posteriorly abrupt adrostral depressions and lacks the broad triangular area of the carapace from which the rostrum terminates posteriorly.

Material of *A. estuariensis* was examined from Port Isabel and Gilchrist, Texas, and from Mississippi Sound, Alabama, as well as the Gulf of Mexico material used by Christoffersen (1984). *Alpheus estuariensis* was not found in this survey, and thus is probably of uncommon occurrence in the northern Gulf of Mexico. *Alpheus estuariensis* is distinguishable from *A. heterochaelis* in that it lacks the balaeniceps-type minor claw in males, and lacks the movable spine on the ischium of the fifth pereopod. In addition, the minor claw of *A. estuariensis* is very slender relative to that of *A. heterochaelis.*

Alpheus angulatus was the most common species that the author collected from Florida and from Louisiana, and has apparently been mistaken for *Alpheus heterochaelis* in a number of museum collections. This is because they are both similarly colored, and commonly taken in a single sampling (both have been collected simultaneously at most of the author's collecting localities).

In one case, *Alpheus angulatus* has been mistaken for *A. estuariensis* by Christoffersen (1984). One of the specimens referred to as *A. estuariensis* (USNM 98137) from Louisiana represents *A. angulatus* and not *A. estuariensis. Alpheus angulatus* differs from *A. estuariensis* in that the former has a more robust minor claw, whereas the spine on the merus of the first pereopod is lacking in *A. estuariensis.* In addition, the upper and lower notches of the major chela are wider of *A. estuariensis* than those of *A. heterochaelis* and of *A. angulatus,* and the distal end of the propodus is sharply truncated in *A. estuariensis.*

Alpheus angulatus has previously been referred to as the Carolinian *A. armillatus* (Hay & Shore 1918; Knowlton 1970; Chace 1972; Williams 1965, 1984). Except by examining the color pattern, the two species are difficult to distinguish. Both *A. armillatus* and *A. angulatus* have the typical *A. armillatus*-type rostrum, consisting of a broad, flattened triangular area posteriorly, and posteriorly abrupt adrostral furrows. Milne-Edwards' (1837) description of *A. armillatus* was brief and lacking in detail. However, the locality was given as the Antilles. The species was named "the banded *Alpheus*" for its conspicuous banded color pattern; this pattern is lacking in *A. angulatus.* Verrill (1922) stated that *A. armillatus* from Bermuda, when recently caught, was identifiable by its conspicuous transverse bands of white on the body and rings of color on the legs and antennae, and provided a photograph (plate 20, fig. 4b) showing such a pattern. Zeiller (1974, p. 76) provided a color photograph of *A. armillatus* revealing the conspicuous banded pattern on the abdomen, with the body and chelae colored overall brown speckled with white. In *A. angulatus,* the body is darker and speckled with dark red-brown spots, with speckling lacking on the chelae.

Hay & Shore (1918) listed *A. angulatus* as *A. armillatus* from North Carolina. Although the author was informed that Hay & Shore's (1918) collection may no longer exist (R. B. Manning, pers. comm.), the color description by Hay & Shore for the *A. armillatus* from Beaufort, North Carolina, matches that of *A. angulatus.* In addition, the figures provided by Hay & Shore of *A. armillatus* match *A. angulatus* with respect to the shape of the rostrum and minor chela. They also mentioned the rarity of this species at Beaufort, North Carolina, which also confirms the authors' findings (one *A. angulatus* individual was caught with 54 *A. heterochaelis* individuals). The color pattern difference between the Carolinian *A. armillatus* and the tropical *A. armillatus* also led Knowlton (1970) to speculate that the Carolinian form may represent a separate species.

The likelihood that *A. armillatus,* as currently known, represents a species complex seems more plausible now than ever, since differences in color patterns have been demonstrated to have systematic importance in *Alpheus* (Knowlton & Mills 1992). Hendrix (1971) described three color morphs of *A. armillatus* from Miami, Florida (the normal banded pattern, a blue-grey morph, and a yellow morph), and suggested that they may represent distinct species. The author was unable to locate the specimens used by Hendrix (1971), so confirmation is lacking if any of his color morphs of *A. armillatus* from the Miami region correspond with *A. angulatus.*

Hendrix (1971) mentioned in his description that *A. armillatus* (all three color morphs included) had a movable ventral spine on the ischium of the fifth pereopod, which is lacking in *A. angulatus.* Specimens of *A. armillatus* from the Smithsonian-Bredin Expedition (Chace 1972) examined from the Leeward Islands (Lesser Antilles) contain such a spine (appearing more conspicuous in smaller specimens), and also differ from *A. angulatus* in the shape of the ventral margin of the carapace; the latter having a pronounced ventral angle posterior to the second pereopods (Fig. 1C) lacking in the Antillian specimens. Other specimens identified as *A. armillatus* by Chace (1972) from the east coast of the Yucatan peninsula, Mexico, had characteristics matching *A. angulatus* (color pattern information was lacking). In addition, specimens from Haiti identified as *A. armillatus* by Coutière (MNHN-Na 2171) match the characteristics present for *A. angulatus.*

Hendrix (1971) provided a description of *A. nuttingi* (Schmitt, 1924) as the first record of that species from the continental U.S.A. His description differs from the original description of the holotype in that the latter lacks a spine on the merus of the first pereopods; this spine is present both on *A. nuttingi* and *A. angulatus.* However, *A. angulatus* differs from *A. nuttingi* (both of Schmitt 1924, and Hendrix 1971) in that *A. angulatus* possesses movable spines on the ischium of the third and fourth pereopods, and the "*A. armillatus*-type" rostrum is absent in *A. nuttingi.*

Alpheus normanni Kingsley, a "Macrochirus-group" species, was examined from South Padre Island, Texas, Dauphin Island, Alabama, and Crystal River, Florida. This species is mentioned here because it too has occasionally been labeled as *A. heterochaelis* in some collections. This is probably due to both *A. normanni* and *A. heterochaelis* having the balaeniceps-type minor claw in males or have both been taken simultaneously. *Alpheus normanni* is distinguished from the Edwardsii-group species mentioned herein in that the major chela of *A. normanni* lacks a lower notch, being only notched dorsally; the dorsal notch is sharply undercut proximally. In addition, *A. normanni* has angularly produced ocular hoods anteriorly, not smooth or evenly rounded as in these Edwardsii-group species (Hendrix 1971). It is also brighter green in color relative to *A. heterochaelis* and *A. angulatus.*

The geographic range of *A. heterochaelis* is apparently widespread throughout the temperate and tropical western Atlantic. Despite past taxonomic ambiguity surrounding this species, records confirm the presence of *A. heterochaelis* from eastern and southeastern North America, the Caribbean region, eastern Central America, and northeastern South America. However, *A. armillatus* should now be considered to have a tropical distribution. Previous records of *A. armillatus* from temperate North America correspond with *A. angulatus*; the latter differs from the former in color pattern and in some discrete characters. The geographic range of *A. angulatus* includes the Gulf of Mexico and northwestern Atlantic, and appears to extend into the Caribbean region. Additional ranges of *A. angulatus* are not currently known. The geographic range of *A. estuariensis* appears just as Christoffersen (1984) described, although this species does not seem to be abundant in the northern Gulf of Mexico.

Originally, a single Edwardsii-group *Al-*

pheus species, *A. heterochaelis,* was known in coastal waters from the northern Gulf of Mexico and northwestern Atlantic. Prior to this study two such species, *A. heterochaelis* and *A. estuariensis,* had been reported from the northern Gulf of Mexico. In this study, *A. angulatus* was found to be equally as common as *A. heterochaelis* and more common than *A. estuariensis* in the northern Gulf of Mexico and northwestern Atlantic. The new species resembles *A. nuttingi,* and strongly resembles *A. armillatus,* both of which may in fact consist of more than one species throughout the western Atlantic. In short, the taxonomic and biogeographic relationships existing for western Atlantic alpheids is far from being resolved.

Acknowledgments

The author thanks the following people for their help in the collection of snapping shrimp: L. S. McClure, M. K. Wicksten (Texas A&M University), E. C. Rives, J. S. Whorff, D. Hockaday and F. Judd (University of Texas-Pan American Marine Field Station, South Padre Island, Texas), M. Dardeau (MESC), M. Demetz, L. Edmiston and G. Bailey (Apalachicola National Estuarine Research Reserve), D. Felder and T. Zimmerman (University of Southwestern Louisiana), and B. Kirby-Smith and K. Reinsel (Duke Marine Laboratory, Beaufort, North Carolina). S. K. Davis, I. F. Greenbaum, and H. Wilson (Texas A&M University) provided the cryogenic field equipment and storage space for shrimp in their ultracold freezers. The following museum curators were helpful with the loaning of snapping shrimp specimens: R. B. Manning (USNM), D. K. Camp (FBSC), M. Dardeau and T. S. Hopkins (MESC), A. Chaney (TAI), D. Guinot and N. Nguyen (MNHN), and R. Harrell (LU). Thanks also to M. K. Wicksten, R. E. Knowlton, N. Knowlton, and J. Goy for their advice on alpheid systematics. M. K. Wicksten, J. Goy, and I. F. Greenbaum provided reviews. This study was funded in part by Sigma Xi Grants-In-Aid of Research GIAR 9912 (to M. R. McClure) and Advanced Research Program ARP grant 160603 (to M. K. Wicksten).

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Appendix

Material Examined

Alpheus heterochaelis.—Collected Material: Texas: South Padre Island, Laguna Madre, north of Brazos-Santiago Pass near old Coast Guard Station, 0.5 m, *n* = 31, 17 Apr 1993; Port Aransas, north jetty at Saint Joseph Island, intertidal, *n* = 19, 18 Dec 1991; Galveston Bay, off Sportsman's Road, 0.5 m, *n* = 14, 14 Sep 1991, South jetty, 0.5 m, *n* = 1, 17 Jan 1992. Alabama: Dauphin Island, Mobile Bay, 0.5 m, *n* = 4. Florida: Pensacola, Escambia Bay, 0.5 m, *n* = 1, 18, 19 Mar, 1993; Apalachicola Bay, St. George Island State Park, 1.0–1.5 m, *n* = 3, 25 May, 1992; Panacea, *n* = 5, 26 Feb, 1992; Fort St. George Inlet, 8 miles south of Amelia Island, intertidal, *n* = 1 (neotype, USNM 268646), 25 May, 1992. North Carolina: Beaufort, near Duke Marine Lab, 0.5 m, *n* = 54, 25, 26 Jun 1993. Borrowed Material: Texas: USNM 72186, Ranson Island, *n* = 1; USNM 82116, Galveston, Offat's Bayou, *n* = 2; TAI 166, Salt Lake, Indianola, *n* = 1; TAI 167, Port Isabel, *n* = 1; TAI 169, Bahia Azul, *n* = 1; TAI 551, Bahia Azul, *n* = 1. Mississippi: USNM 64243, Dier Island, *n* = 2. Alabama: MESC 6179-3671, Mobile Bay, *n* = 2; MESC 6179-3672, Pt. Pines, *n* = 2; MESC uncat., Dauphin Island, airport marsh, *n* = 2. Florida: USNM 57635, Key West, *n* = 2; MESC 6179-5143, St. Joseph Bay, *n* = 1; FBSC I 110, Bush Key, Pinellas Co., *n* = 3; FBSC I 188, Bush Key, *n* = 2; FBSC I 364, Egmont Key, Pinellas Co., *n* = 8; FBSC I 1496 Boca Ciega Bay, *n* = 1; FBSC I 2177, Tampa Bay, *n* = 1; FBSC I 2177 Tampa Bay, *n* = 1; FBSC I 5126, Bush Key, *n* = 1; FBSC I 6244, Pumpkin Bay, Collier Co., *n* = 1; FBSC I 6338, Pakalatchee Bay, *n*

= 7; FBSC I 6378 Mullet Key, Pinellas Co., $n = 1$; FBSC I 7628, Sawyer and Sistu Keys, Boca Ciega Bay, $n = 12$; FBSC I 7685, Crystal River, $n = 2$; FBSC I 14419, W. McIllvaine Bay, $n = 1$; FBSC I 7745, Crystal River, $n = 12$. Georgia: USNM 181864, 181865, 181866, 181867, Sapelo Island, $n = 1$ each.

Alpheus angulatus, new species.—Collected Material: Texas: South Padre Island, Laguna Madre, north of Brazos-Santiago Pass near old Coast Guard Station, 0.5 m, $n = 2$, 4 Jul 1992 (holotype, USNM 266804 and paratype, USNM 266805); $n = 2$, 17 Apr, 1993; Port Aransas, north jetty at Saint Joseph Island, intertidal, $n = 3$, 18 Dec 1991; Galveston Bay, off Sportsman's Road, 0.5 m, $n = 2$, 14 Sep 1991, South jetty, 0.5 m, $n = 4$, 17 Jan, 1992. Louisiana: Terribonne Bay, Lighthouse island south of LUMCON-Cocodrie, 0.5 m, $n = 34$, 19 Jul 1993; Florida: Pensacola, Escambia Bay, 0.5 m, $n = 45$, 18, 19 Mar 1993; Apalachicola Bay, St. George Island State Park, 1.0–1.5 m, $n = 28$, 25 May 1992; Panacea, $n = 1$, 26 Feb 1992; Fort St. George Inlet, 8 miles south of Amelia Island, intertidal, $n = 34$, 25 May 1992. North Carolina: Beaufort, near Duke Marine Lab, 0.5 m, $n = 1$, 25, 26 Jun 1993. Borrowed Material: Texas: TAI 168, Mustang Island, $n = 1$. Louisiana: USNM 98138, Lake Ponchartrain, $n = 1$. Alabama: MESC uncat., west end Dauphin Island (subsample), $n = 3$. Florida: USNM 57635, Key West, $n = 1$; FBSC I 1293 Tierra Verde, Pinellas Co., $n = 1$; FBSC I 2901, St. George Bay near Apalachicola, $n = 3$; FBSC I 2931, Magnolia Beach, Andrews Bay, $n = 2$; FBSC I 3626, Mullet Key, Pinellas Co., $n = 3$; FBSC I 6297, Gullivan Bay, Collier Co., $n = 5$; FBSC I 7601, "Marine Research Lab", Pinellas Co., $n = 2$; FBSC I 7745 (subsample), Crystal River, $n = 1$; FBSC I, 2 miles south of Hillsburough River, $n = 1$. South Carolina: USNM 63549, Jericho Creek, $n = 7$. North Carolina: USNM 128061, Beaufort, Lennoxville Point, $n = 1$. Haiti: MNHN-Na 2171, $n = 2$. Mexico: USNM 135891, Quintana Roo, Ascension Bay, $n = 12$.

Alpheus estuariensis.—Borrowed Material: Brazil: USNM 144014, Sao Paulo, paratypes, $n = 3$; USNM 25800, Mamanquape, paratype, $n = 1$; USNM 222042, $n = 4$; MESC 6179-10461, Raiba, $n = 4$. CUBA: USNM 96455, Laguna de Paso Malo, $n = 3$. U.S.A.: Texas: USNM 63546, Jetty at Galveston Bay (Evermann 1891 coll.), $n = 2$; TAI uncat., Port Isabel, $n = 4$; LU uncat., East Galveston Bay at Gilchrist, $n = 4$. Louisiana: USNM 98137, Lake Pontchartrain, $n = 1$. Alabama: MESC uncat., Mississippi Sound, $n = 1$. Florida: USNM 90957, Duval Co., $n = 4$.

Alpheus armillatus.—Borrowed Material: Lesser Antilles: USNM 135869, Leeward Islands, Guadaloupe, $n = 14$; USNM 135870 (subsample), Leeward Islands, Antigua, $n = 4$.

Alpheus nuttingi.—Borrowed Material: USNM 68700, Holotype and 2 additional specimens from Barbados, W. Schmitt, 1918.

Alpheus normanni.—Collected Material: Texas: South Padre Island, Laguna Madre, north of Brazos-Santiago Pass near old Coast Guard Station, 0.5 m, $n = 3$, 17 Apr 1993. Borrowed Material: Alabama: MESC uncat., "Mussels 2-1", $n = 3$; MESC uncat., west end Dauphin Island (subsample), $n = 1$. Florida: FBSC I 7745 (subsample), Crystal River, $n = 1$.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(1):98–101. 1995.

A new species of freshwater crab of the genus *Strengeriana* from Colombia (Crustacea: Decapoda: Pseudothelphusidae)

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Abstract.—A new species of the genus *Strengeriana* Pretzmann, 1971, *S. florenciae,* from the Central Cordillera of Colombia is described. The new species closely resembles *Strengeriana bolivarensis* Rodríguez & Campos, 1989, but can be easily distinguished by the shorter and bilobed mesial process and by the absence of a proximal spine at the lateral lobe of the first male gonopod.

The genus *Strengeriana* Pretzmann, 1971, comprises a group of small and primitive pseudothelphusid crabs that inhabit mountain streams. Including the new species, the genus now comprises 14 species, distributed in the Sierra Nevada de Santa Marta, and the Western, Central, and Eastern Cordilleras of the Colombian Andes, at altitudes ranging from 700 to 1800 m above sea level.

The systematics and biogeography of the genus were reviewed by Rodríguez & Campos (1989), and three new species of *Strengeriana* have been recently described by Campos & Rodríguez (1993). Explorations of the Central Cordillera of Colombia have revealed the presence of an additional new species described herein.

The terminology used in the description of the first gonopod is according to the criteria established by Smalley (1964), and Rodríguez (1982). The material is deposited at the Museo de Historia Natural, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN-MHN). The abbreviations cb and cl are used for carapace breadth and carapace length, respectively.

Family Pseudothelphusidae Rathbun, 1893
Tribe Strengerianini Rodríguez, 1982
Genus *Strengeriana* Pretzmann, 1971

Strengeriana florenciae, new species
Fig. 1

Material examined.—Bosque de Florencia, Corregimiento Florencia, Municipio Samaná, Caldas Department, 1800 m alt., 10 Nov 1993, J. V. Rueda: 1 male holotype, cb 19.2 mm, cl 11.5 mm; (ICN-MHN-CR 1347); 1 male paratype, cb 15.0 mm, cl 9.6 mm; (ICN-MHN-CR 1348). Vereda El Dorado, Corregimiento Florencia, Municipio Samaná, Caldas Department, 1700 m alt., 28 Jul 1994, M. R. Campos: 7 males, cb 22.8, 22.0, 21.5, 19.4, 18.2, 15.5, 13.0 mm, cl 13.8, 13.1, 12.6, 11.9, 11.4, 9.8, 8.5 mm; 5 females, cb 19.3, 18.3, 17.1, 16.2, 12.7 mm, cl 12.2, 11.3, 10.7, 10.3, 8.1 mm; (ICN-MHN-CR 1351).

Diagnosis.—Male first gonopod with short, inwardly turned, bilobed mesial process and lateral lobe with 2 processes, one semicircular, distal, and the other rudimentary, proximal.

Description.—Carapace narrow (cb/cl = 1.67). Cervical grooves straight and deep, reaching lateral margins. Anterolateral margin with depression behind orbits, followed by 7 papillae and second shallow depression at level of cervical groove; rest of margins with approximately 11 papillae, regularly spaced. Postfrontal lobes are small, ovally

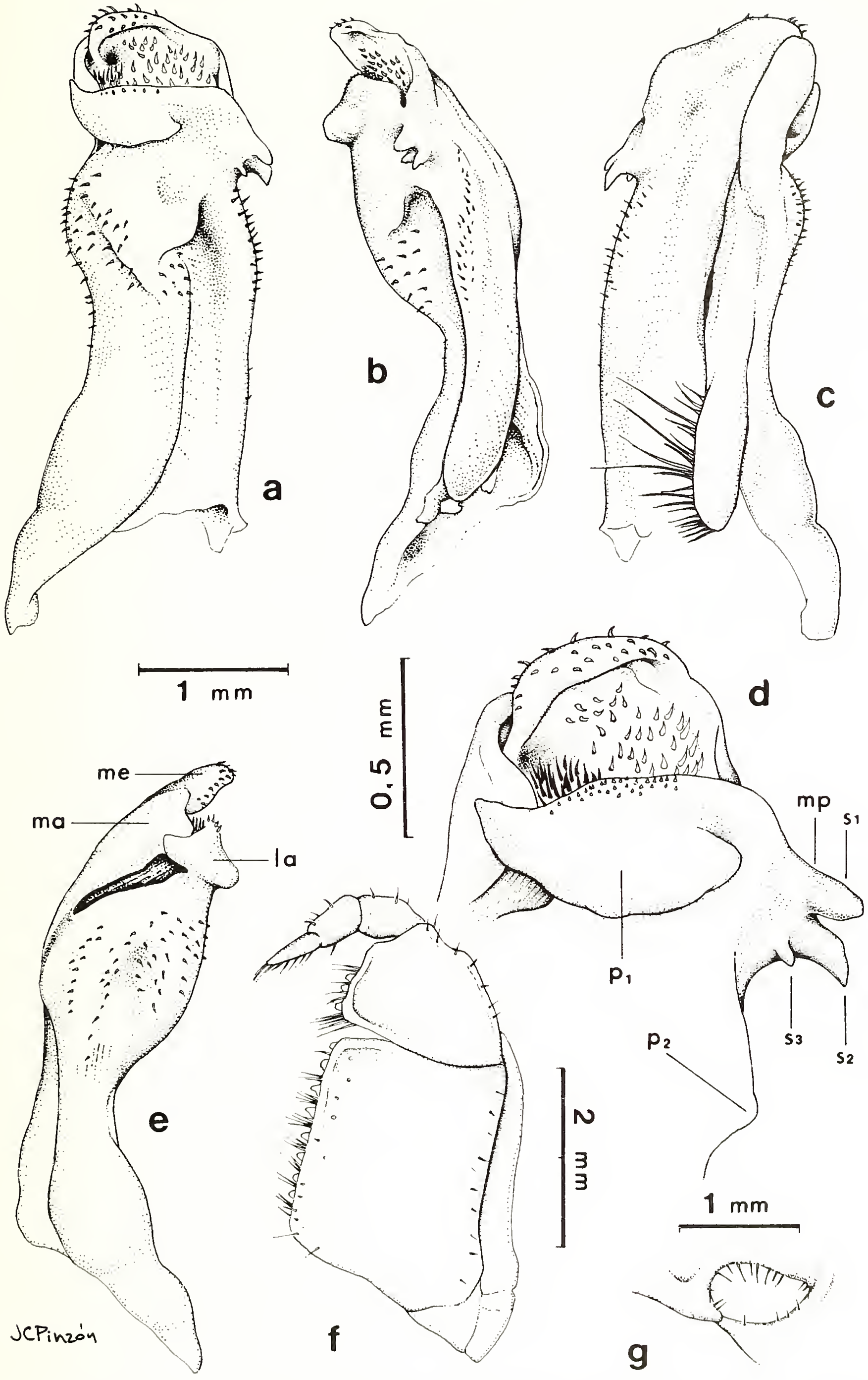

Fig. 1. *Strengeriana florenciae,* new species, holotype, first left gonopod: a, total view, cephalic; b, same, mesial view; c, same, caudal view; d, same, detail of apex, cephalic view; e, same, lateral view; f, third maxilliped, left; g, aperture of efferent channel, left. la, lateral lobe; ma, marginal lobe; me, mesial lobe; mp, mesial process; p_1, p_2, lateral processes; s_1, s_2, distal spines of the mesial process; s_3, lateral spine of the mesial process.

shaped and low. Median groove absent. Surface of carapace between front and postfrontal lobes inclined anteriorly and towards mid-line. Upper border of front bilobed in dorsal view, with conspicuous tubercles. Lower margin strongly sinuous in frontal view, with tubercles. Surface of front between upper and lower borders high. Lower orbital margins each with row of tubercles. Surface of carapace smooth, covered by small papillae; the limit between the regions is indistinct.

Palm of larger chela (left) strongly inflated; fingers not gaping. Walking legs slender, but not unusually elongated, the largest being those of second and third pairs, which are of similar length (total length 1.31 times the breadth of carapace); merus in third pair 3.5 times longer than wide. Dactylus with 5 rows of large spines, diminishing in size proximally; arrangement of spines on dactylus of third left pereiopod as follows: anterolateral and anteroventral rows with 5 spines plus 2 proximal papillae, external row with 5 spines plus 2 papillae and 1 pair of proximal papillae, posteroventral and posterolateral rows with 4 spines. Exognath of third maxilliped overreaches lateral margin of ischium of endognath; merus of third maxilliped shows acute angle on distal half of external margin (Fig. 1f). Orifice of efferent branchial channel closed by spine at jugal angle and by extension of lateral lobe of epistome (Fig. 1g).

Male first gonopods short, slightly arched in caudo-cephalic plane (Fig. 1b). Apex formed by 3 distinct lobes: mesial (Fig. 1e, me), marginal (caudal) (Fig. 1e, ma) and lateral (Fig. 1e, la); mesial and marginal lobes rounded, cup-shaped, with borders strongly demarcated; border of mesial lobe strongly bent at cephalic and caudal ends. Mesial lobe with short, inwardly turned, bilobed mesial process (Fig. 1d, mp), ending in 2 conical spines (Fig. 1d, S_1, S_2), and another spine located near basis of the lateral surface of process (Fig. 1c, S_3); mesial lobe forms with lateral lobe a long slit where the genital pore is located (Fig. 1c, d). Lateral lobe forming an inflated protuberance covered with spinules (Fig. 1a, c), and 2 lateral processes, one semicircular, distal, and the other rudimentary, proximal (Fig. 1d, p_1, p_2). Internal cavity of mesial lobe densely covered by spines; with strong, dark spines near genital pore, and small spinules over distal border of lateral lobe (Fig. 1d). In addition to strong caudal setae, gonopod bears tiny setae on mesial and lateral sides (Fig. 1a, b, c).

Etymology.—The name of the species refers to the Corregimiento of Florencia, where the type was collected.

Remarks.—This species resembles *Strengeriana bolivarensis* Rodríguez & Campos, 1989, in the shape of the first male gonopod, but differs in the shape of the mesial lobe. The mesial process is longer and entire in *S. bolivarensis*; while shorter and bilobed in *S. florenciae. Strengeriana bolivarensis* has a proximal spine at the lateral lobe, whereas *S. florenciae* lacks this spine.

Acknowledgments

I thank J. V. Rueda for collecting the specimens. I am also very grateful to Dr. Rafael Lemaitre and the referees for their constructive comments. The illustrations were prepared by J. C. Pinzón.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(1):102–106. 1995.

A new callianassid (Decapoda: Thalassinidea) from the southern Caribbean Sea

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Abstract.—A new species of callianassid, *Sergio guaiqueri,* similar to *S. guara* (Rodrigues, 1971) is described from the northeastern coast of Venezuela. The new species differs in having larger, more inflated cornea; in the shape of margins of merus and carpus of the major cheliped, and in dentition of the dactyl of the major cheliped.

Manning & Felder (1991) placed the genus *Neocallichirus* Sakai, 1988, in the subfamily Callichirinae, and included six western Atlantic species. Manning (1993) later added two new species to this genus, but noted that it could be divided into two groups of species based on the shape of the telson and uropodal endopod. Subsequently, Manning & Lemaitre (1994) restricted the genus *Neocallichirus,* and proposed the new genus *Sergio* for four western Atlantic species forming one of those groups: *S. guassutinga* (Rodrigues, 1971), *S. guara* (Rodrigues, 1971), *S. mirim* (Rodrigues, 1971), and *S. trilobatus* (Biffar, 1970). With the discovery of *S. guaiqueri* new species, the genus now contains five species in the western Atlantic. Specimens from Venezuela reported by Blanco Rambla & Liñero Arana (1994) as *Neocallichirus* sp. actually represent the new species described herein.

Specimens of the new species were collected in the northeastern coast of Venezuela with a Petersen grab on board R/V *Guaiquerí II.* Measurements (mm) were made with an ocular micrometer. Carapace length (cl) was measured along the middorsal line of the carapace from the tip of the rostrum to posterior margin; total length (tl) was measured from tip of rostrum to posterior margin of telson. The holotype has been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and paratypes in the Museum of the Instituto Oceanográfico de Venezuela, Cumaná (IOV).

Family Callianassidae Dana, 1852
Subfamily Callichirinae Manning & Felder, 1991
Genus *Sergio* Manning & Lemaitre, 1994
Sergio guaiqueri, new species

Figs. 1–3

Neocallichirus sp. Blanco Rambla & Liñero Arana, 1994:20–22, figs. 4–5.

Material.—Venezuela: north of Jose, Anzoátegui State (10°08′40″N, 64°50′10″W), Petersen grab, 9 May 1991, 24 m, clay-silt bottom: 1 male (cl 4.2 mm, holotype, USNM 265294); 3 males (tl 28.3–49.1 mm, paratypes, IOV).

Diagnosis.—Carapace with 3 unarmed anterior projections; median extending less than half length of eyestalks. Eyestalk with cornea subterminal, inflated. Propodus of third maxilliped longer than wide, distal margin sinuous. Major cheliped with ventral serrations on merus, carpus as long as palm; dactylus with 3–4 small teeth. Telson nearly 2 times wider than long; posterior

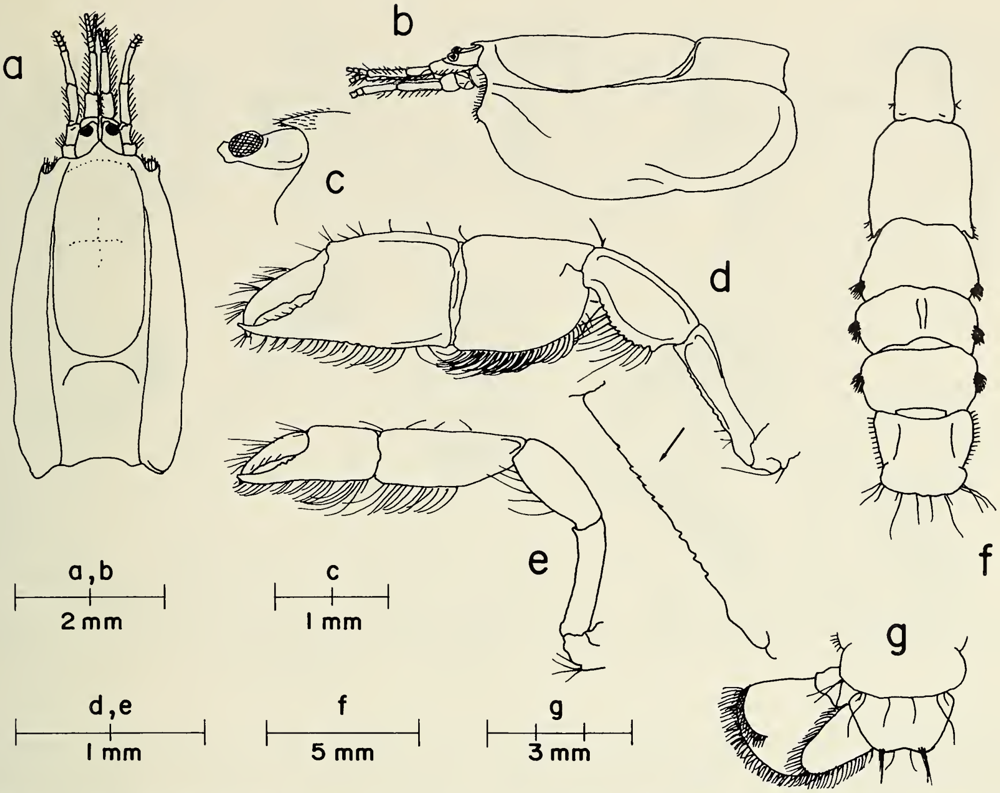

Fig. 1. *Sergio guaiqueri*, new species. a–c, f, g, holotype male, USNM 265294, cl 4.2 mm; f, g, paratype male, IOV, cl 2.5 mm. a, Carapace and cephalic appendages (dorsal view); b, Same (lateral view); c, Anterior portion of carapace and eyestalk; d, Major cheliped (inner face); e, Minor cheliped (outer face); f, Abdomen; g, Telson and left uropod.

margin divided by a median cleft. Uropodal endopods longer than wide.

Description.—Front with 3 anterior projections, median subtriangular, flattened, extending less than half length of eyestalks, with scattered setae on dorsal surface and few setae on ventral surface near the apex. Carapace rounded dorsolaterally; linea thalassinica distinct, reaching posterior margin of carapace; cervical groove distinct, delimiting posterior margin of dorsal oval (Fig. 1a, b).

Abdominal somites smooth; somite 1 smallest, with 2 short setae at each side on posterior half; somite 2 largest, with small setae posteriorly; somites 3–5 wider than long, with 1 tuft of dense setae posterolaterally on each side; somite 6 bilobed, anterior lobe larger than posterior, with long setae on posterior margin (Fig. 1f).

Eyestalk dorsally flattened, not extending to end of first segment of antennular peduncle; cornea subterminal, hemispherical, pigmented; anterior margin of eyestalk with angled projection (Fig. 1c). Antennular peduncle shorter than antennal peduncle; segment 3 of antennular peduncle longer than segments 1 and 2. Segment 4 of antennal peduncle as long as segment 5, segments 1–3 short.

Mandible with 1 sharp tooth on molar process; incisor process with 10 sharp teeth, median longest; mandibular palp 3-segmented, third article longest, bearing

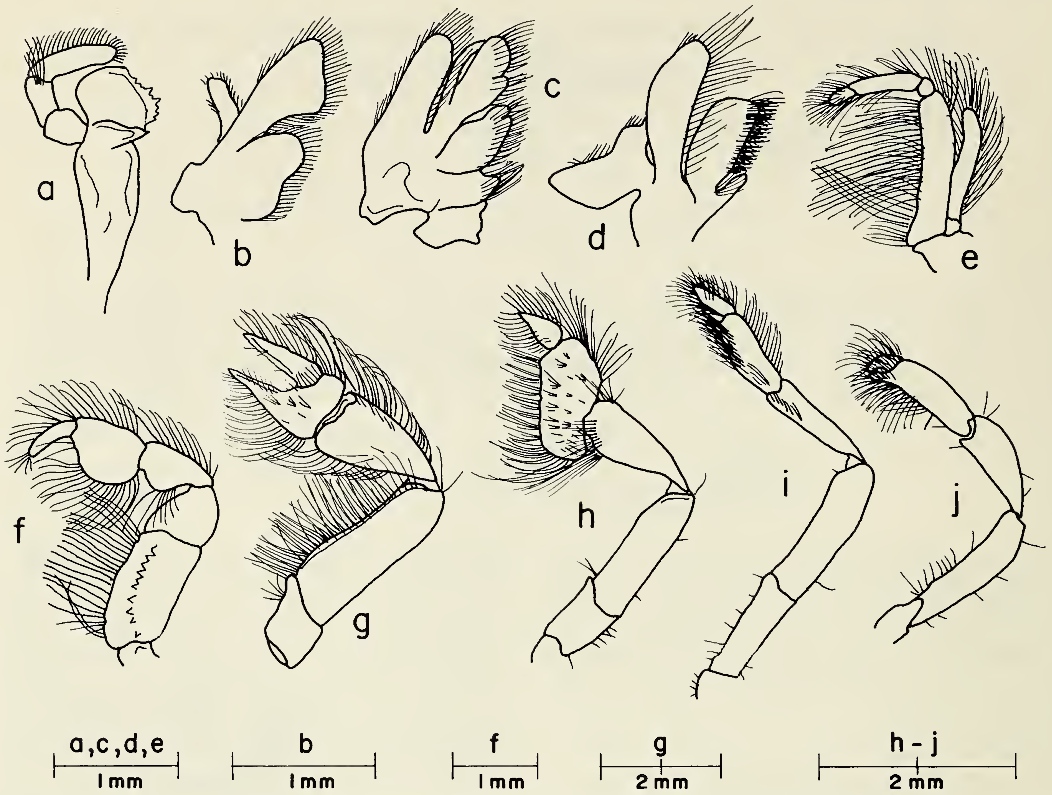

Fig. 2. *Sergio guaiqueri,* new species, paratype male, IOV, cl 2.5 mm. a, Mandible; b, Maxillule; c, Maxilla; d, First maxilliped; e, Second maxilliped; f, Third maxilliped (inner face); g, Second pereopod; h, Third pereopod; i, Fourth pereopod; j, Fifth pereopod.

numerous setae on outer surface (Fig. 2a). Maxillule with elongate lobe on coxo-basal endite, palp slender, unsegmented. Maxilla with elongate lobes on both coxal and basal endites, scaphoganthite with anterior lobe rounded (Fig. 2b, c).

First maxilliped with short basal endite. Second maxilliped with exopod shorter than merus of endopod, dactyl short. Third maxilliped without exopod; ischium-merus subpediform, ischium with crista dentata on inner surface, with about 10 teeth; propodus longer than wide, distal margin emarginate, concave (Fig. 2d–f).

Chelipeds dissimilar, unequal. Major cheliped strong, ischium elongate, widening distally, ventral margin finely serrated; merus broad, ventrally denticulate, bearing long setae, convex, without hooks or spines; carpus subquadrate, longer than wide, ventral margin evenly convex, smooth; propodus with palm as long as carpus, ventral margin irregular, except on fixed finger, with long setae; cutting edge of fixed finger with 3–4 small teeth; dactylus slightly shorter than palm, with tufts of setae on dorsal margin, curved ventrally, tip hooking over outer surface of fixed finger, cutting edge with 3–4 small teeth on proximal half (Fig. 1d).

Ischium of minor cheliped narrow, margins diverging distally; merus broad on distal half, lacking ventral keel, serrations or hooks; carpus elongate, more than 2 times longer than wide, with long setae on ventral margin; dactylus longer than palm, both dactylar and fixed finger with cutting edges denticulate (Fig. 1e).

Second pereopod chelate, fixed finger and

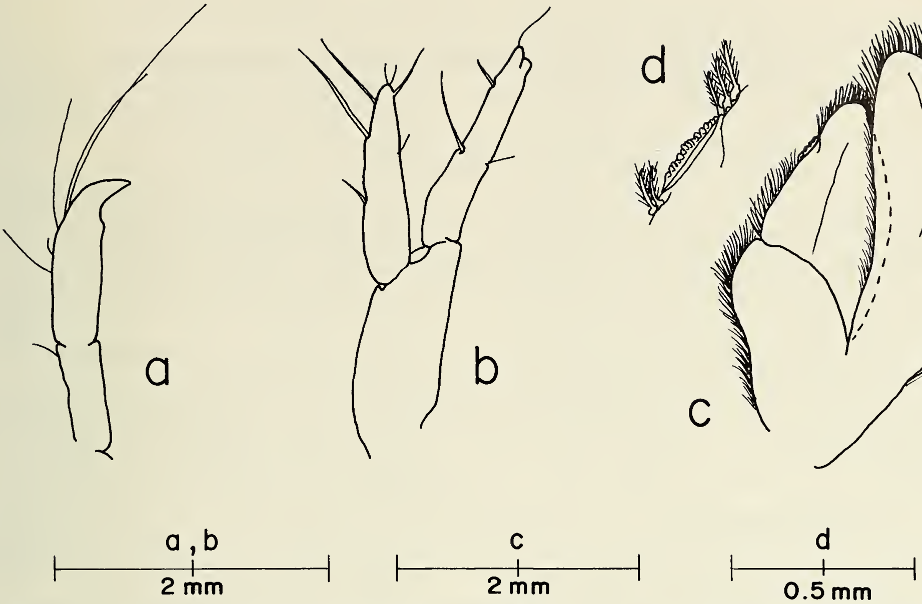

Fig. 3. *Sergio guaiqueri,* new species, paratype male, IOV, cl 2.5 mm. a, First pleopod; b, Second pleopod; c, Third pleopod; d, Appendix interna of third pleopod.

dactylus symmetrical, both cutting edges pectinate; carpus widening distally. Margins of chela and carpus setose; ventral margin of merus with row of evenly spaced long setae. Third pereopod with carpus widening anteriorly; propodus 2 times wider than long, outer face covered with numerous tufts of short setae; dactylus short, articulating on upper anterior margin. Fourth pereopod subchelate, with carpus and propodus broader distally; propodus and dactylus with setae, densely setose grooming apparatus on ventral margin of propodus. Fifth pereopod chelate, propodal finger short; dactylus elongate, apex rounded. Propodus and dactylus setose; carpus widening distally (Fig. 2g–j).

Telson short, nearly 2 times wider than long, subtrapezoidal, posterior margin divided by shallow median cleft into broadly rounded posterolateral lobes. Uropods longer than telson; uropodal protopod bilobed, lacking spines; exopod broad, longer than endopod, upper exopodal plate shorter than lower plate, posterior margin flattened; endopod elongate, longer than wide, margins converging distally, apex rounded (Fig. 1g).

First pleopod of male uniramous, 2-segmented, bearing a few setae, terminal segment hooked at tip (Fig. 3a). Second pleopod biramous, endopod and exopod of about the same length, blade-like exopod, with a few setae; endopod with a slender lobe and few setae. Appendix interna and appendix masculina absent (Fig. 3b). Pleopods 3–5 alike, exopods and endopods foliaceous; endopods with small appendix interna embedded on inner margins; margins of endopods and exopods with plumose setae (Fig. 3c, d).

Distribution.—Known so far only from north of Jose, Anzoátegui State, Venezuela.

Etymology.—The specific name honors an ancient indian tribe Guaiquerí from the northern Venezuelan coast, and the research vessel of the IOV.

Remarks.—*Sergio guaiqueri,* new species, is most closely related to *S. guara.* The two can be separated by differences in the shape of the corneae, margins of carpus and merus, and cutting edge of the dactyl of the major cheliped. In the new species, the corneae are larger, and more inflated than in *S. guara*; the interior margin of carpus of the major cheliped is smooth, and the lower margin of merus is convex and denticulate, whereas in *S. guara* the carpus of major cheliped has the proximal half of its interior margin serrated, and the merus has a strong serrated tooth near the proximal extremity of the lower margin. Additionally, the cutting edge of the dactyl of the major cheliped has only 3–4 small teeth in *S. guaiqueri,* whereas in *S. guara* the cutting edge has four strong irregular teeth.

Acknowledgments

The authors are indebted to Dr. R. Lemaitre and Dr. R. B. Manning, USNM, for their helpful advice concerning the status of the species and who were kind enough to examine the holotype, and offering numerous valuable suggestions to the manuscript. We are grateful to Dr. D. L. Felder, University of Southwestern Louisiana, for his constructive comments on an earlier version of this manuscript. We especially wish to thank F. Arocha P., Rosenstiel School of Marine and Atmospheric Science, University of Miami, for providing most of the necessary literature.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(1):107-116. 1995.

Heteranthessius hoi, a new species (Copepoda: Pseudanthessiidae) from a sea-anemone in the Straits of Gibraltar, with remarks on the genus

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Abstract.—An unknown species of *Heteranthessius* is described as *H. hoi* and is compared with the three previously known species: *H. dubius* (T. Scott 1903), *H. scotti* Bocquet et al., 1959 and *H. furcatus* Stock, 1971. This is the first time male and female of this genus have been found together. The diagnostic characters of this species are two claws on the terminal segment of the second antenna and third segment of leg 4 exopodite with the armature formula II, I, 5. The diagnosis of the genus is modified to incorporate these and other features.

Resumen.—Se describe una nueva especie del género *Heteranthessius, H. hoi,* y se compara con las tres especies conocidas hasta ahora: *H. dubius* (T. Scott 1903), *H. scotti* Bocquet et al., 1959 y *H. furcatus* Stock, 1971. Esta es la primera vez que se ha encontrado el macho y la hembra de este género juntos. Las características típicas de la especie son: dos garfios terminales del último segmento de la segunda antena y la armadura del tercer segmento del exopodito de la pata cuarta, II, I, 5. Se modifica la diagnosis del género incorporando éstas y otras características.

In the course of research on copepod fauna associated with marine invertebrates from the Straits of Gibraltar and nearby areas, a female and male of copepod belonging to the genus *Heteranthessius* were found in the coelenteron of the sea-anemone *Aiptasiogeton pellucidus* (Hollard 1848). The genus *Heteranthessius* was erected by T. Scott (1904) for *Paranthessius dubius* T. Scott, 1903. *Paranthessius* T. Scott was replaced by *Heteranthessius* since the former name had been preoccupied by *Paranthessius* Claus, 1889, another copepod crustacean.

Three species have been recognized in *Heteranthessius*: *H. dubius* (T. Scott 1903), *H. scotti* Bocquet et al., 1959 and *H. furcatus* Stock, 1971. *Heteranthessius dubius* was described from a male dredged in British waters. *Heteranthessius scotti* was found in washings of the calcareous alga *Lithophyllum incrustans* from Brittany. *H. furcatus* was collected in the branchial cavity of the ascidian *Microcosmus sabatieri*; this was the first time that the genus was found in Mediterranean waters. Two males of an undetermined *Heteranthessius* species were collected recently from the Irish coasts (Holmes & Gotto 1992). In this paper, *Heteranthessius hoi,* new species, is described and compared with the other species of the genus. The diagnosis of *Heteranthessius* is modified to accommodate the new features shown by *H. hoi.*

Material and Methods

Aiptasiogeton pellucidus was collected on stones from the infralittoral zone (4 m deep).

The copepods were removed by dissection of the sea-anemone and preserved in 70% ethanol. Because the purpose of host dissection was not to search for symbiotic copepods, the male specimen was slightly damaged. The specimens were stained with chlorazol black, dissected under a steromicroscope. Permanent mounts were made in lactophenol and sealed using entellan. All figures were drawn with the aid of a camera lucida. The letter after explanation of each figure refers to the scale at which it was drawn.

Order Poecilostomatoida Thorell, 1859
Family Pseudanthessiidae Humes & Stock, 1972
Genus *Heteranthessius* T. Scott, 1904

Diagnosis (modified from Humes & Stock 1973).—Body of female transformed, prosome swollen. Body of the male cyclopiform, elongate. Urosome in female 5-segmented, in male 6-segmented. Caudal ramus with 5 or 6 setae. First antenna 7-segmented. Second antenna 4-segmented, with one or 2 claws. Mandible consisting of broad basal area and 2 unequal slender, recurved lashes with denticulated edges. In females lashes may be partially fused or overlapping, so that it is difficult to distinguish them. First maxilla with 2 terminal elements. Second maxilla with terminal armature consisting of one long spine, terminally bifurcate in female, plus a short seta. Maxilliped in female non-prehensile, 3-segmented with rounded or pointed tip, in male prehensile, 4-segmented (that distal part of claw represents a fourth segment). Legs 1–4 with 3-segmented rami except leg 4 endopod which consists of a single small segment or knob with one or 2 terminal elements. Setae on all 4 legs short in female, long and plumose in male. Leg 4 exopodite with terminal segment having III, I, 5 or II, I, 5. Leg 5 without a free segment and represented only by two setae.

Found free, associated with ascidians or actinian coelenterates.

Type species: *Heteranthessius dubius* (T. Scott 1903).

Heteranthessius hoi, new species
Figs. 1–5

Type material.—1 ♀ and 1 ♂ from the sea-anemone *Aiptasiogeton pellucidus* (Hollard 1848) at Patricia, Cádiz (Spain), Feb. 1990. The holotype female and allotype male have been deposited in the Museo Nacional de Ciencias Naturales of Madrid, Spain (MNCN lot n° 20.04/334).

Description.—Female: Body transformed (Fig. 1a, b); length (not including setae on caudal rami) 2 mm and greatest width 1 mm, based on one specimen in 70% ethanol. Ratio of length to width of prosome 1.5:1. Ratio of length of prosome to that of urosome 3.8:1. Separation of pedigers weakly defined. Genital segment (Fig. 1c) wider than long, 258 × 387 μm. Genital areas located dorsolaterally on widest part of segment. Postgenital segments from anterior to posterior 45, 58, and anal segment 142 μm long. Caudal ramus about 3 times longer than wide. One outer anterolateral seta 96 μm, dorsal seta 32 μm, outermost terminal seta 96 μm, intermost terminal seta 109 μm, and two long median terminal setae 167 μm (outer) and 251 μm (inner). All setae naked. Rostrum rounded posteroventrally.

First antenna (Fig. 1d) about 408 μm long, lengths of 7 segments (measured along their posterior nonsetiferous margins) 48 (87 μm along anterior margin), 132, 48, 45, 64, 42 and 29 μm, respectively. Formula for armature 4, 12, 2, 4, 4+1 aesthete, 2 and 6 setae. All setae naked.

Second antenna (Fig. 1e) 4-segmented. First segment, 74 μm along its outer edge, 154 μm along its inner edge; remaining segments, 106, 42, 87, respectively. Formula for armature: 1, 1, 3, and 3 setae + 2 unequal claws. All elements naked.

Labrum (Fig. 1f), with two posteroventral lobes, with medial projection. Paragnaths smooth.

Mandible (Figs. 1g, 5a) with concave side

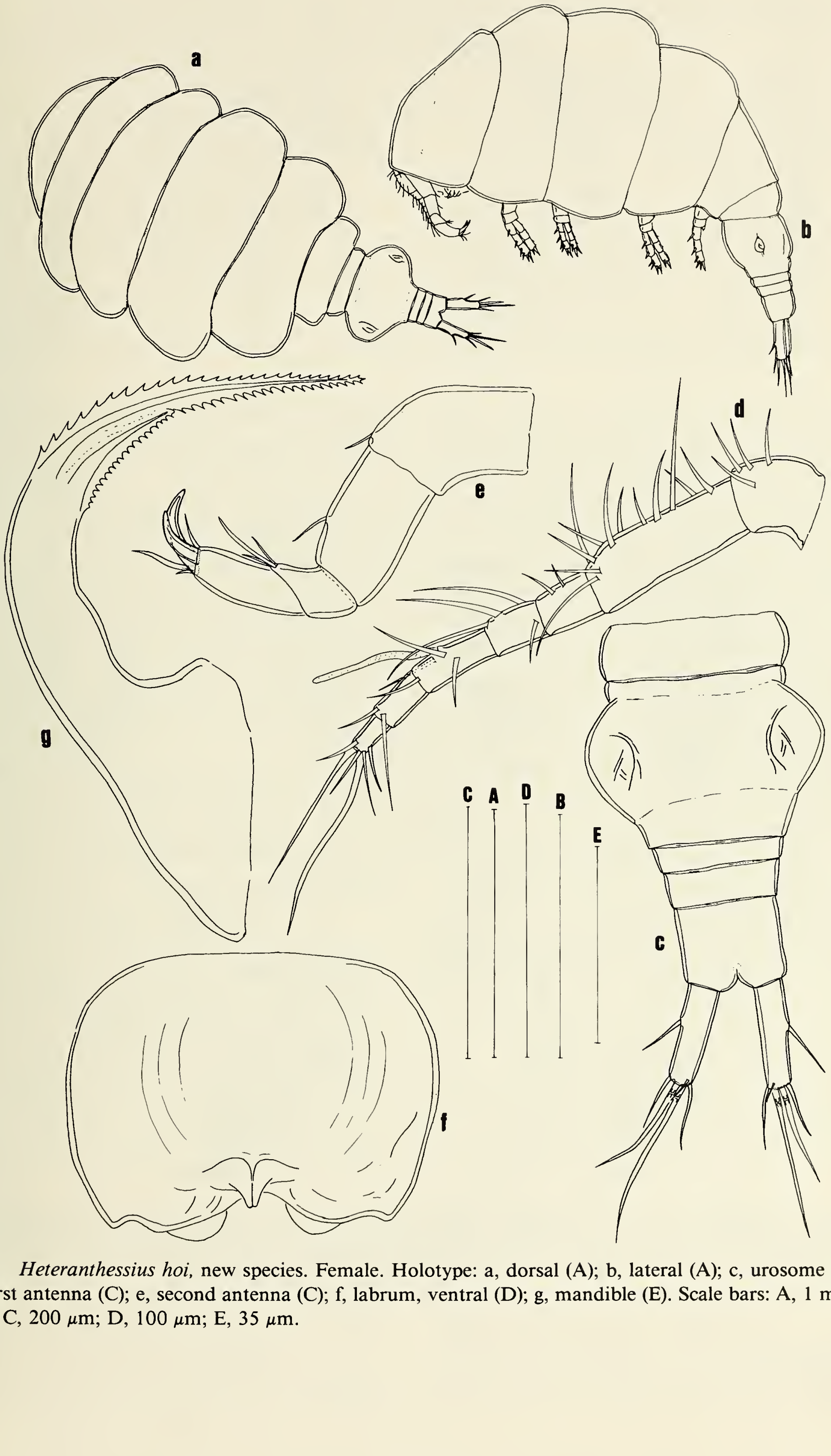

Fig. 1. *Heteranthessius hoi,* new species. Female. Holotype: a, dorsal (A); b, lateral (A); c, urosome dorsal (B); d, first antenna (C); e, second antenna (C); f, labrum, ventral (D); g, mandible (E). Scale bars: A, 1 mm; B, 400 μm; C, 200 μm; D, 100 μm; E, 35 μm.

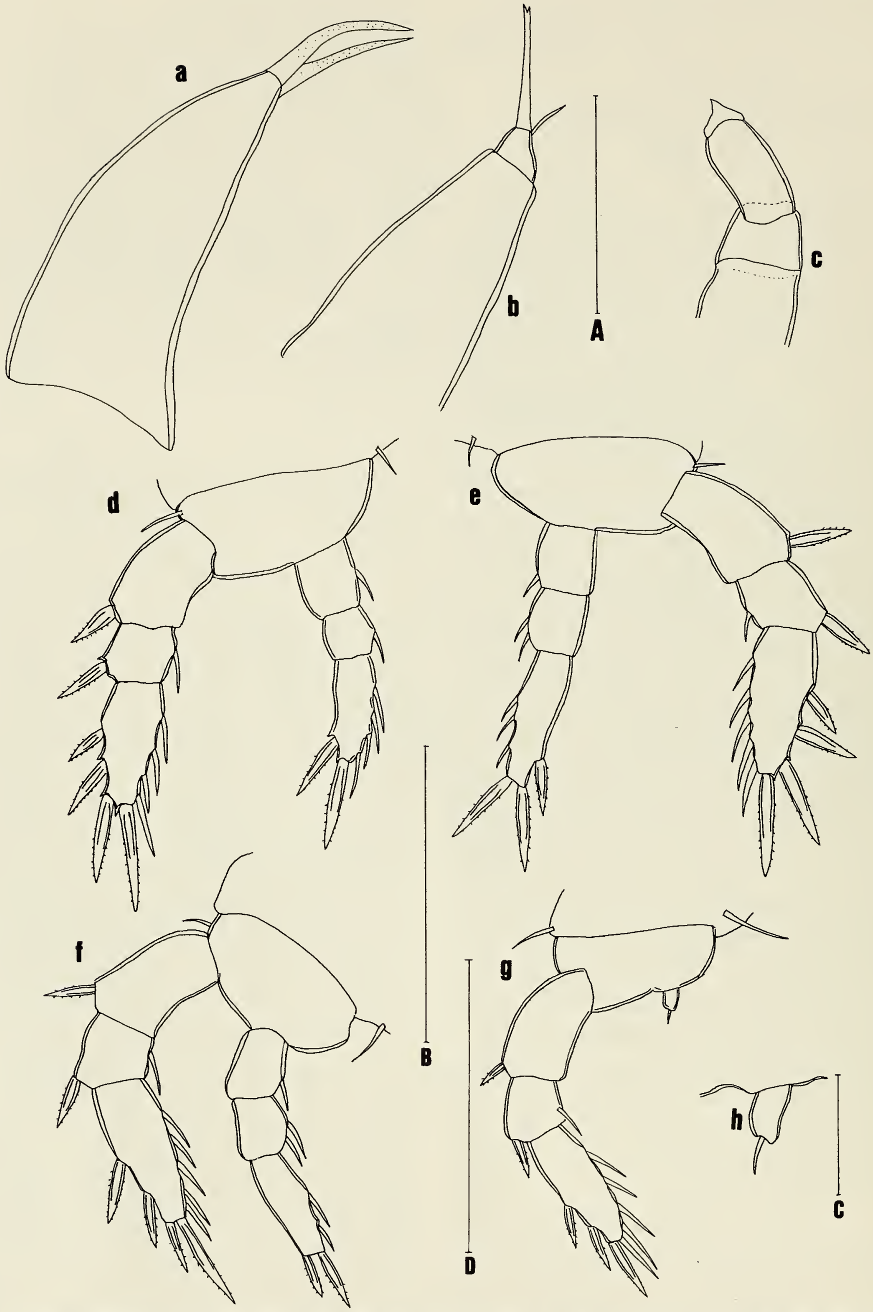

Fig. 2. *Heteranthessius hoi,* new species. Female. Holotype: a, first maxilla (A); b, second maxilla (D); c, maxilliped (D); d, leg 1, anterior (B); e, leg 2, anterior (B); f, leg 3, anterior (B); g, leg 4, anterior (B); h, leg 4 endopodite, anterior (C). Scale bars: A, 35 μm; B, 200 μm; C, 30 μm; D, 100 μm.

Table 1.—Comparison of the armature of legs 1–4 of the known females of *Heteranthessius*. (Roman numerals = spines; arabic numerals = setae; exp = exopodite; enp = endopodite.)

Leg		*H. scotti* Bocquet et al., 1959	*H. furcatus* Stock, 1971	*H. hoi*, new species
1st	exp:	I-0; I-0/I-1; II,I,3/III,I,4	I-0; I-1; III,I,4	I-0; I-1; III,I,4
	enp:	0-0; 0-0; II,4	0-0; 0-1; II-4	0-1; 0-1; II-4
2nd	exp:	I-0; 0-0; II,I,5/II,I,4	I-0; I-1; III,I,5	I-0; 0-1; II,I,5
	enp:	0-0; 0-0; III,3/III,0	0-0; 0-2; III-3	0-1; 0-2, III-3
3rd	exp:	I-0; I-1; III,I,5	I-0; I-1; III,I,5	I-0; 0-1; III,I,5
	enp:	0-0; 0-2; II,2/I,0	0-0; 0-2; III,2	0-1; 0-2; II-2
4th	exp:	I-0; I-1; III,I,5	I-0; I-1; III,I,5	I-0; I-1; II,I,5
	enp:	I-0	II-0	I-0

produced into 2 spinulose lashes. First lash long; second smaller and apparently partly fused to long lash.

First maxilla (Fig. 2a) unilobated and elongate with 2 terminal setae subequal in length. Second maxilla (Fig. 2b), 2-segmented, first segment unarmed, second trapezoidal, small with a strong terminally bifid spine (13.8 μm) and one seta (6.3 μm). Maxilliped (Fig. 2c) 3-segmented. First and second segments unarmed, third small and pointed.

Legs 1–4 (Figs. 2d.g) with 3-segmented rami, except leg 4 endopodite (Fig. 2h) which consists of single small segment with one seta shorter than segment. Formula for armature as in Table 1. Setae of leg rami, basis and coxae small and naked.

Leg 5, represented by 2 naked setae in other species of genus, not observed here.

Male: Body cyclopiriform (Fig. 3a). Pediger 1 fused with cephalosome, remaining pedigers clearly defined. Length (excluding setae on caudal rami) 1.4 mm, greatest width 423 μm, based on one specimen in 70% ethanol. Ratio length to width of prosome 2:1. Ratio length of prosome to that urosome 1.6:1.

Leg 5 (Fig. 3c) small, 11 × 18 μm, and bearing two setae. Genital segment (Fig. 3b) as long as wide. Four postgenital segments from anterior to posterior 74 × 143, 52 × 134, 35 × 95, and 69 × 95 μm.

Caudal ramus resembling that of female, 122 × 52 μm, length/width ratio 2.3:1. Setae plumose, except dorsal seta. Rostrum rounded posteroventrally. First antenna (Fig. 3e) similar to that of female, formula for armature 4, 11+2 aesthetes, 3, 3+1 aesthete, 2, 7+1 aesthete. Second antenna (Fig. 3f) similar to that of female, but terminal claws more slender and longer. Labrum (Fig. 3g) and paragnaths as in female.

Mandible (Figs. 3h, 5b) more slender than that of female, with lashes well separated. First maxilla (Fig. 4a) smaller than that of female, with length of both setae similar to length of segment. Second maxilla (Fig. 4b) similar to female; second segment bearing a long (not bifid) spine and one seta.

Maxilliped (Fig. 4c) 4-segmented; first, second and third segments unarmed; last segment transformed into long curved claw with one seta at basis. Inner surface of claw with spinules.

Legs 1–4 (Fig. 4d–g) with 3-segment rami. Leg 4 endopodite reduced unisegmented with one long seta 3.8 times as long as segment. Formula for armature as in Table 2. Setae of rami and coxae of legs plumose; those on basis naked.

Leg 5 (Fig. 3c) with 2 naked setae, subequal in length.

Leg 6 (Fig. 3d) consisting of two scarcely plumose setae 47 μm and 44.5 μm.

Spermatophore not observed.

Sexual dimorphism.—The body is transformed with an inflated prosome in the fe-

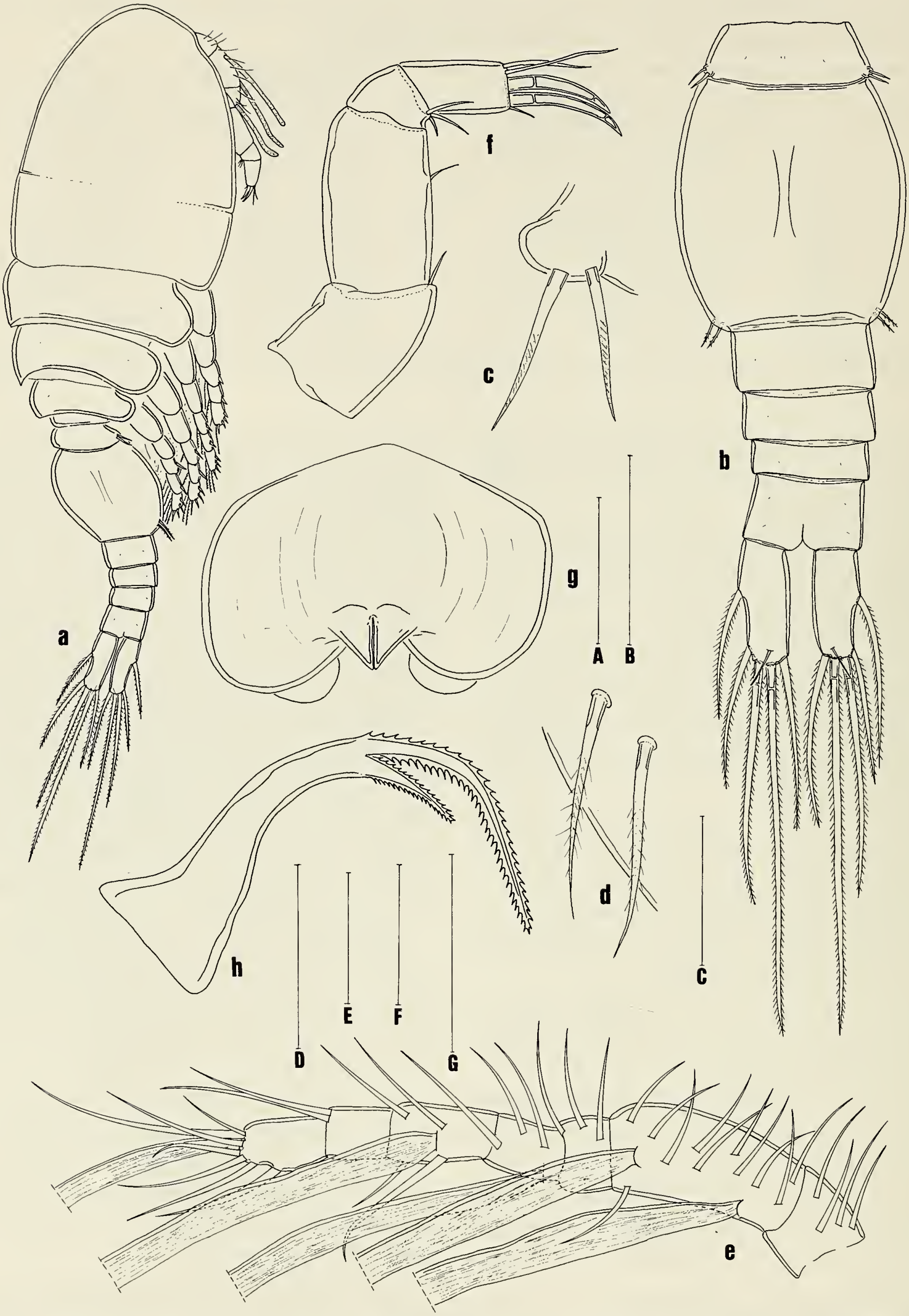

Fig. 3. *Heteranthessius hoi,* new species. Male. Allotype: a, dorsolateral (A); b, urosome, dorsal (B); c, leg 5, dorsal (C); d, leg 6, ventral (C); e, first antenna (D); f, second antenna (E); b, labrum, ventral (F); c, mandible (G). Scale bars: A, 300 μm; B, 200 μm; C, 30 μm; D, 100 μm; E, 100 μm; F, 50 μm; G, 30 μm.

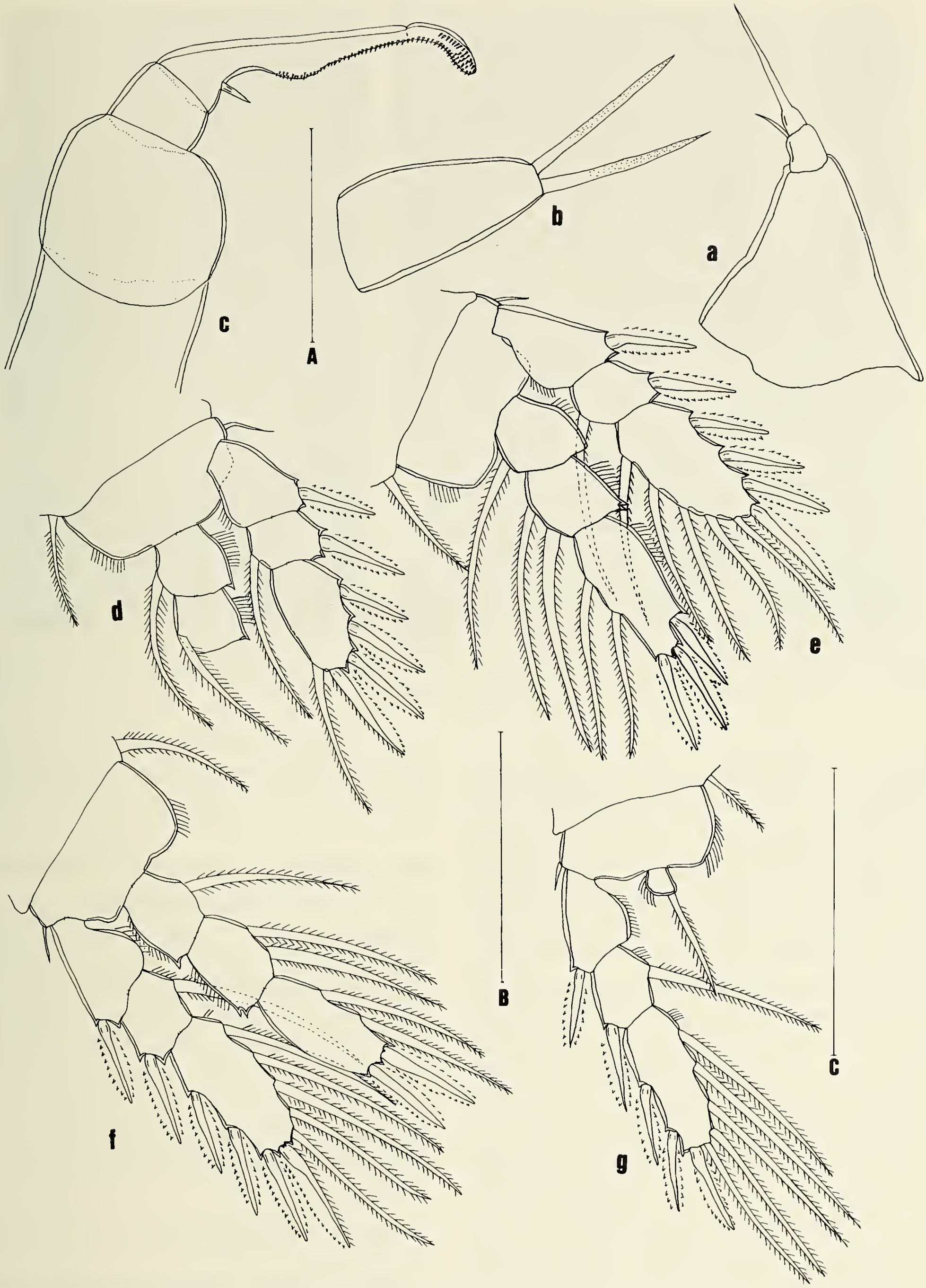

Fig. 4. *Heteranthessius hoi,* new species. Male. Allotype: a, second maxilla (B); b, first maxilla (A); c, maxilliped (B); d, leg 1, anterior (C); e, leg 2, anterior (C); f, leg 3, anterior (C); g, leg 4, anterior (C). Scale bars: A, 40 μm; B, 100 μm; C, 200 μm.

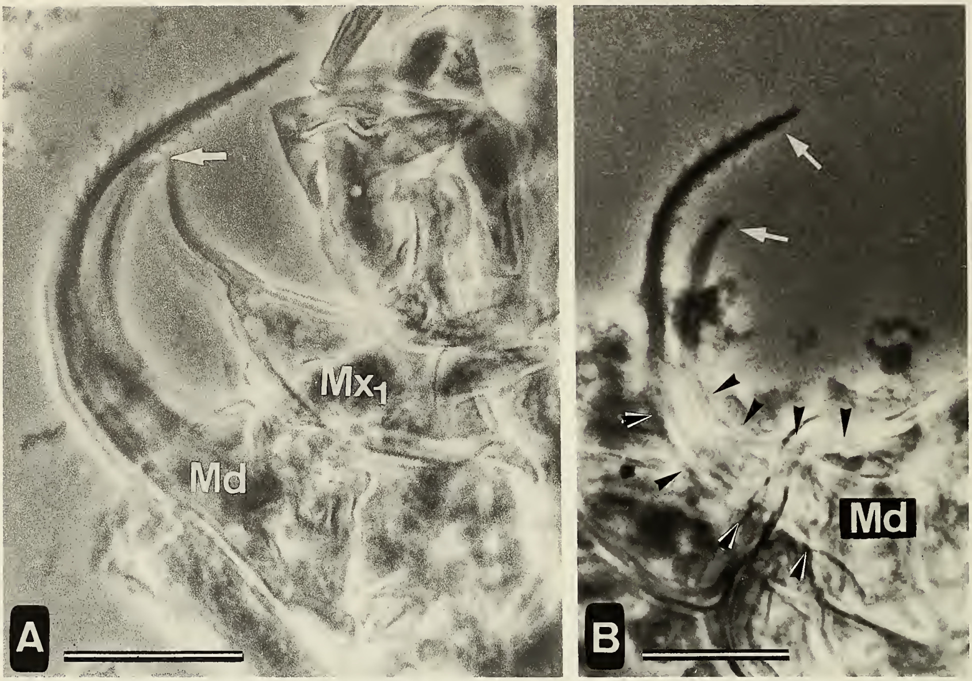

Fig. 5. *Heteranthessius hoi,* new species: A, mandible of female; B, mandible of male. Notice lashes (white arrows) and basal portion (black arrows). Scale bars: 30 μm.

male, but cyclopiriform in male. The first antenna possesses only one aesthetasc in the female but five in the male. Terminal claws of the second antenna are more slender in the male than in the female. The lashes of the mandible are more divergent in the male than in the female. The elements of the first maxilla are proportionately longer in the male than in the female. The terminal spine of the second maxilla is bifurcated in the female and simple in the male. Sexual dimorphism in the maxilliped is as in other lichomolgoidean genera, 4-segmented and prehensile in the male and very simplified and reduced in the female. The armature of legs 1–4 is reduced in the female and free-swimming type in the male. The caudal rami are longer in the female than the male. Setae of the caudal rami are plumose in the male and naked in the female.

Etymology.—This species is dedicated to Dr. Ju-Shey Ho (Long Beach, California) in recognition of his valuable contributions to the knowledge of parasitic and commensal copepods.

Key to species of the genus *Heteranthessius*

Known Females
(*Heteranthessius dubius* is not included)

1. Terminal segment of second antenna with 2 claws; third segment of leg 4 exopodite having armature formula II, I, 5 .... *H. hoi*
   Terminal segment of second antenna with one claw; third segment of leg 4 exopodite having armature formula III, I, 5 2
2. Length/width ratio caudal ramus 3:1 or longer; third segment of maxilliped pointed; single segment of leg 4 endopodite with 2 elements .... *H. furcatus*
   Length/width ratio of caudal ramus less than 2.3:1; third segment of maxilliped rounded; single segment

of leg 4 endopodite with one element . . . . *H. scotti*

Known Males
(*Heteranthessius scotti* and *H. furcatus* are not included)

1. Terminal segment of second antenna with 2 claws; third segment of leg 4 exopodite having armature formula II, I, 5 . . . . *H. hoi*
   Terminal segment of second antenna with one claw; third segment of leg 4 exopodite having armature formula III, I, 5 . . . . *H. dubius*

Table 2.—Comparison of the armature of legs 1–4 of the known males of *Heteranthessius*. (Roman numerals = spines; arabic numerals = setae; exp = exopodite; enp = endopodite.)

Leg		*H. dubius* (T. Scott, 1903)	*H. hoi*, new species
1st	exp:	I-0; I-1; III,I,4	I-0; I-1; III,I,1(?)
	enp:	0-I; ?; ?	I-0; 0-1; ?
2nd	exp:	?; ?; ?	I-0; I-1; III,I,5
	enp:	0-1; 0-2; III-3	0-1; 0-2; III-2
3rd	exp:	I-0; I-1; III,I,5	I-0; 0-1; III,I,5
	enp:	0-1; 0-2; III-2	0-1; 0-2; II-2
4th	exp:	I-0; I-1; III,I,5	I-0; I-1; II,I,5
	enp:	0-0	0-1

Discussion

With the discovery of *Heteranthessius hoi*, four species of the genus are now known. The host specificity at the generic level is not clear because hosts of *Heteranthessius dubius* and *H. scotti* are unknown; *H. furcatus* was found in an ascidian and *H. hoi* in a sea-anemone. *Heteranthessius* are rarely found. *H. dubius* is known from the male, and *H. scotti* and *H. furcatus* from the female. Only *Heteranthessius hoi* is known from both sexes.

Two features of the genus *Heteranthessius* are not in a good agreement: the setation of the first antenna and the structure of the mandible. As to the formula of the first antenna, none of the described females of the genus (*H. scotti, H. furcatus* and *H. hoi*) has the same setation. The armature of *H. scotti* is 3, 9, 2, 4, 4 + 1, 3, 6; that of *H. furcatus* 3, 12, 4, 3, 4 + 1, 3, 6 + 1, and that of *H. hoi* 4, 12, 2, 4, 4 + 1, 2, 6. The three species have in common only the armature of the fifth segment, which bears 4 setae and 1 aesthete; *H. furcatus* has a second aesthete in the last segment. There is no concordance in the formula of the first antenna between the known males. The setation of *H. dubius* is 1, 5 + 2, 3 + 1, 1, 3 + 1, 2 + 1, 5 + 1 whereas that of *H. hoi* is 4, 11 + 2, 3, 3 + 1, 4 + 1, 2, 7 + 1. Such differences in the setation of the first antenna is rather rare for the genera Lichomolgoidea, they usually differ only in the number of aesthetes. These disimilarities in the armature of the first antenna (including differences between male and female) may indicate that *Heteranthessius* is highly a variable genus as reported for the genera *Amarda* Humes & Stock, 1972 and *Indomolgus*, Humes & Ho, 1966 (Humes & Stock 1973).

The genus *Paranthessius* Scott, 1903 was erected for *P. dubius*, which has two lashes on the mandible. However, *Heteranthessius scotti* and *H. furcatus* were described with a single lash. The study of both sexes in *H. hoi* has allowed us to corroborate the existence of two lashes in this structure (Fig. 5). As these lashes may be partially fused or overlapping in the female, the mandibles of *H. scotti* and *H. furcatus* should be re-examined. Until then, the diagnosis of the superfamily Lichomolgidea Humes & Stock, 1972 must be slightly modified to accommodate the mandible of the *Heteranthessius* species as follow: "Mandible simple, without terminal elements, but often attenuate into a slender lash, rarely two lashes." *Heteranthessius hoi* may be easily distinguished from the remaining species of the genus by the presence of two claws on the terminal segment of the second antenna and the third segment of the leg 4 exopodite having II, I, 5. The female of *Heteranthessius hoi* differs from *H. scotti* and *H. furcatus* in the armature of legs 1–4 (see Table 1), particularly in the endopodal segments of legs 1–3 and terminal segment of leg 4 exopodite. The labrum of a *Heteranthessius* species is described and illustrated for the first time. Setae on the segments of the second antenna are larger in *H. hoi* than in the remaining species. *Heteranthessius hoi* is similar to *H. scotti* in the shape of the first maxilla. The second maxilla of *H. hoi* has a smaller basal segment than that in the remaining species. The maxilliped of *H. hoi* and *H. furcatus* are acuminate terminally, but rounded in *H. scotti.* The caudal ramus is equal to or more than 3:1 longer than wide in *H. hoi* and *H. furcatus,* and 2.2:1 in *H. scotti.*

The male *Heteranthessius hoi* differs from *H. dubius* in the armature of legs (see Table 2). On inner margin of the third exopodite segment of the first leg, only one seta was observed in *H. hoi.* Because the right side of the copepod was damaged, the actual difference in the armature of this segment is impossible to ascertain. The unisegmented leg 4 endopodite is slightly larger in *H. hoi* than in *H. dubius.* This segment also bears a long plumose seta which is lacking in *H. dubius.* The mandible is longer and slender in *Heteranthessius hoi* than *H. dubius,* and the two basal elements present in *H. dubius* are lacking in *H. hoi.* The first maxilla carries two moderately long elements, longer in *H. hoi* than in *H. dubius.*

Acknowledgments

We thank Dr. A. G. Humes (Woods Hole, Massachusetts) and Dr. J. H. Stock (Amsterdam) for generous help with information and literature, and Dr. R. V. Gotto (Belfast, Northern Ireland) for revising the first draft of this manuscript and for valuable suggestions.

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Description of *Amphiascoides atopus*, a new species (Crustacea: Copepoda: Harpacticoida) from a mass culture system

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Abstract.—*Amphiascoides atopus,* a new species, is described from a mass culture system. Its natural habitats and distribution are unknown. This new species shares the possession of seven setae on the exopod 3 of leg 4 with ten other species in the genus. *Amphiascoides atopus* can be distinguished from congeneric species by the shape, relative length, and ornamentation of the setae on the leg 5 in both male and female. Possession of three setae grouped together on the proximal region of the second endopod segment of leg 2 distinguishes the males of this species from all other described males in this genus.

A species of harpacticoid copepod has been successfully kept in a mass culture system in our laboratory at the Department of Zoology and Physiology, Louisiana State University, Baton Rouge, LA. Approximately 300,000 individuals have been harvested from 2.5 m² culture surface area almost every day for more than six months, with no sign of population decline. Specimens used to start this culture were obtained from a commercial bioassay laboratory, where it was identified as a fouling species in culture tanks of marine fish and invertebrates. It was identified as an undescribed species of *Amphiascoides.* It was not possible to determine the source of the individuals present in the tanks as the origin of the various specimens was from many localities in the United States including other laboratories. Therefore, the natural habitat and the distribution of this new taxon remain unknown. In the United States three species of *Amphiascoides* (*A. lancisetiger* Lang, 1965, *A. petkovskii* Lang, 1965, *A. dimorphus* Lang, 1965) have been described from the coast of California and were collected from tidal pools, shell-sand intertidal, among algae and among stones (Lang 1965). On the Atlantic coast, the cosmopolitan *A. debilis* has been recorded from Scituate, MA living among algae by Rosenfield (1967). Specimens in the culture system display strong photophobia and have been successfully cultured in trays containing small stones, suggesting that they might come from the habitats typically reported for *Amphiascoides.* The culture system has been kept at a temperature of 23–26°C and 30‰ salinity.

Specimens examined came directly from our mass culture system. Hundreds of individuals were drawn from the system using a Pasteur pipet and fixed with formalin 4%. Type material was sorted under a stereo-dissecting microscope. Whole specimens were examined in lactic acid and dissected parts mounted in Hoyers mounting medium. All figures were drawn using a camera lucida connected to a Zeiss microscope. Details were checked on an Olympus BX 50 microscope using phase contrast. Type material and an additional lot of specimens were deposited in the collections of the National Museum of Natural History, Smithsonian Institution. Terminology follows that of Huys & Boxshall (1991).

Order Harpacticoida Sars, 1903
Family Diosaccidae Sars, 1906
Genus *Amphiascoides* Nicholls, 1941
Amphiascoides atopus, new species
Figs. 1–3

Material.—Holotype female, ethanol preserved (USNM 259892). Allotype male, ethanol preserved (USNM 259893).

Paratypes: two females dissected and preserved on slides (USNM 259894); two males dissected and preserved on slides (USNM 259898); 10 females (USNM 259895) and 10 males (USNM 259896) ethanol preserved. Additional lot with approximately one hundred adults and copepodites, ethanol preserved (USNM 259897). All specimens were drawn from culture system collections.

Description of female.—Length (tip of rostrum to end of caudal rami) of holotype, 841 μm; paratypes 780–1000 μm ($n = 10$). Body (Fig. 1a) moderately slender, slightly tapering towards the end. Rostrum (Fig. 1b) prominent, with pair of small sensory setae and tip finely serrate. Urosome (Fig. 1c), with ventro-lateral row of spinules on all segments; genital double somite with dorsolateral sign of subdivision; genital field with attached spermatophore as shown in Fig. 1c; third segment with ventral row of spinules; anal somite with distal border spinulate ventrally; operculum and pseudoperculum lacking. Caudal rami (Fig. 1d, e) about twice wider than long and bearing short spinules on inner margin; setae II, IV and V well developed; seta II as long as seta VI; seta VII triarticulate; setae II, III, VI and VII naked; seta IV spinulose on outer margin and with few spinules on inner margin, seta V sparsely spinulose on both margins.

Antennule (Fig. 1f). Eight-segmented. Armature as follows: (Roman numeral = segment; Arabic numeral = seta): I—1; II—10; III—5; IV—3 + aesthetasc; V—1; VI—4; VII—2; VIII—6 + aesthetasc.

Antenna (Fig. 1g). Coxa short, asetose. Allobasis partially divided by an incomplete suture on outer face and with one inner seta. Second endopod segment with two strong spines and row of spinules laterally; distal edge with one spiniform seta, four geniculate setae and one slender seta confluent at base with outermost geniculate seta. Exopod 3-segmented; proximal segment with plumose seta, second segment very short and asetose, terminal segment with one lateral and two apical setae, all pinnate.

Mandibular palp (Fig. 1h). Broad basis with three pinnate and one naked seta on distal edge. Endopod elongate, 2-segmented and with one strong and pinnate basal seta on and two sub-apical setae on first segment and three apical setae on second segment. Exopod 2-segmented, first segment with one basal seta, second segment with three plumose apical setae.

Maxillule (Fig. 1i). Praecoxa with row of spinules medially and at base of coxa; arthrite with two surface setae and seven elements on inner margin, two proximal-most elements ornamented with spinules. Coxa partially fused to basis and lacking epipodite and bearing two setae. Basis with one spinular row, two sub-distal and three distal setae. Exopod with two setae, inner-most pinnate; endopod with three setae, the outer-most pinnate.

Maxilla (Fig. 1j). Syncoxa with spinule rows medially and distally and with three endites, first two bearing two setae and distal endite bearing three setae. Allobasis with distal margin of endite bearing a fused claw and one seta. Endopod 3-segmented with one seta on first two segments and three setae on distal segment.

Maxilliped (Fig. 1k). Well developed and prehensile. Syncoxa with spinule rows and three stout and pinnate setae. Basis with a row of long spinules and two naked setae on inner margin. Endopod 1-segmented with a terminal claw twice as long as the segment and two accessory setae.

Leg 1 (Fig. 2a) with intercoxal sclerite wider than long, without ornamentation;

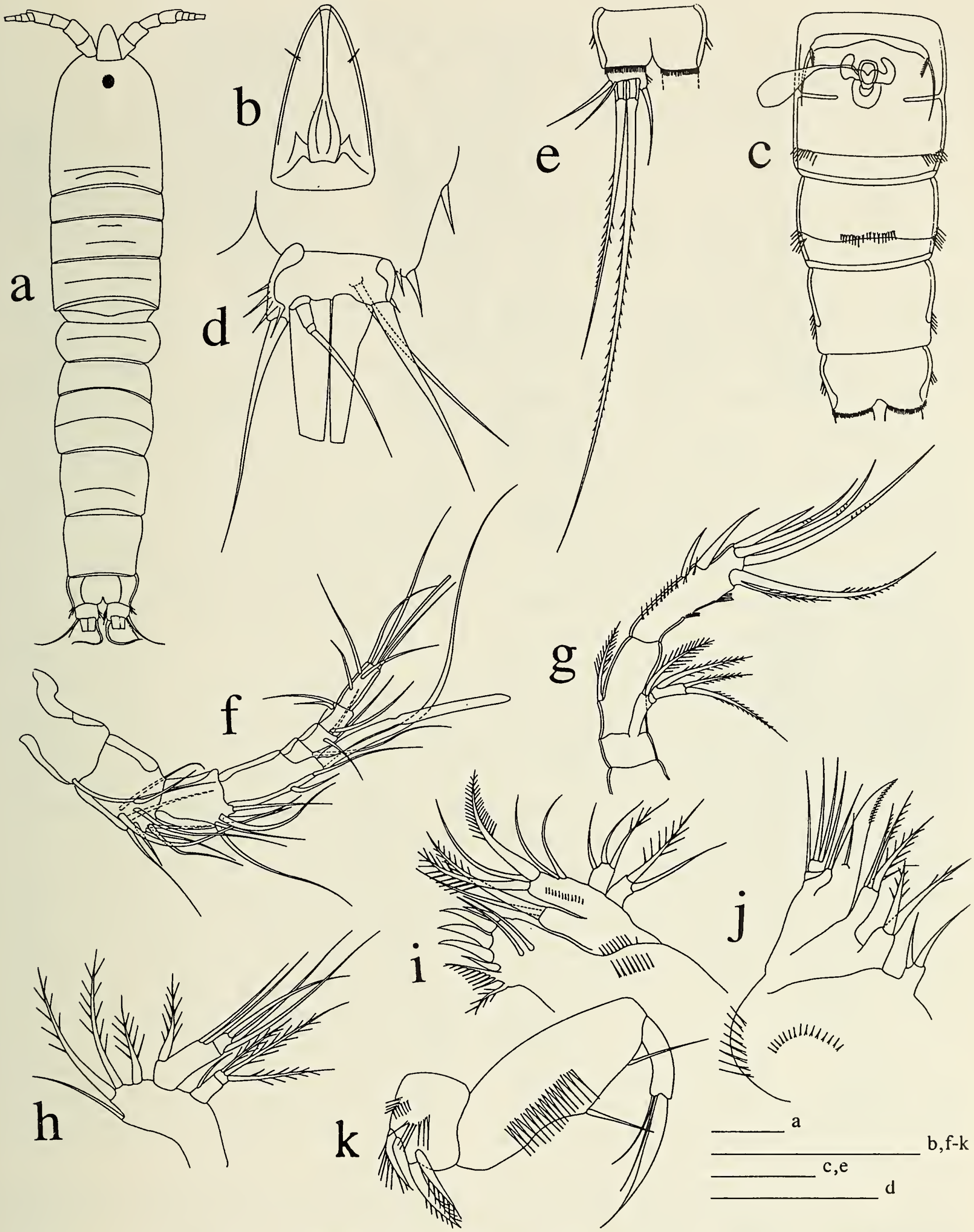

Fig. 1. *Amphiascoides atopus,* Female: a. Habitus, dorsal; b. Rostrum; c. Urosome (first somite omitted), ventral; d. Caudal ramus, dorsal; e. Anal somite and caudal ramus, ventral; f. Antennule; g. Antenna; h. Mandibular palp; i. Maxillule; j. Maxilla; k. Maxilliped. Scale bars: a, c, e = 100 μm; b, d, f–k = 50 μm.

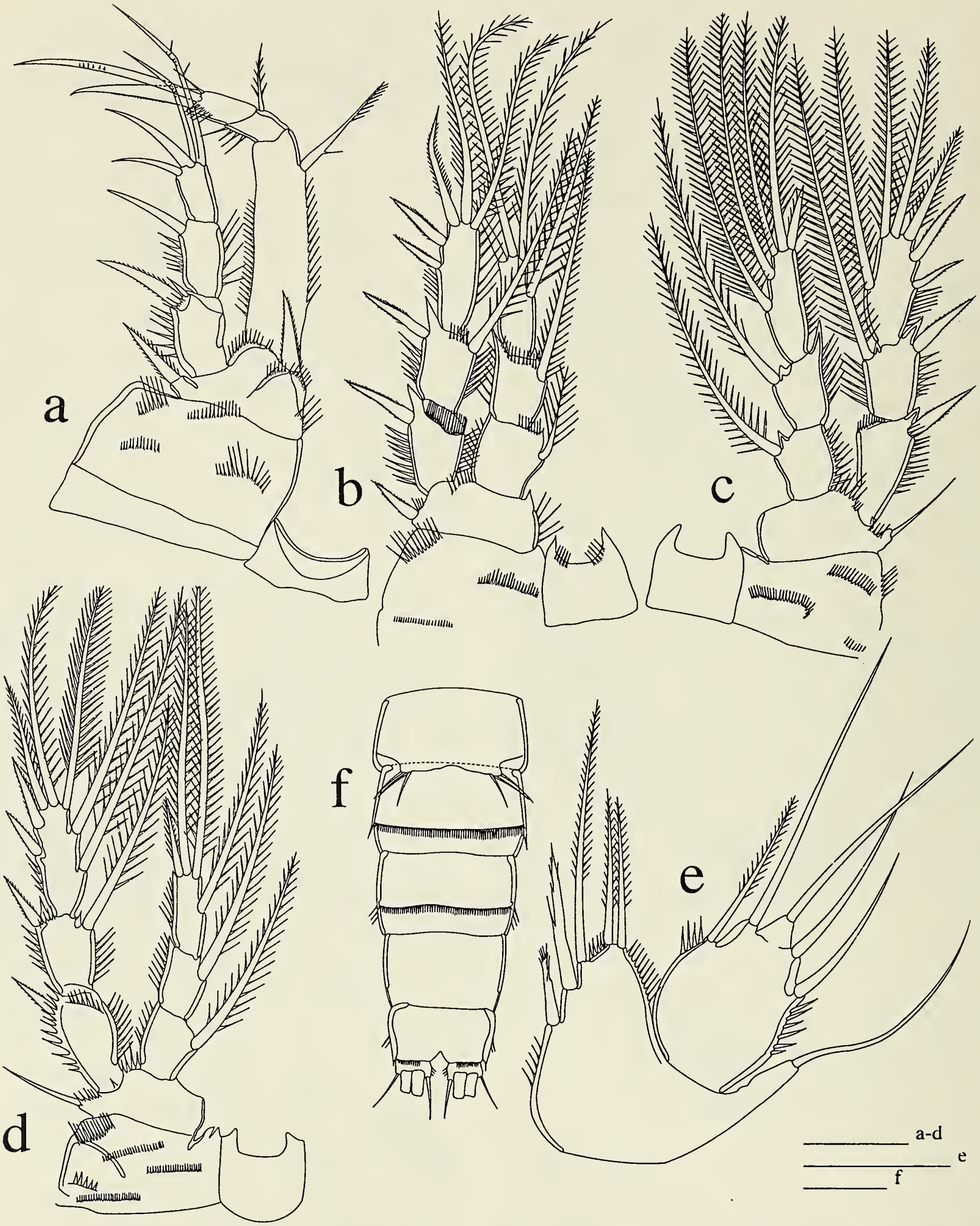

Fig. 2. *Amphiascoides atopus,* Female: a. Leg 1; b. Leg 2; c. Leg 3; d. Leg 4; e. Leg 5. Male: f. Urosome (first somite omitted). Scale bars = 100 μm.

coxa with four rows of spinules on anterior face; basis with rows of spinules on inner and distal margin and at base of inner spine; outer seta spiniform and as long as inner spine, both finely serrate; exopod and endopod 3-segmented; exopod with long spinules present on outer margin of proximal segment and both margins of second seg-

Table 1.—Spine and seta formula for legs 1 to 4.

	Coxa	Basis	Exopod segment 1 2 3	Endopod segment 1 2 3
Leg 1	0-0	1-I	I-0; I-0; I,I,2	0-1; 0-1; 0,2,1
Leg 2	0-0	1-0	I-0; I-1; III,I,1	0-1; 0-1; 1,2,1
Leg 3	0-0	1-0	I-0; I-1; III,I,2	0-1; 0-1; 1,2,2
Leg 4	0-0	1-0	I-0; I-1; III,I,3	0-1; 0-1; 1,2,1

ment; proximal and second segment lacking inner setae; terminal segment with two outer spines and two apical setae; first segment of the endopod reaching beyond the distal margin of the exopod, with spinules on outer and inner margins, and armed with inner seta plumose on inner margin of posterior end; second and third segments spinulose on outer margin; second segment with one plumose seta on inner margin; terminal segment with outer apical seta serrate on outer margin, inner apical seta geniculate and slender inner seta.

Legs 2 to 4 (Fig. 2b–d) with intercoxal sclerite about as long as wide and with spinules only on leg 2. Exopod 3-segmented; outer margin of all segments with a row of spinules; inner row of spinules present on all segments on leg 2, second segment on leg 3, and on first two segments on leg 4; distal margin spinulate on exopod 1 of all legs and exopod 2 leg 2. Endopod 3-segmented and with row of spinules on outer margin of all segments except endopod 3 leg 2; inner and distal margins spinulate only on endopod 1 and 2 leg 2. Spine and seta formula for legs 1 to 4 are shown in Table 1. Setation using system devised by Lang (1934) as follows:

	exopod	endopod
leg 1	0:0:0.2.2	1:1:1.2.0
leg 2	0:1:0.2.3	1:1:1.2.1
leg 3	0:1:1.2.3	1:1:2.2.1
leg 4	0:1:2.2.3	1:1:1.2.1

Leg 5 (Fig. 2e) with baseoendopod and exopod distinct. Baseoendopod with inner expansion reaching about midpoint of exopod, ornamented with a row of spinules and armed with three inner and two apical setae; two innermost setae irregularly spinulate; outer seta naked. Exopod 1.5 times longer than wide, with row of spinules on inner and outer margins and armed with five setae, the innermost pinnate and the remaining naked. Leg 6 (Fig. 1c) represented by two setae, inner seta short and pinnate on inner margin, outer setae long and naked.

Description of the male.—Length (tip of rostrum to end of caudal rami) of allotype 828 μm; paratypes 724–882 μm (n = 10). Body similar to the female. Urosome (Fig. 2f) with second and third somites not fused. Third and fourth segments with ventro-lateral row of spinules; anal somite with distal border spinulate ventrally. The male is identical to the female in all other respects.

Antennule (Fig. 3a) 8-segmented, geniculation between sixth and seventh segments. Armature as follows: (Roman numeral = segment; Arabic numeral = seta): I—1; II—8; III—7; IV—7 + spine + aesthetasc; V—1; VI—1 + 2 spines; VII—4; VIII—5 + aesthetasc.

Leg 2 endopod (Fig. 3b) 2-segmented; endopod 1 with row of spinules on outer margin and one short and pinnate seta on midpoint of inner margin. Endopod 2 produced to a strong mucruniform projection bearing three setae on inner margin, all grouped together on the proximal region of the segment, above a triangular lateral projection; proximal-most seta the shortest, sparsely spinulose on both margins; median seta the longest, 1.3 times longer than the segment and spinulate on inner margin; distal-most

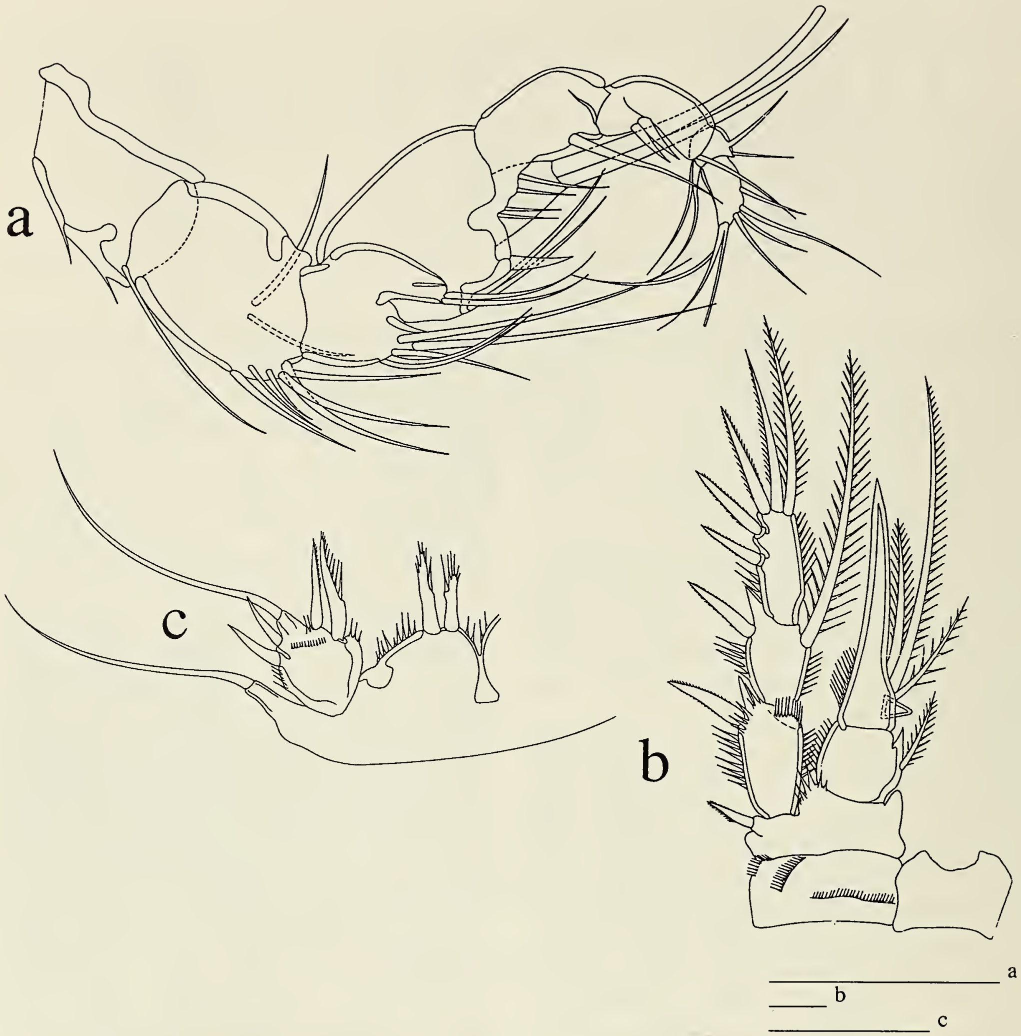

Fig. 3. *Amphiascoides atopus,* Male: a. Antennule; b. Leg 2; c. Leg 5. Scale bars = 50 μm.

seta the most robust, spinulate on both margins.

Leg 5 (Fig. 3c) with confluent baseoendopods, not separated by intercoxal sclerite; inner expansion with row of spinules and armed with two irregularly spinulate spines, outermost one slightly longer; outer seta naked and very long. Exopod 1.3 times longer than wide and ornated with minute spinules and bearing five elements; innermost spine the longest, spinulate distally on inner margin; second inner spine minutely pinnate distally on inner margin; middle setae naked and 2.5 times longer than the segment; two outer spines naked and equal in length. Leg 6 (Fig. 2f) represented by three naked setae set on a ventrolateral common plate.

Distribution.—Unknown.

Etymology.—The specific name is a Neo-Latin formation from Greek *a*-'without' + *topos*- 'place', used as an adjective with the masculine form *atopus.* It is used as an allusion to the fact that the type material has not been collected from the species natural habitats, as they remain unknown.

Remarks.—To the genus *Amphiascoides*

belong twenty named species and *Amphiascoides* sp. Becker & Schriver, 1979, from which hitherto only the male has been described. Both males and females of *A. atopus* can be distinguished from the other species of the genus by the shape, relative length and ornamentation of the setae on the leg 5.

Amphiascoides atopus shares with *A. brevifurca* (Czernivaski), *A. neglectus* (Norman & T. Scott), *A. subdebilis* (Willey), *A. lancisetiger* Lang, *A. petkovskii* Lang, *A. dimorphus* Lang, *A. nichollsi, A. bulbiseta* Pallares, *A. koltuni* and *A. breviarticulatus* Kunz, the leg 4 exopod three bearing 7 setae. The remaining species in this genus (*A. debilis* (Giesbrecht), *A. dispar* (T. Scott & A. Scott), *A. limicolus* (Brady), *A. littoralis, A. nanus* (Sars), *A. nanoides* (Sars), *A. sterilis, A. golikovi,* and *A. paradebilis* Tschislenko, have this segment armed with 6 setae. This character is not described for *A. proximus,* a poorly described species that is distinguished from *A. atopus* and all other species in the genus by possessing the baseoendopod leg 5 of the female with only four setae.

Among the species armed with seven setae on the leg 4 exopod 3, *A. brevifurca* differs from *A. atopus* by lacking inner setae on endopod 2 leg 1. *Amphiascoides nichollsi* is distinguished from *A. atopus* by having two projections on the tip of the rostrum, leg 1 endopod 1 1.3 times longer than the exopod. *Amphiascoides neglectus* differs from *A. atopus* in having the leg 1 endopod 1 1.4 times longer than the exopod and in the shape of the exopod leg 5, 2.6 times longer than wide. *Amphiascoides subdebilis* is distinguished from *A. atopus* in having the caudal seta VI shorter than seta III, leg 1 endopod 1 1.4 times longer than the exopod. *Amphiascoides lancisetiger, A. petkovskii,* and *A. dimorphus,* the three North American species described by Lang (1965), differ from *A. atopus* in having the mandibular exopod 3-segmented and bearing five setae and endopod with seven (*A. lancisetiger*) or eight setae (*A. petkovskii* and *A. dimorphus*), maxillule with four setae on the endopod and 11 (*A. lancisetiger*) or 10 elements (*A. petkovskii* and *A. dimorphus*) on the arthrite, maxilla with 2-segmented endopod, and leg 1 endopod 1 extending far beyond exopod. *Amphiascoides lancisetiger* and *A. petekovskii* further differ from *A. atopus* in having three terminal setae on the distal segment of the antenna exopod. *Amphiascoides bulbiseta* differs from the species here described in having the leg 1 endopod 1 1.5 times longer than the exopod, three terminal setae on the distal segment of the antenna exopod and caudal seta III modified. *Amphiascoides breviarticulatus* differs from *A. atopus* in having three terminal setae on the distal segment of the antenna exopod and inner seta of the leg 6 almost as long as the genital double segment. Finally, *Amphiascoides koltuni* also differs from *A. atopus* in having the leg 1 endopod 1 1.4 times longer than the exopod.

The male of *A. atopus* is readily distinguished from all described males of *Amphiascoides* and from *Amphiascoides* sp. Becker & Schriver, 1979, by the shape and insertion of the setae on the endopod 2 leg 2. This segment is always modified in *Amphiascoides,* but only in *A. atopus* are the three setae grouped together on the proximal region of the segment. In all other species the three setae are inserted on different positions on the inner margin. *Amphiascoides dispar* bears only four setae on the leg 5 exopod in the male, differing in this respect from *A. atopus* and all the other species in the genus. Males are unknown in *A. proximus* (T. Scott), *A. sterilis* (Monard), *A. littoralis* (T. Scott), *A. nichollsi* Lang, and *A. golikovi* Tschislenko. The leg 2 is not represented for *A. koltuni* Tschislenko, but it is apparent from the description that it is similar to *A. subdebilis* (Willey).

Morphological data were obtained from Lang (1948) for all species represented in his publication. Data were complemented by Noodt (1955) for *A. brevifurca*; Bodin

(1964), Noodt (1955), and Pallares (1975) for *A. subdebilis*; Tschislenko (1967) for *A. debilis*; Mielke (1974) for *A. nanus*; Becker (1970) for *A. dispar*. Original descriptions were used as the sole source for the remaining species cited.

A mass culture system of *A. atopus* (adult dry weight of 5 μg) may generate enough copepods to be used in mariculture as a high nutritional value food source for a wide variety of larval fish and shellfish (Sun & Fleeger, pers. comm.). The potential use of *Amphiascoides* as an alternative food source in fish farming has already been suggested in the literature (Walker 1970, Kahan 1979, Shirgur 1989).

Acknowledgments

Specimens were obtained from the culture system designed and maintained by Dr. Bin Sun. We are grateful to Jeff Tamplin for kindly inking the line drawings and to Dr. Janet Reid for her help with the bibliography. Support from Louisiana Sea Grant (Project Number R/A-35-PD) is gratefully acknowledged. G. Lotufo is financially supported by CNPq (Brazilian Federal Government).

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(1):125–129. 1995.

Hydroids colonizing the carapaces of the ostracode *Philomedes brenda* from the Beaufort Sea, Arctic Ocean

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Abstract.—A hydroid in the superfamily Bougainvillioidea or Pandeoidea colonizing the carapaces of the mydocopid ostracode *Philomedes brenda* (Baird 1850) collected in the Beaufort Sea, Arctic Ocean, is described and illustrated.

The Beaufort Sea forms that part of the Arctic Ocean lying north of Alaska and Canada, eastward of Point Barrow and westward of Banks Island and Prince Patrick Island. During a study of myodocopid ostracodes collected in bottom sediments of the continental shelf and slope of the Beaufort Sea from 1971 to 1976, an athecate hydroid was observed colonizing the outer surface of carapaces of the myodocopid ostracode *Philomedes brenda* (Baird 1850) (Kornicker 1988: abstract, fig. 2a, b).

The only previous report of Hydrozoa attached to the carapaces of myodocopid ostracodes was that of Baker (1975:78, fig. 17b, c, j) who observed them attached to *Euphilomedes carcharodonta* (Smith 1952), *Scleroconcha trituberculata* (Lucas 1931) and *Eusarsiella "tubipora"* (Darby 1965) on the southern California continental shelf. Baker (1975:78) reported that the same species appeared to be present on all three ostracode species and that both feeding and reproductive polyps were present, but it was not possible to identify the hydrozoan.

The purpose of the present paper is to describe the morphology of the hydrozoan on the Arctic ostracodes, and to further identify it. For the latter purpose the junior author made a nematocyst slide preparation from one of the hydranths. The nematocyst categories are of types widespread in the superfamilies Bougainvillioidea and Pandeoidea. Without more evidence concerning the life cycle of the hydroid it is not prudent to carry the identification to family or genus.

Hydroids of the Arctic Seas of Russia have been monographed by Naumov (1969), and those of northern Canada by Calder (1970, 1972). The Beaufort Sea species seems different from any mentioned in these works.

Specimens were prepared for the Scanning Electron Microscope by critical point drying. All specimens, including those in alcohol, have been placed in collections of the National Museum of Natural History, Department of Invertebrate Zoology, and have been assigned USNM numbers. Bottom collections were made with a Smith-McIntyre Grab (SMG) covering 0.1 square meters.

Class Hydrozoa
Subclass Hydroida
Order Leptolida
Superfamily Bougainvillioidea
or Pandeoidea
Figs. 1–3

Material.—All hydroids are on carapaces of *P. brenda* that have been given USNM

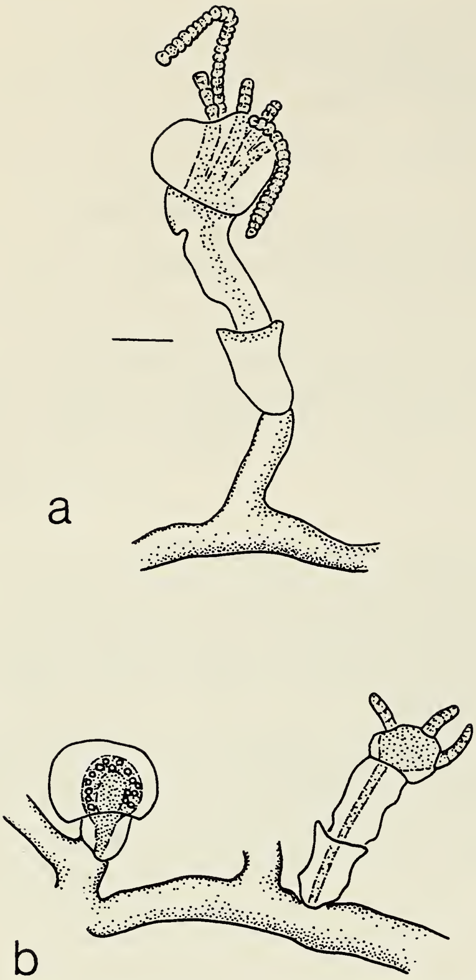

Fig. 1. Hydroid on *P. brenda* USNM 193284B: a, Hydranth with tentacles and T-shaped segment of pseudohydrorhiza; b, Hydranth with tentacles, medusa bud, and segment of pseudohydrorhiza. (Scale bar 0.1 mm.)

numbers. USCGC *Glacier,* cruise WEBSEC71, 12 Sep 1971, station C7184, sample SMG-1017-11; 76°16′48″N, 150°18′30″W, 831 m: USNM 193284A, adult female, USNM 193284B, ovigerous female. Ice Station OCS-1, 29 Oct 1975, 71°19′06″N, 152°34′00″W, 59 m: sample SMG-1092-16, USNM 158419A, ovigerous female; sample SMG-1091-12, USNM 158422, adult female. Ice Station OCS-1, sample SMG-1093-17, 30 Oct 1975, 71°21′36″N, 152°35′00″W, 102 m, USNM 158466, adult female. Ice Station OCS-2, station PPB-100, sample SMG-1137-14, 19 May 1976, 71°26′30″N, 152°38′42″W, 99 m, USNM 158536, adult female. Ice Station OCS-6, station PP-100, 3 Nov 1976, 71°21′54″N, 152°33′24″W, 99 m: sample SMG-1491-09, USNM 193282, adult female; sample SMG-1494-10, USNM 193283, ovigerous female.

Distribution.—Beaufort Sea, 59–831 m.

Description (Figs. 1–3).—Colonies on carapaces of adult and ovigerous females of *P. brenda* (carapace length 2.80–3.06 mm) (Figs. 2a, b, f, 3a, b, d). Pseudohydrorhiza filiform (stolon width about 0.07 mm; individual stolon length about 0.5 mm or less) (Fig. 3d); polyp with maximum length about 0.75 mm; hydrocaulus unbranched; hydranths with filiform tentacles forming single whorl (length of longest hydranths and tentacles about 0.46 mm) (Figs. 1, 2c–e, 3a, b, e, f); larger hydranths with 4–6 tentacles (Fig. 1a), but most with 2–4 (Figs. 2c–e, 3e, f); stalks with wrinkled perisarc and either cylindrical (Fig. 3a–c) or with indentation at base (Fig. 3b), some with proximal flaring section (Fig. 1). Sparse oval processes (possibly medusa buds or sporosacs, maximum diameter 0.17 mm) originating directly from pseudohydrorhiza (Fig. 1b).

Nematocyst complement of a hydranth comprising desmonemes (4.1 μm long × 2.8 μm wide) and heterotrichous microbasic euryteles (6.5 μm long × 2.8 μm wide). One specimen with a developing gonophore; development too early to determine whether it would become a medusa or a fixed gonophore.

Discussion.—The ostracode *P. brenda* has pan-Arctic distribution (Kornicker 1982:4). Juveniles 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 adults, both sexes become capable of swimming and rise in the water to couple. After mating, the female either rubs or breaks off its swimming

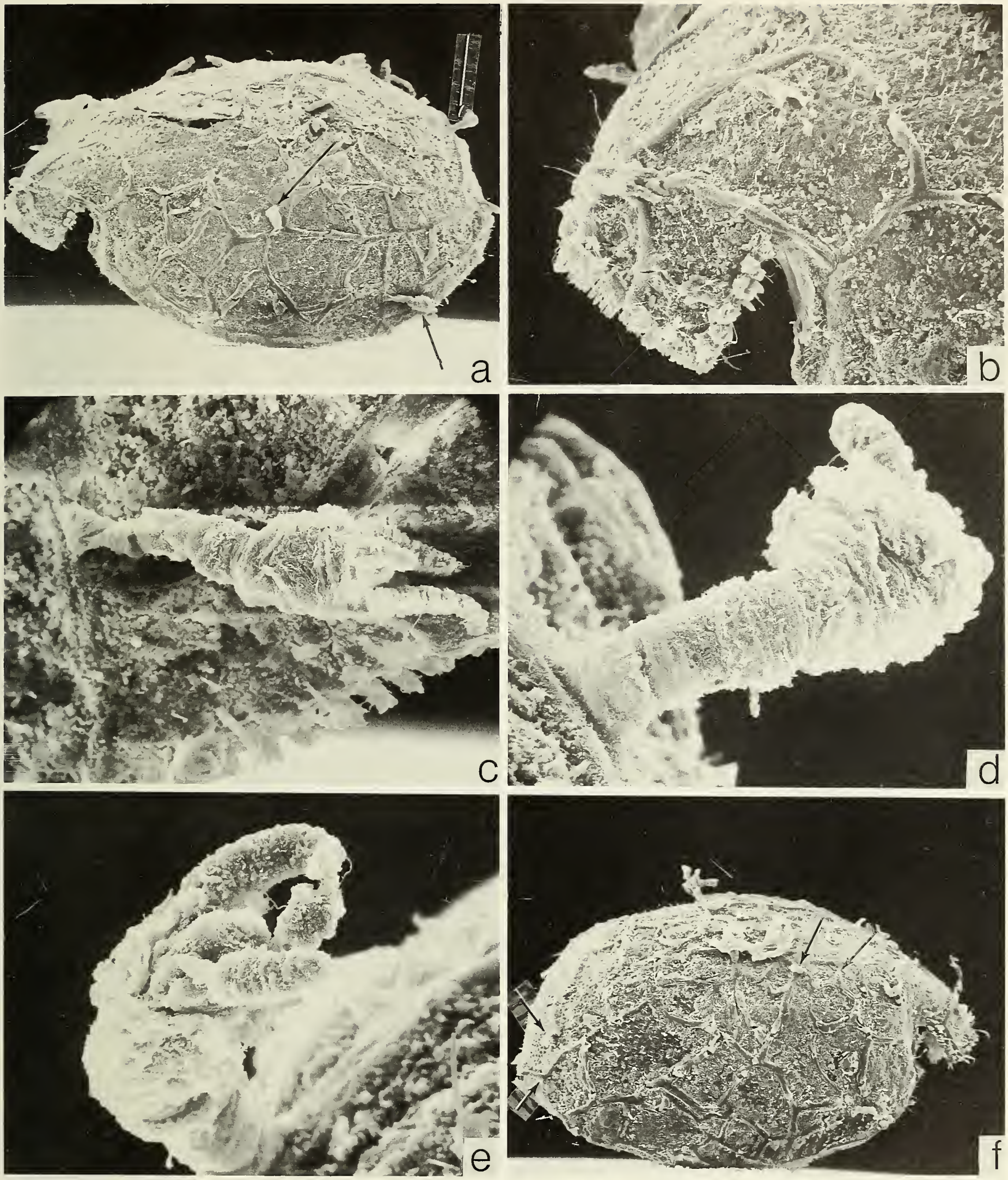

Fig. 2. Hydroid on left valve of *P. brenda* USNM 158536 (length 3.06 mm): a, Pseudohydrorhiza and 3 hydranths (arrows), ×22.8; b, Detail of pseudohydrorhiza, from a, ×67; c, Detail of hydranth on lower right of a, ×171; d, Detail of hydranth on upper right of a, ×336; e, Hydranth in d reoriented, ×336. Hydroid on right valve of USNM 158536: f, Pseudohydrorhiza and 4 hydranths (arrows), ×22.8.

bristles and is again restricted to the bottom (Elofson 1969:165). The eight females having attached hydrozoans all have broken swimming bristles, indicating that they had mated and returned to the bottom. The presence of hydrozoans on adult females only, and not on juveniles, suggests that the hydroids may have become attached when

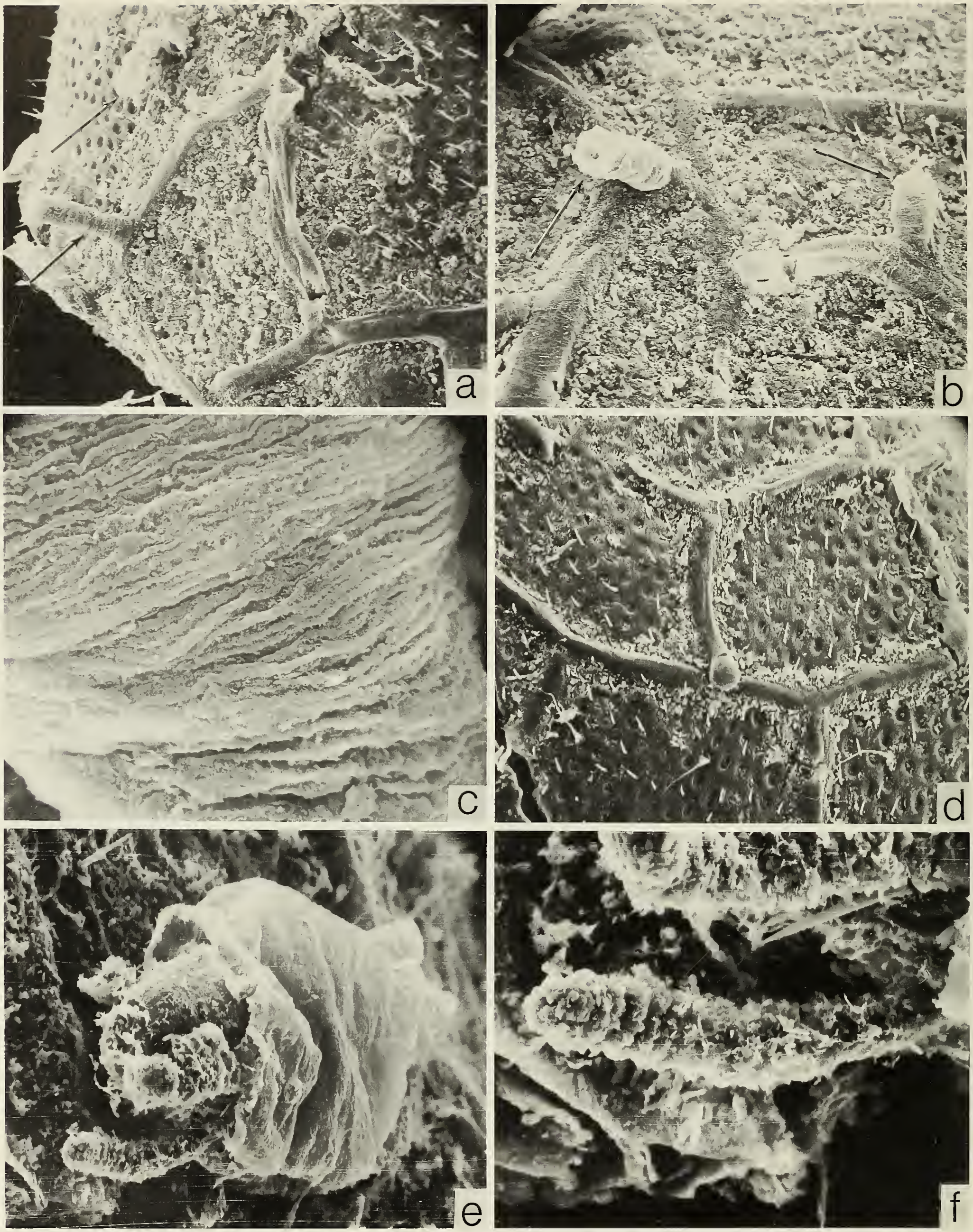

Fig. 3. Hydroid on left valve of *P. brenda* USNM 158536: a, Detail from left end of Fig. 2f showing 2 hydranths (arrows), × 101; b, Detail of upper right of Fig. 2f showing hydranths (arrows), × 174; c, Detail showing surface crinkles of right hydranth shown in b, × 1448. Hydroid on right valve of *P. brenda* USNM 158466 (length about 3 mm): d, Detail of pseudohydrorhiza near anterior of valve, × 119; e, Hydranth with tentacles, × 326; f, Detail of tentacles in e, × 724.

the ostracode was swimming in the water column. The absence of hydroids on adult males, which probably spend more of their adult life swimming than females, could be the result of having collected relatively few such specimens, which probably die soon after mating. According to Elofson (1969: 160, 161, 165) adult females of *P. brenda* live several years. Although the density of hydrozoan growth on the carapaces (Figs. 2, 3) could be interpreted to suggest colonization over a long period, it is known that some hydroid colonies grow rapidly after planula settlement, i.e., a few days or weeks.

Acknowledgments

Collections from the Beaufort Sea by Dr. A. G. Carey, School of Oceanography, University of Oregon, were supported by the Mineral Management Service through an interagency agreement with the National Oceanographic and Atmospheric Administration as part of the Alaskan Outer Continental Shelf Environmental Assessment Program and by NSF Grants GA-36679 and OCE75-14703. The senior author thanks P. F. S. Cornelius, British Museum; J. J. Kohlmeyer, The University of North Carolina; S. D. Cairns, and F. M. Bayer, Smithsonian Institution; for correspondence or discussions. We thank Thomas E. Bowman and Stephen D. Cairns, Smithsonian Institution, and an anonymous reviewer, for reviewing the manuscript.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(1):130–135. 1995.

Laonome albicingillum, a new fan worm species (Polychaeta: Sabellidae: Sabellinae) from Taiwan

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Abstract.—A new sabellid polychaete species, *Laonome albicingillum,* is described. The species is a dominant component of a mangrove estuary in northern Taiwan, and differs from all other currently recognized *Laonome* species in that it has thoracic neuropodial companion setae. An emended definition for the genus is provided.

During studies of benthic communities in a mangrove estuary in northern Taiwan, an undescribed sabellid species was discovered that occurred in densities of up to 19,000 individuals per m^2. This species, assignable to the genus *Laonome* Malmgren, is described herein. The types are deposited in the Institute of Zoology, Academia Sinica, Taipei, Taiwan (ASIZIP); the Allan Hancock Foundation Polychaete Collection of the Natural History Museum of Los Angeles County, California, U.S.A. (LACM-AHF); and the National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (USNM).

Family Sabellidae
Laonome Malmgren, 1866, emended

Type species.—*Laonome kroyeri* Malmgren, 1866 by monotypy.

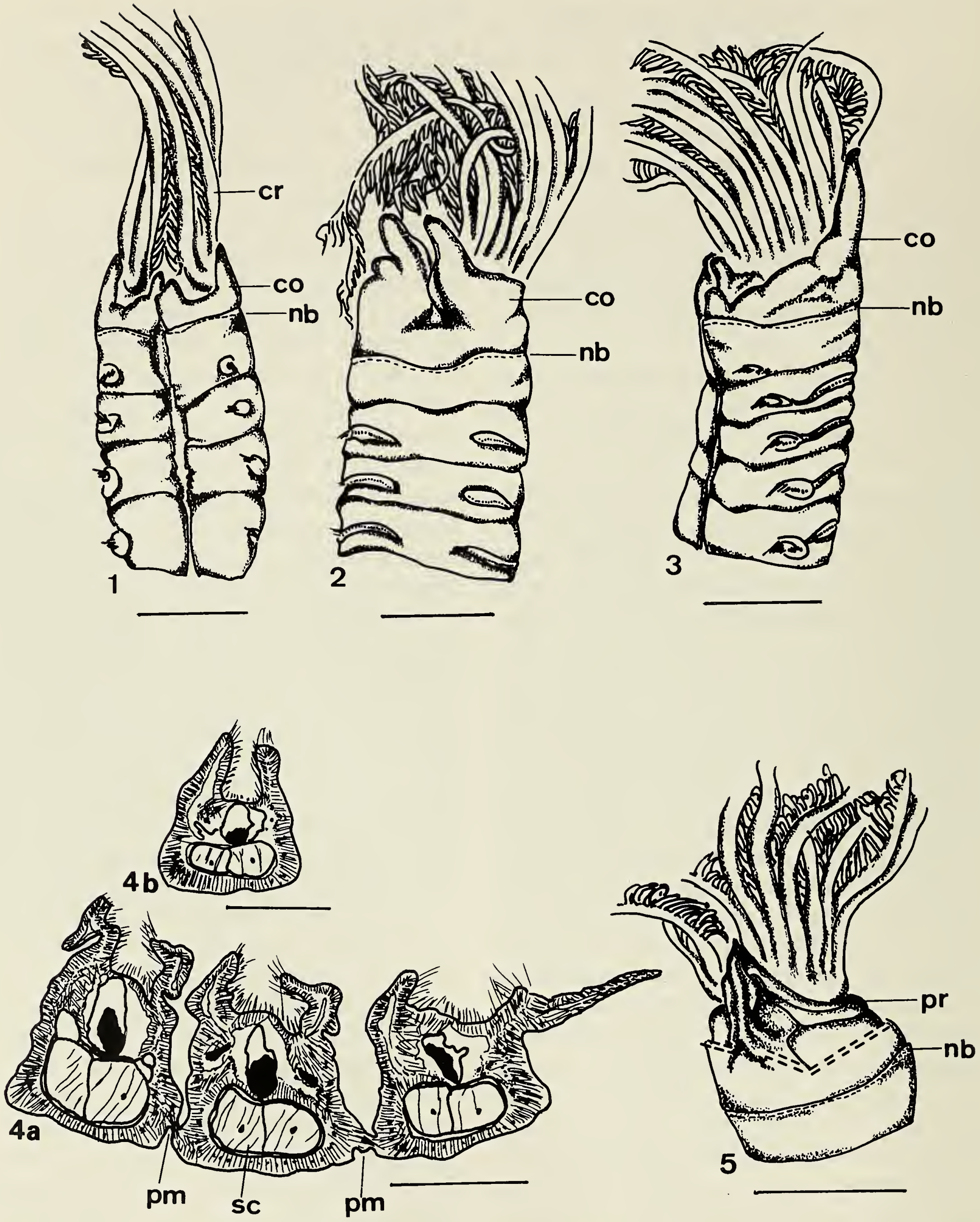
Diagnosis.—Medium-size sabellin species with (usually) eight thoracic and numerous abdominal setigers. Axis of radiolar skeleton in cross section with two cells. Palmate membrane absent or present; radiolar flanges absent. Dorsal lips without dorsal radiolar appendages; dorsal pinnular appendages absent. Ventral lips fused. Parallel lamellae absent or present as a single medial lamella. Posterior peristomial ring collar present. Superior thoracic notosetae elongate narrowly hooded; inferior setae paleate. Thoracic neuropodial uncini with series of small teeth above main fang, breast well developed, handles absent. Companion setae present or absent. Abdominal uncini with series of small teeth above main fang, breast well developed, handles absent.

Remarks.—This diagnosis is essentially the same as that provided by Fitzhugh (1989: 76–77; see also Fauchald 1977:139) except with regard to the presence of companion setae. Historically, *Laonome* has been defined by the combined absence of companion setae and handles on thoracic and abdominal uncini. Fitzhugh (1989) also included the absence of dorsal radiolar appendages as a feature denoting monophyly of the genus. The presence of companion setae in *L. albicingillum* does not affect recognition that this species is closely related to other members of the genus because the absence of both radiolar appendages and uncini handles are still sufficient to establish monophyly. However, Fitzhugh's (1989) diagnosis was based primarily on specimens of a single species, *Laonome kroyeri,* and the suite of characters of these two species may, upon examination of other species, indicate that they are representative of two related monophyletic groups, which may subsequently be recognized as separate genera or subgenera (T. Perkins, in litt.).

Laonome albicingillum, new species
Figs. 1–17

Material examined.—Intertidal mudflat, Chu-Wei mangrove swamp (25°10′N, 121°27′E), Tan-Shui estuary, Taipei County, northern Taiwan, 17 Mar 1992: holotype (ASIZIP 25), 17 paratypes (ASIZIP 22–24, 26–34, 37–41), 49 paratypes (LACM-AHF 1706). Same locality: Apr 1993, 1 paratype (ASIZIP 35). Same locality: 23 May 1994, 27 paratypes (USNM 170551).

Description.—Holotype complete, with 8 thoracic and 71 abdominal setigers; total body length 57 mm (branchial crown 6 mm), body width at collar 1.6 mm. Complete paratypes with 54–79 setigers, body (exclusive of crown) 13–52 mm long (crown 2–6 mm), width at collar 0.45–1.60 mm; most specimens with 8 thoracic setigers, some with 6 or 7. Branchial crown radioles without eyespots or pigmentation (Figs. 1–3). Branchial lobes each with 5–12 pairs of radioles in specimens with 54–79 setigers; number of radioles usually positively correlated with size of animal; radiole surfaces smooth, no appendages or flanges on outer margins (Figs. 1–3); radioles quadrangular in cross section. Axis of radiolar skeleton usually with two, occasionally four, rows of cells (Fig. 4). Palmate membrane joining radioles proximally at about 1/10 of radiole length (Fig. 4a), very thin and transparent. Anterior peristomial ring not developed ventrally as a narrow lobe-like extension (Fig. 5). Dorsal lips triangular, fused with one another by thin lamella along ventralmost margins, just above mouth (Fig. 6). Dorsal lips without radiolar appendages (Fig. 6). Ventral lips quadrangular, extending from inner, ventral margins of branchial lobes, about ⅔ length of dorsal lips (Figs. 6, 7). Ventral lips fused to one another along ventral midline (Fig. 7), extending ventrally as single lamella, fused to inner midventral margins of collar (Figs. 2, 7). Posterior peristomial ring collar completely separate middorsally (Figs. 1, 6) and midventrally (Figs. 2, 7), midventral margins turned inward and fused with ventral lip lamella. Ventral collar margin about ⅔ higher than dorsal (Fig. 3). Dorso-lateral collar margins with deep V- or U-shape incisions (Figs. 1, 3, 6). Midventral collar margins as narrow, elongate, triangular flaps (Figs. 2, 3). Anterior margin of setiger 1 completely encircled, except middorsally, by very narrow, white band (Figs. 1–3, 5, 6); best observed when specimen is stained with methyl green (see below). Setiger 1 separated externally from posterior peristomial ring by "intersegmental groove." Notosetal fascicles of setiger 1 situated slightly more dorsal than remaining thoracic notopodia (Figs. 1, 3). Setiger 1 fascicles slightly oblique; setae elongate narrowly hooded. Notosetal fascicles of setigers 2–8 with superior setal group forming arc over inferior transverse setal row (Fig. 8). Superior notosetae elongate narrowly hooded (Fig. 9); inferior notosetae paleate with mucronate tip (Fig. 10), 14–17 per fascicle. Thoracic neurosetal tori extend to ventrolateral margins of segments (Fig. 2). Ventral shields present but indistinct. Uncini with several rows of small, equal-size teeth above main fang; handles absent; breast well developed, expanded, extending beyond tip of main fang (Figs. 12, 13); 38–79 uncini per torus. Companion setae arranged as single row anterior to uncini, 34–54 per fascicle; distal end a thin, tear drop-shaped membrane terminating to a fine point (Fig. 11). Abdominal neurosetal fascicles arranged in two transverse rows in anterior setigers and single rows in posterior setigers. Anterior rows of anterior abdominal neurosetae elongate narrowly hooded (Fig. 15), posterior rows modified, elongate narrowly hooded (Fig. 16). Posterior abdominal neurosetae similar to setae in posterior rows but somewhat more elongate. Abdominal uncini similar to those of thorax (Fig. 14). Pygidium elongate, conical, distinct from last abdominal setiger (Fig. 17). Anus ventral, near anterior pygidium margin. Hermaphroditic. Live animals pale



Figs. 1–5. *Laonome albicingillum,* new species. 1, Paratype (ASIZIP 24), anterior end, dorsal view. Dashed line indicates narrow white band around setiger 1. 2, Holotype (ASIZIP 25), anterior end, ventral view. 3, Holotype (ASIZIP 25), anterior end, right side. 4, Paratype (ASIZIP 35), a, cross section of three radioles near base of crown shows thin palmate membrane and arrangement of skeletal axis cells. b, cross section of radiole in median region. 5, Paratype (ASIZIP 40), anterior end, ventro-lateral view, left side. Scale bar in Figs. 1–3 & 5: 1 mm; in Fig. 4: 100 μm. Double dashed lines indicate collar being removed. co: collar; cr: branchial crown; nb: narrow white band; pm: palmate membrane; pr: anterior margin of anterior peristomial ring; sc: skeletal axis cell.

green; alcohol-preserved specimens light brown to cream colored. Tubes composed of mucus, fine mud, sand, and detritus. Methyl green staining patterns were as follows: first setigers deeply stained except the narrow white band and notopodia; radioles and dorsal and ventral lips not stained; margins of fecal groove in abdomen deeply stained; in anterior segments dorsal surface of body taking less stain than ventral surface but in posterior segments both surfaces well stained.

Etymology.—The specific name is derived from the Latin *albi,* whitish, and *cingillum,* little girdle, referring to the occurrence of a whitish narrow band on the anterior margins of setiger 1.

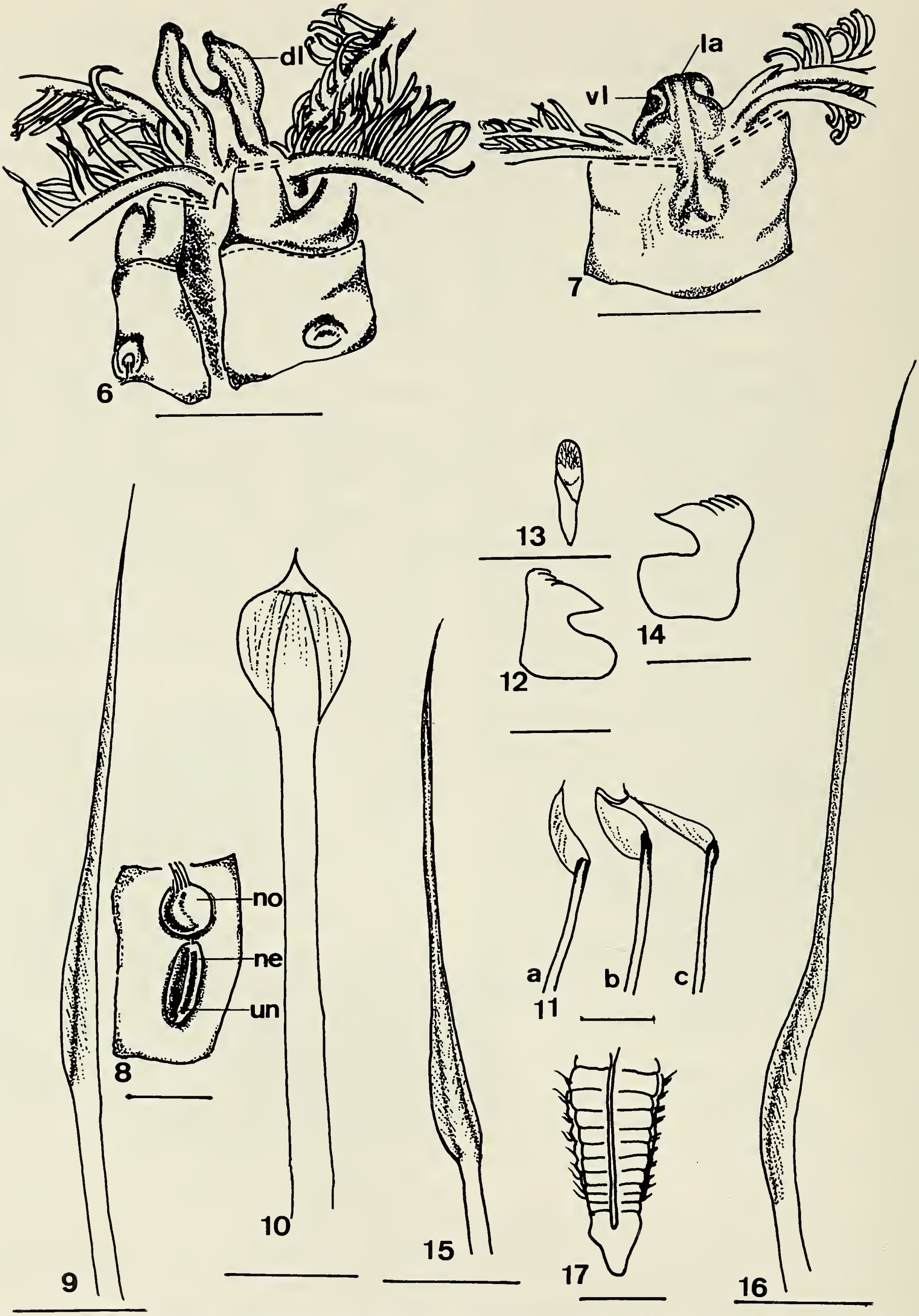
Habitat.—The type locality is an intertidal mud flat in a mangrove swamp adjacent to a river bank. Sediment salinity varies from 17–28‰, whereas salinity of the overlying water varies from 2–21‰. The median grain size diameter on the mud flat is from 0.06–0.14 mm, with a modal grain size diameter of 0.01–0.12 mm. The sediment silt and clay content ranges from 16–50%. Vegetation of the adjacent swamp is dominated by the mangrove, *Kandelia candel.*

Reproduction.—*Laonome albicingillum* is hermaphroditic. Gametes are limited to the abdomen, with the 10 anteriormost setigers (setigers 9–19) producing oocytes and the following 20–30 setigers producing sperm. Coelomic oocytes are irregular in shape and spawned eggs are spherical, 140–160 μm in diameter. Spawning appears to occur from October to May. Embryos and larvae are planktonic with non-planktotrophic larval stage. Development from the fertilized egg to larval settlement only requires 26–33 hours.

Taxonomic remarks.—Of the 14 species that have been described as members of *Laonome* (cf. Hartman 1959, 1965; Hutchings & Murray 1984), exclusive of the current account, only the following five are now maintained in the genus: *L. kroyeri* Malmgren, 1866; *L. tridentata* Moore & Bush, 1904; *L. elegans* Gravier, 1906; *L. indica* Southern, 1921; and *L. triangularis* Hutchings & Murray, 1984. *Laonome albicingillum* is readily distinguished from these species by the presence of companion setae. In other respects, *L. albicingillum* closely resembles *L. indica* (Southern 1921: pl. XXX, fig. 26B) in that the midventral collar margin is well developed into a pair of elongate triangular processes. Except for these processes, the collar of *L. indica* appears to be of uniform height (Southern 1921: pl. XXX, fig. 26A). The collar of *L. triangularis* is oblique (Hutchings & Murray 1984: fig. 32.5), but lacks dorsolateral incisions. Most previous descriptions of *Laonome* species have not been very detailed with regard to the branchial crown. Thus, as to the presence or absence of a palmate membrane, closer inspection might reveal the systematic importance of this character in the genus. As regards the companion setae, their presence or absence also may be systematic important.

The midventral lamella which extends from the fused ventral lips to the ventral margins of the collar appears to be comparable to the parallel lamellae seen in many sabellids. It appears probable that in the case of *Laonome albicingillum* these lamellae are fused for most of their length, resulting in the presence of a single lamella. Southern (1921:653; pl. XXX, fig. 26B) described the presence of a "median lobe" in *L. indica* that appears very similar to the midventral lamella in *L. albicingillum.* Fitzhugh's (1989, pers. comm.) definition of *Laonome* was based primarily on his examination of the type species, *L. kroyeri,* from which he inferred that species in the genus lack parallel lamellae. As he made no further distinctions in this character, the presence of what are presumed to be fused lamellae in *L. albicingillum* might be of systematic importance.

Until all other *Laonome* species can be examined, I do not know to what extent the white band at the anterior margin of setiger



Figs. 6–17. *Laonome albicingillum,* new species. 6, Paratype (ASIZIP 26), dorsal view of dorsal lips. 7, Paratype (ASIZIP 27), ventral view of ventral lips. 8, Paratype (ASIZIP 22), lateral view (left side) of setiger 5 showing arrangements of superior and inferior noto- and neurosetal fascicles. 9, Paratype (ASIZIP 22), elongate, narrowly hooded seta from setiger 3. 10, Paratype (ASIZIP 22), paleate seta from setiger 3. 11, Paratype (ASIZIP

1 can be of diagnostic use. This band may be similar to the so-called postsetal "glandular" girdle that has been reported in several sabellid genera, such as *Euchone* (Banse 1970) and *Potamethus* (Knight-Jones 1983). These "glandular" girdles are, however, located on setiger 2 and are postsetal.

Acknowledgments

I wish to thank Dr. K. Fitzhugh, Natural History Museum of Los Angeles County (LACM), Mr. T. Perkins, Florida Marine Research Institute and Dr. G. Rouse, Smithsonian Institution (USNM) for much help in examining the type specimens, to Dr. K. Fauchald and Ms. L. Ward, USNM, for providing references, advice and encouragement during the study. I am also very grateful to Dr. Fitzhugh and Mr. Perkins for their critical reading of the manuscript. Thanks are also due to Dr. C. P. Chen, Institute of Zoology, Academia Sinica, for help in field work and encouragement. This study was supported by National Science Council of the Republic of China grants NSC810209B00105 and NSC820211-B001020.

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25), a, companion seta from setiger 6; b,c, from setiger 4. 12, Paratype (ASIZIP 23), thoracic uncinus from setiger 3, lateral view. 13, Paratype (ASIZIP 22), thoracic uncinus from setiger 3, frontal view. 14, Paratype (ASIZIP 22), abdominal uncinus from setiger 11, lateral view. 15, Paratype (ASIZIP 37), elongate narrowly hooded seta from anterior row of neurosetal fascicle, setiger 10. 16, Paratype (ASIZIP 37), elongate narrowly hooded seta from posterior row of neurosetal fascicle, setiger 10. 17, Paratype (ASIZIP 29), posterior end of body, ventral view. Scale bar in Figs. 6 & 7: 1 mm, in Figs. 8 & 17: 500 μm, in Figs. 9 & 10, 13, 15 & 16: 50 μm, in Figs. 11 & 12, 14: 25 μm. dl: dorsal lips; la: ventral lip lamella; ne: neurosetal fascicles; no: notosetal fascicles; un: uncini; vl: ventral lips. Other indications are same as in the previous figures.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(1):136–146. 1995.

A juvenile of the scaled squid, *Pholidoteuthis adami* Voss, 1956 (Cephalopoda: Oegopsida), from the Florida Keys

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Abstract.—I describe a heretofore unknown, small juvenile (54 mm mantle length) of *Pholidoteuthis adami,* a member of the uncommonly captured, systematically confused lepidoteuthid squids. I used scanning electron microscope photomicrographs to examine the dermal cushions and tentacular suckers, which are distinguishing features in the adult. I compared these features with larger specimens of 108 mm and 179 mm mantle length. The dermal cushions of the smallest specimen are conical, but in the larger specimens they are flatter, oblong in shape or roughly pentagonal, and closer together and often touching one another at the base. In all growth stages the dermal cushions are interiorly vacuolated. The tentacular suckers of the smallest specimen have oval openings. However, in the larger juveniles the tentacular suckers are laterally compressed and have narrow openings as in the adult. The structure of the dermal cushions of the juveniles and apparent developmental patterns suggest that a congeneric relationship with the type of the genus, *P. boschmai,* may not be valid.

The "scaled" squid *Pholidoteuthis adami* is a pelagic species that reaches 780 mm in mantle length (ML; Roper et al. 1969). Adult *P. adami* have two peculiar features: roughly pentagon-shaped dermal cushions on the mantle, and tentacular suckers that are laterally compressed and have narrow openings. This species occurs in shelf and slope waters throughout the Caribbean and Gulf of Mexico and adjacent northwest Atlantic Ocean and may have fisheries potential (Roper et al. 1984). However, *P. adami* was described only relatively recently by Voss (1956), and is infrequently collected, although it has been observed in large schools at night at the surface in the upper Gulf of Mexico. Additional accounts of *P. adami* in the literature are few: it has been reported from the northern Gulf of Mexico (Lipka 1975), off the eastern United States (Rathjen 1981), off Suriname and French Guiana (Okutani 1983), off Venezuela (Arocha et al. 1991), and observed on the Cape Hatteras slope in a submersible (Vecchione & Roper 1991). Additionally, 38 juvenile and adult specimens from the largely unreported collection of the Rosenstiel School of Marine and Atmospheric Science (RSMAS) Invertebrate Museum were mostly captured in shelf and slope waters in the upper Gulf of Mexico and off Columbia.

The genera *Pholidoteuthis, Lepidoteuthis,* and *Tetronychoteuthis* have been placed in the family Lepidoteuthidae because they all possess prominent, scale-like dermal structures on the mantle. However, the systematics of these taxa are confused. Their status was evaluated by Roper & Lu (1989), who recommended that *P. adami* be placed in the family Lepidoteuthidae based on the similar morphologies of the gladii and structure of the dermal cushions of *P. adami* and *Lepidoteuthis grimaldii.* However, Nesis & Nikitina (1990) revised the Lepidoteuthidae and concluded that *Pholidoteuthis* should be in a separate family, Pholidoteuthidae, and that the two nominal species of *Tetronychoteuthis, T. massyae* and *T. dussumieri,* are synonymous with *Pholidoteuthis boschmai. Pholidoteuthis boschmai* is found in the eastern Atlantic and southern Indian oceans and may not be congeneric with *P. adami* based on marked differences in the gladii (Toll 1982).

The dermal structures of these squid were described in detail by Roper & Lu (1990) and were designated as dermal cushions in *Pholidoteuthis adami* and *Lepidoteuthis grimaldii,* and papillose tubercles in *Tetronychoteuthis massyae* in recognition of their different morphologies. The structures of all three genera are composed of fibrous connective tissue and are extremely vacuolated. The dermal cushions of *P. adami,* and other vacuolated tissue in the mantle, may contain ammonium ions to aid in buoyancy. Additionally, Roper & Lu (1990) postulated that dermal cushions may aid these squid in reduction of hydrodynamic drag by controlling laminar flow in the boundary layer to reduce turbulence.

I describe here an exceptionally well-preserved, previously unknown, small juvenile *P. adami* from the Straits of Florida off the Florida Keys. Additionally, I utilize scanning electron microscopy (SEM) to characterize the dermal cushions and tentacular suckers of a size series of three juveniles in order to elucidate the development of these features, and to help understand the relationship of *P. adami* with other lepidoteuthids.

Materials and Methods

Seasonal zooplankton and physical oceanographic surveys were conducted off the Florida Keys from May 1989 to Jan 1991 by the Southeast Florida and Caribbean Recruitment project (SEFCAR; Lee et al. 1992). Discreet depth zooplankton samples from the surface to 200 m were collected with a Multiple Opening and Closing Net and Environmental Sensing System (MOCNESS) with a 1 m^2 fishing mouth (Wiebe et al. 1976). I analyzed distribution of planktonic cephalopods from four SEFCAR cruises from Aug 1989 to May 1990 (Goldman & McGowan 1991, Goldman 1993). One juvenile *P. adami* of 54 mm ML and 104 mm total length was captured on 14 Feb 1990, 2035–2041 h GMT, during the R/V *Calanus* cruise CA9002, off the central Florida Keys at 24°31.93′N, 81°03.20′W. The depth of capture was between 78–101 m over a 200 m bottom depth. The specimen was fixed in a 10–15% formalin-seawater solution and subsequently transferred to 70% ethanol. It has been deposited in the RSMAS Invertebrate Museum (UMML 31.2636). I examined two additional specimens from the collections of that museum. These are larger juveniles of 108 mm ML (UMML 31.2369; R/V *Oregon* 4902, 28 May 1964) and 179 mm ML (UMML 31.465; R/V *Oregon* 3221, 4 Mar 1961).

I prepared specimens for SEM photomicrography in different ways. Samples from the museum specimens were dehydrated in ethanol, hardened with hexamethyldisilazane (HMDS) and dried in a desiccator for 24 h, then sputter coated them with palladium. These preparations resulted in severe shrinkage of the mantle tissue. The dermal cushions collapsed and were flat. However, the tentacular suckers, which contain hard chitin rings, were unaffected by shrinkage.

I re-hydrated and re-fixed a second group of samples from the same specimens in 2% glutaraldehyde for 1.5 h. After dehydration in ethanol, one set of tentacle and mantle samples was hardened with HMDS and another set was dried by critical point drying (CPD). The set of re-fixed samples treated with HMDS exhibited severe shrinkage. However, the samples dried by CPD produced dramatically improved results; dermal cushions looked spongy and were highly vacuolated. The latter technique was used on samples from the SEFCAR specimen.

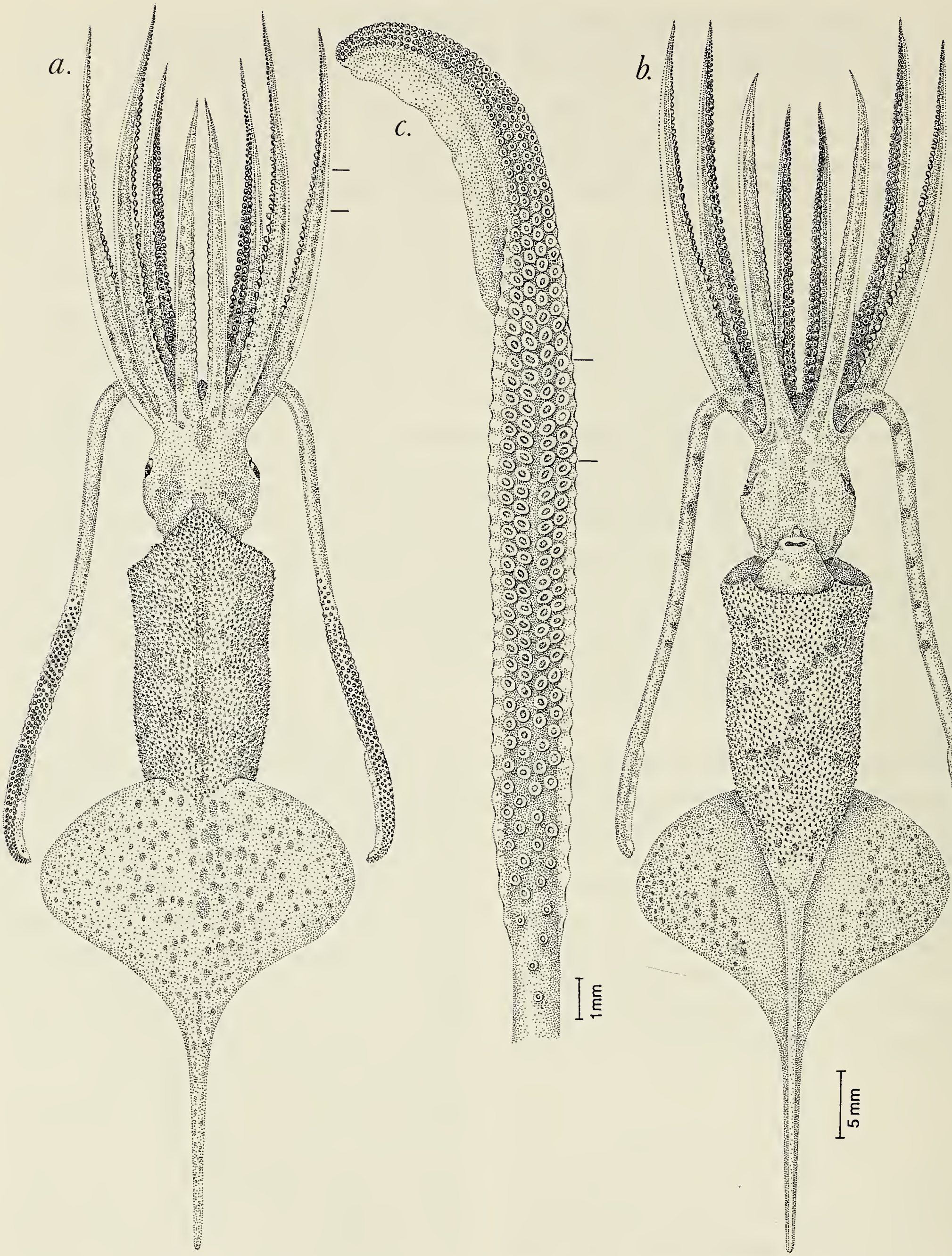

Fig. 1. Juvenile *Pholidoteuthis adami* from the Florida Keys, 54 mm ML, UMML 31.2636: (a) dorsal view, unlabeled bars indicate section illustrated in Fig. 2a, (b) ventral view, and (c) closeup of left tentacular club, unlabeled bars indicate section illustrated in Fig. 2c.

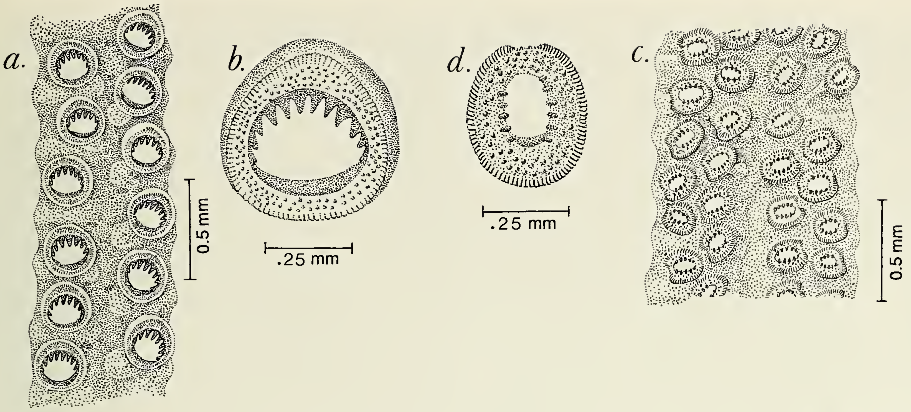

Fig. 2. Juvenile *P. adami,* 54 mm ML: (a) ventral view of middle section from right arm III, lowest sucker is 24th from base in dorsal row, (b) largest right arm III sucker, 18th from base in ventral row, (c) section from left club manus, and (d) sucker from left club manus.

Results

Description of 54.2 mm ML, female juvenile.—(Figs. 1–2).

Mantle: Walls firm. Thickness varies from about 0.3 to 0.4 mm. Constricted just posterior to the anterior mantle margin. Bulges in center where mantle width (MW) is maximum. Laterally compressed, presumably an artifact, so that MW is 8.7 mm (16.1% of ML) measured laterally, 12.7 mm (23.4% of ML) dorso-ventrally. Anterior margins flare outward. Tapers sharply at about midway along length of fins where muscular tissue terminates and forms a long tail. Mid antero-ventral margin slightly emarginate between small, sharp lateral angles. Mid antero-dorsal margin produced into a large, broad, blunt angle.

Dermal cushions: Found only on mantle. Evenly spaced, ca. 100–150 μm apart, but sparse on posterior ventral mantle (Fig. 3a). Conical in shape; sharply pointed. Height about 100–200 μm (Fig. 3b). Diameter at base varies from about 50 to 80 μm. Covered with very thin, polygonal plates, possibly epithelial cells; frequently lost at point of cone (Fig. 3c). Interior vacuolated (Fig. 3d). Mantle tissue underneath dermal cushions is slightly vacuolated.

Gladius: Not extracted. Partially visible dorsally through mantle but does not bisect mantle muscle. Forms a ridge along dorsal mantle that turns into a groove between the fins. Visible in tail. Covered by thin, dermal tissue on posterior ventral surface. Length probably about the same as ML.

Fins: Large, rounded, very broad and muscular. Posteriorly concave and extend as fringe on long, slender tail which projects about 16 mm posterior to expanded portion of fins. Anteriorly convex with small lobes. Width is 22.7 mm (41.8% of ML); length is 20.5 mm (37.8% of ML).

Funnel: Short, stout. Not set deeply in funnel groove. Funnel valve large. Funnel organ with large, roughly oval ventral pads, and inverted V-shaped dorsal pad with anterior median papilla and what appear to be broad, low median ridges on the lateral arms.

Funnel-mantle locking cartilage: Straight and simple, very prominent. Funnel element, long with deep, wide median groove. Mantle element, long, thick ridge.

Head: Short; width less than MW, 8.0 mm (14.8% of ML); head length (HL) is 11.8 mm (21.8% of ML). Rounded posteriorly. Eyes occupy about 50% of HL and do not greatly protrude. Eyelids round with pronounced anterior sinus. Posterior, muscular thickening on eyelids and loose, membra-

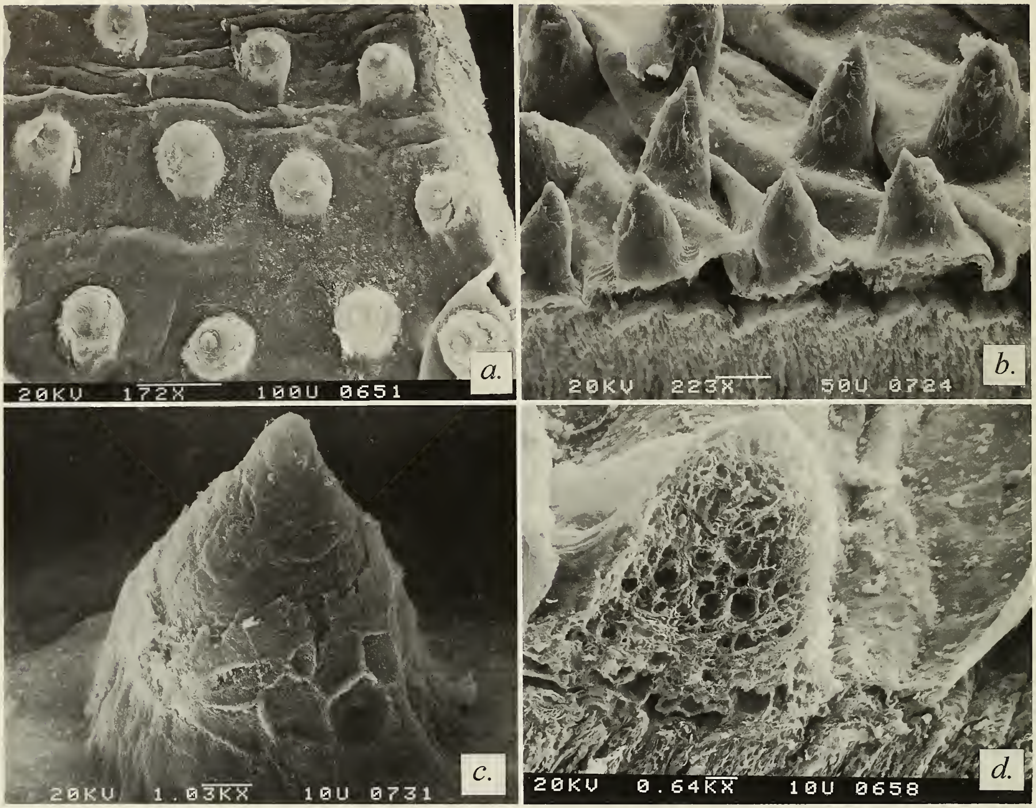

Fig. 3. Dermal cushions from mantle, 54 mm ML: (a) top view, scale: 100 μm (b) lateral view, scale: 50 μm, (c) closeup, scale: 10 μm, and (d) cross section, scale: 10 μm.

nous tissue between eyes and base of arms. One pair of small nuchal folds on either side of funnel groove.

Arms: Long, narrow; attenuate gradually. All keeled for their entire lengths. Arms III most prominently keeled. Arm formula III > II > IV > I on right side but III = II > IV > I on left. Length varies from 23.6 to 29.5 mm (43.5–54.4% of ML). Oral surface with low, trabeculate protective membranes on both margins of all arms. Trabeculae short, narrow and attached to bases of sucker stalks. Suckers biserial, spherical in shape, of approximately uniform size for nearly entire length of all arms. Chitinous sucker rings of proximal suckers with 10–12 large, pointed teeth on distal margins and several very small, rounded teeth on proximal margins. Small distal suckers, with about eight large teeth distally but no teeth proximally.

Tentacles and clubs: Tentacles nearly twice as long as arms; length is 44.1 mm (81.4% of ML). Cross section is elliptical, almost triangular. Club only slightly expanded. Club very long; about 22.5 mm (ca. 51% of tentacle length). Aboral swimming keel originates approximately mid club and extends to distal end. Proximal half of club and stalk with separate, low median aboral keel. Low trabeculate protective membranes equally developed on both margins of clubs proximal of dactylus. Membranes most developed on long manus. Four series of suckers on full length of club; ventral and dorsal pairs of suckers on manus slightly separated by a sucker-free median area (Fig. 2c). Neither suckers or knobs on stalks. Suckers on manus about 350 μm across on longest axis; oval, almost circular, with wide openings (Fig. 4) and not compressed like

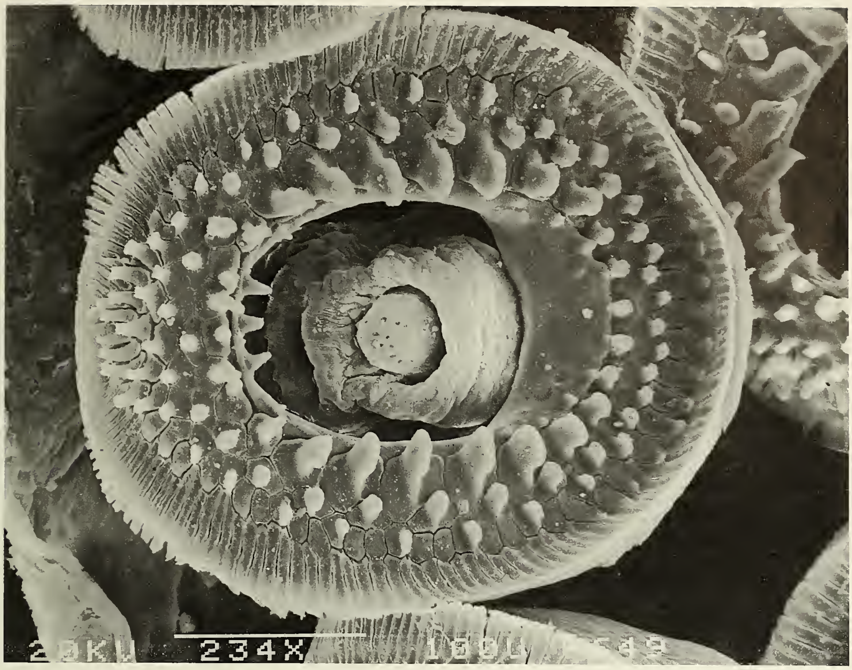

Fig. 4. Mid manal tentacular sucker, 54 mm ML, scale: 100 μm.

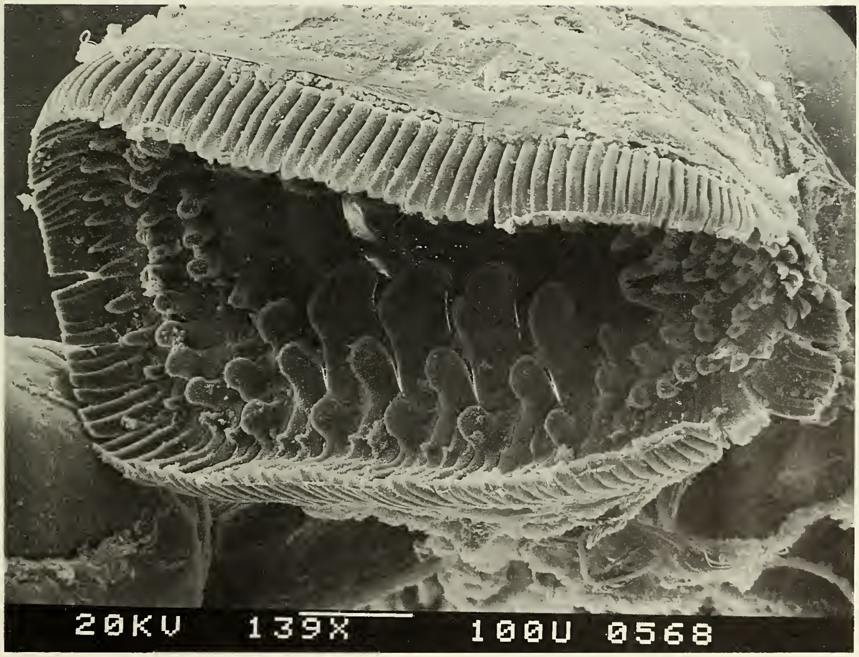

Fig. 5. Mid manal tentacular sucker, 108 mm ML, UMML 31.2369, scale: 100 μm.

suckers in large *P. adami.* Suckers on carpus and dactylus more circular. Suckers on short carpus ca. 80% diameter of those on manus, suckers on moderately short dactylus ca. 60% diameter of those on manus. Peripheral fringe of outer chitinous rings of suckers composed of tooth-like plates; larger, blunt, tooth-like structures present on medial plates with those near interior margins of suckers much larger. Three pronounced teeth on interior distal margins of inner chitinous ring.

Buccal mass: Small; projects outward. Seven large lappets with well-developed connectives attached dorsally to arms I–II, ventrally to arms III–IV. Buccal membrane prominent; translucent but firm. No buccal suckers.

Beak and radula: Not extracted. Protruding rostrums of upper and lower beaks darkly pigmented.

Chromatophores: Present on all parts of specimen; mostly round or oval. Red-brown, mostly flared, vary in intensity from faint to vivid. Numerous and large along dorsal midline of mantle. Large, widely spaced on dorso-lateral and ventral surface of mantle. Form distinct wine-glass pattern on ventral surface. Dense on dorsal surfaces of fins and tail, and ventrally on outer halves of fins; absent on interior halves and ventral surface of tail. Few, mostly contracted, on ventral surface of funnel. Some widely scattered on ventral surface along dorsal margin of funnel groove, midline of head and anterior and posterior to eyes. Few large, irregularly spaced on dorsal surface of head posterior to eyes, and some on posterior and anterior center of head. Two or three indistinct horizontal rows along entire length of arms. Several very small, elongate on distal and proximal edges of suckers. Aboral row along full length of tentacular stalk, dense pattern aborally on club. On oral surface of club, scattered around the bases of the suckers stalks.

Tentacular suckers and dermal cushions of 108 mm and 179 mm ML juveniles.— Tentacular suckers: Mostly oblong and laterally compressed with narrow openings at 108 mm ML, some partially open (Fig. 5). Laterally compressed with narrow openings at 179 mm ML, identical to the condition described for the adult by Voss (1956). Length from about 1000 to 1200 μm at both 108 and 179 mm ML. Tooth-like structures on the infundibulum similar but more robust than at 54 mm ML.

Dermal cushions: Flat-topped and broad, not conical and pointed like in the specimen of 54 mm ML. Positioned relatively much closer, like in adult (Roper & Lu 1990). About 100 μm in height and 300–400 μm across at 108 mm ML; roughly circular or oblong, may have been slightly flattened during handling of specimen; vacuolated (Fig. 6). About 175–250 μm in height and about 500 μm across at 179 mm ML; roughly square or pentagonal; closer together than at 108 mm ML, often touching at the base; vacuolated (Fig. 7). Underlying mantle tissue more highly vacuolated than at 54 mm ML (Figs. 6b, 7b).

Discussion

There are notable differences in some morphological features of the SEFCAR specimen compared with the description and illustration of the later growth stages of *P. adami* in Voss (1956). The size of the specimen illustrated in Voss (1956) is given as 136 mm ML in the figure caption. However, this number is questionable: the mantle lengths of the holotype, paratypes, and additional material listed by Voss were all larger. Nevertheless, differences include the fins, which are shorter and more rounded in the small SEFCAR juvenile compared to larger specimens; the tail, which is longer and narrower in the juvenile; and the tentacular suckers, which are open in the small juvenile and not compressed like those of older individuals. Additionally, the development of the dermal cushions in juvenile *P. adami* with growth consists of a change from widely spaced cones to closely set pen-

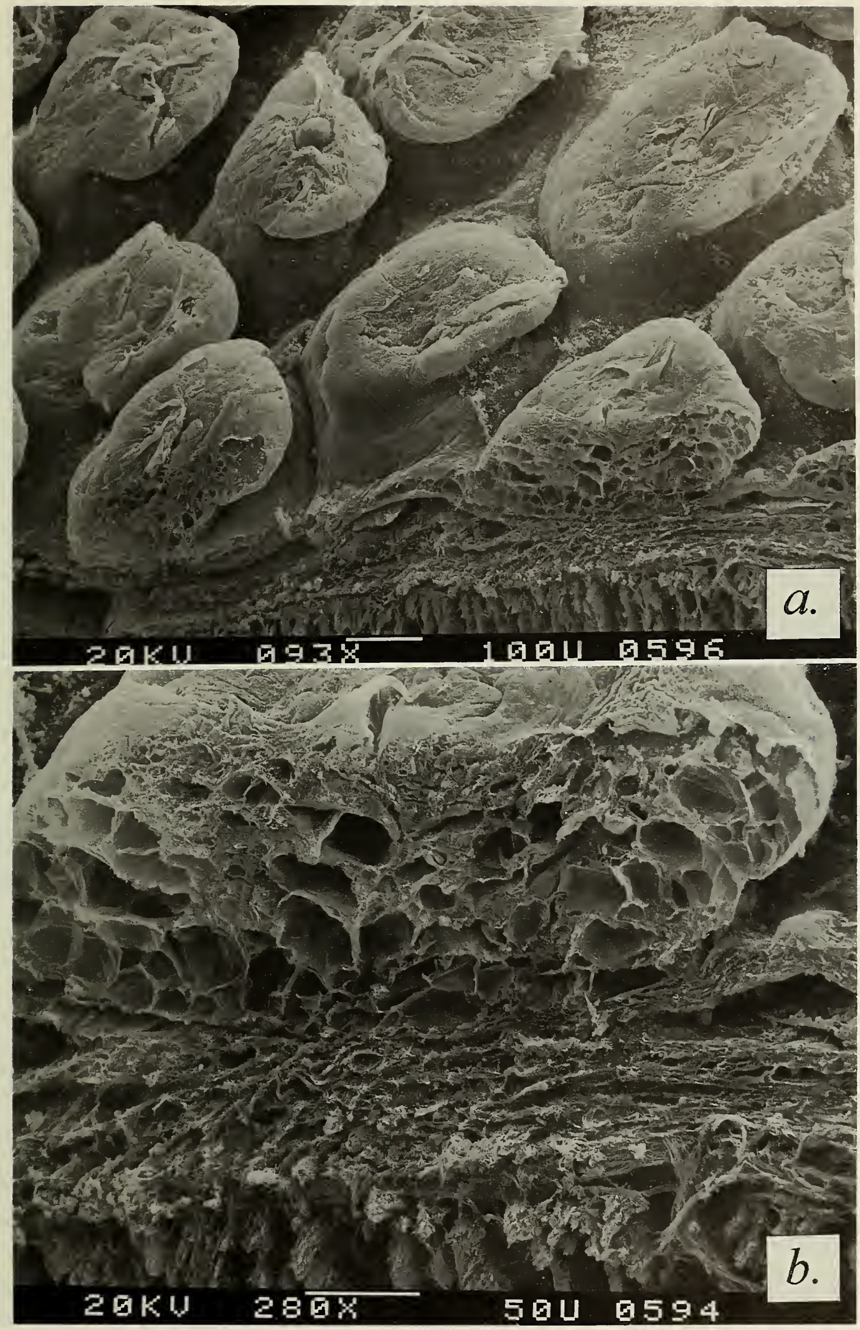

Fig. 6. Dermal cushions from mantle, 108 mm ML: (a) lateral view, scale: 100 μm, and (b) cross section, scale: 50 μm.

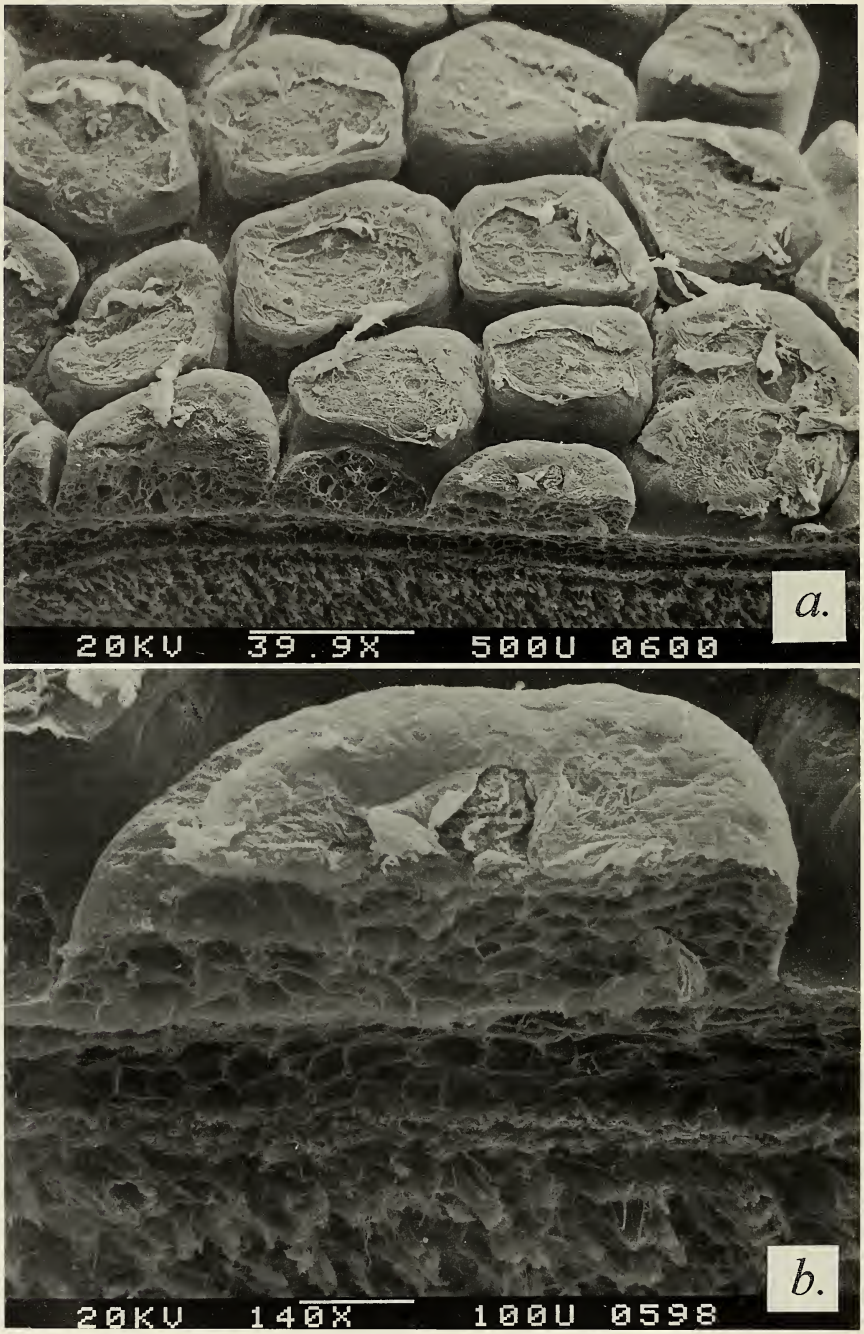

Fig. 7. Dermal cushions from mantle, 179 mm ML, UMML 31.465: (a) lateral view, scale: 500 μm, and (b) cross section, scale: 100 μm.

tagons. The internal structure of the dermal cushions of my *P. adami* juveniles is similar to the vacuolated condition of dermal cushions for the adult described and illustrated by Roper & Lu (1990).

There are also differences in the dermal cushions and tentacular suckers of the SEFCAR specimen compared with the only descriptions of small *Pholidoteuthis* sp.; specimens of 14 mm and 32.8 mm ML in Clarke (1992). Clarke characterized the dermal structures of the specimen of 14 mm ML as the same as those of adults. However, the dermal cushions of the SEFCAR *P. adami* are conical and pointed, so Clarke's 14 mm ML specimen is probably a different species. Furthermore, Clarke stated that the dermal structures of a *Pholidoteuthis* sp. of 32.8 mm ML have small papillae around their margins, similar to the papillose tubercles described by Pfeffer (1912) for the 30 mm ML, juvenile type of *Tetronychoteuthis massyae.* However, there are no marginal papillae on the dermal cushions of the SEFCAR specimen. The papillose tubercles of an immature *T. massyae* of 100 mm ML in Roper & Lu (1990) are similar to the dermal structures of a mature *Pholidoteuthis boschmai* of 286 mm ML in Villanueva & Sanchez (1993), which is in accord with the conclusion of Nesis & Nikitina (1990) that *T. massyae* and *P. boschmai* are conspecific. Therefore, the similarities of the dermal structures of Clarke's 32.8 mm ML *Pholidoteuthis* sp. to the papillose tubercles of *T. massyae* imply that it is *P. boschmai.*

Clarke (1992) described the tentacular suckers of his *Pholidoteuthis* sp. of 14 mm ML as being open and not compressed, and the suckers of his *Pholidoteuthis* sp. of 32.8 mm ML as compressed, the same as in adults. The tentacular suckers of the 54 mm ML SEFCAR specimen, however, are not compressed and are clearly different from those of my older museum juveniles, which have narrow openings like later growth stages of *P. adami* described by Voss (1956). The inconsistency in the size at which compression of the tentacular suckers is present between the specimen at hand and Clarke's specimens is further indication that his specimens are not *P. adami.*

Additionally, the fins in an illustration of Clarke's (1992) specimen of 14 mm ML are proportionally smaller than the SEFCAR juvenile, and the tail is not developed. These and the above incongruities suggest differentiation of Clarke's specimens, at least one of which is likely *P. boschmai,* and my specimen at the generic level. This inference concurs with Toll's (1982) finding that *P. boschmai* and *P. adami* may not be congeneric based on gladius morphology. However, as Roper and Lu (1989) concluded, the status of the type species, *P. boschmai,* must first be resolved before the status of *P. adami* can be revised.

Acknowledgments

I thank N. Voss for reviewing the manuscript and contributing much helpful insight, R. E. Young and an anonymous reviewer for critique that substantially improved the text, C. McSweeny for the illustrations, P. Blackwelder, M. Lynn, and N. Romer for their assistance with the SEM analysis, and M. McGowan for the successful capture of the specimen. This work was supported by National Oceanic and Atmospheric Administration (NOAA) Cooperative Agreements #NA85-WCH-06134 and #NA90RAH00075 to the Cooperative Institute for Marine and Atmospheric Studies (CIMAS), University of Miami. Research operations in the National Marine Sanctuary were conducted under National Marine Sanctuary Permits KLNMS and LKNMS-11-89.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(1):147–152. 1995.

A new species of the gorgonacean genus *Narella* (Anthozoa: Octocorallia) from Hawaiian waters

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Abstract.—A new species of *Narella* collected in Hawaiian waters by the U.S. Bureau of Fisheries steamer Albatross in 1902, but overlooked when the collection of octocorals was originally studied, is now described and illustrated by scanning electron micrographs. The species differs from all others by the elaborate ornamentation of the sclerites of the polyps and the high, thin crests of the coenenchymal scales.

During a review of gorgonacean corals of the genus *Narella* from Hawaiian waters in connection with the identification of specimens recently collected from guyots south of Hawaii, a fragmentary specimen obtained by the U.S. Bureau of Fisheries steamer *Albatross* during its Hawaiian cruise of 1901–1902 was found among the unstudied specimens in the Department of Invertebrate Zoology, U.S. National Museum of Natural History. The bulk of the collection of octocorals obtained around the Hawaiian Islands by the *Albatross* during its cruise of 1901 and 1902 were reported upon by Prof. C. C. Nutting of the State University of Iowa (Nutting 1908), but neither the present fragment nor the complete specimen from which it must have come were mentioned by Nutting in his report. It can be referred without question to the genus *Narella* but its highly distinctive characters exclude it from any species of that genus heretofore described.

Even though the specimen is only a fragment (fig. 1a) from a terminal branch of what must have been a much larger colony, it retains all diagnostic characters necessary for the establishment of a new species. The only feature that remains unknown is the form and branching pattern of the complete colony, a character that may be influenced by environmental factors and is not essential for recognition of the species.

Primnoidae

Genus *Narella* Gray, 1870

Narella Gray, 1870:49.—Deichmann, 1936: 168.

Stachyodes Studer [& Wright], 1887:49.—Wright & Studer, 1889:xlvii, 53.—Kükenthal, 1924:308 (references).

Four species of Primnoidae referred to the genus *Stachyodes* (a junior synonym of *Narella*) were reported from waters around Hawaii by Nutting (1908): *Stachyodes angularis* Nutting, 1908; *S. regularis* "Wright & Studer, 1889"; *S. bowersi* Nutting, 1908; and *S. dichotoma* Versluys, 1906.

The specimens described as the new species *Stachyodes angularis* by Nutting (1908) can be referred to the genus *Calyptrophora* Gray. The specimen Nutting reported as *S. regularis* (erroneously attributed to Wright & Studer) is an incomplete terminal branch of *Narella dichotoma* (Versluys, 1906), and the specimens reported as *Stachyodes dichotoma* represent an entirely different new species of *Narella*, which will be described elsewhere. *Stachyodes bowersi* remains a valid species now referred to *Narella.*

The specimen here described cannot be referred to any species of *Stachyodes* (=*Narella*) previously reported from Hawaiian waters, to any species from Indonesian waters obtained by the *Siboga* Expedition described by Versluys (1906), nor to any species from Japan described by Kinoshita (1907, 1908).

Narella ornata, new species
Figs. 1–3

Material examined.—Hawaii, Kauai: Hanamaulu warehouse S43°W, 8.1 miles, 550–409 fathoms (=1007–748 m), bottom temperature 37.8°F, USFC str. *Albatross* sta. 4019, 21 Jun 1902. One small piece of branch with comatulid crinoid attached. Holotype, USNM 94617 (SEM 2352–2354).

Diagnosis.—*Narella* with both buccal and basal scales distinctly separated adaxially; one pair of small adaxial buccal scales; adaxial opercular scales not remarkably smaller than outer laterals; outer surface of opercular and body scales with radial sculpture developed as prominent, thin crests; cortical sclerites elongate, narrow plates and irregular rods, many with high, thin crests.

Description.—The type specimen (Fig. 1a) is fragmentary so colonial form and manner of branching are unknown. The polyps (Fig. 2) are 3 mm long measured parallel with the branch, directed downward and arranged in whorls of three or four; 7–8 whorls occur in 3 cm of branch length. Members of basal (Fig. 1h) and buccal (Fig. 1g) scale pairs do not meet to form closed but unfused rings around the body of the polyp; medial (Fig. 1f) and buccal (Fig. 1g) scales similar in size; the closed opercular scales form a broad cone (Fig. 3, top) that projects beyond the margin of the buccal pair (Fig. 2, top); one pair of large, squarish adaxial buccal scales is present between the adaxial ends of the buccal scales and below the adaxial opercular scales (Fig. 3, bottom). Tentacles with scattered, minute, elongate scales.

The radial external sculpture (Fig. 1b) of the opercular (Fig. 1d) and body scales (Fig. 1f–h) is conspicuously developed as thin crests, giving the polyps an unusually ornate appearance. The inner surface of the body scales is covered with crowded, complex tubercles (Fig. 1c). The opercular scales (Fig. 1d) are of the usual triangular shape, with a strong, thin, apical keel on the inner surface, and are sculptured externally by a system of thin crests radiating from center of calcification (i.e., the "nucleus"); the adaxial opercular scales are somewhat smaller than the abaxial and lateral scales but are not unusually reduced in size. The sclerites of the cortex (Fig. 1e) are elongate scales and narrow, irregular rods, most having the outer surface ornamented with one or several prominent crests; the inner surface is covered by small, complex tubercles.

Etymology.—Latin *ornatus* = decorated, beautiful, in allusion to the ornate sculpturing of the sclerites. Adjective.

Comparisons.—The most conspicuous feature of this species is the elaborate, cristate sculpture of the body scales and coenenchymal sclerites, unlike any species of *Narella* heretofore recorded.

Remarks.—The nature of this sample suggests that it was cut from a larger specimen of gorgonian in order to segregate the attached crinoid. As it is most unlikely that such a small part of a gorgonian branch with commensal crinoid would have been taken by the trawl, it is highly probable that a larger specimen from which it was cut did exist at one time. However, no trace of such specimen can now be found in the collections of the National Museum of Natural History. The collection of octocorals obtained around the Hawaiian Islands by the *Albatross* during its cruise of 1901 and 1902 were entrusted by the Commission of Fisheries to Prof. C. C. Nutting at the State University of Iowa for study and report. Al-

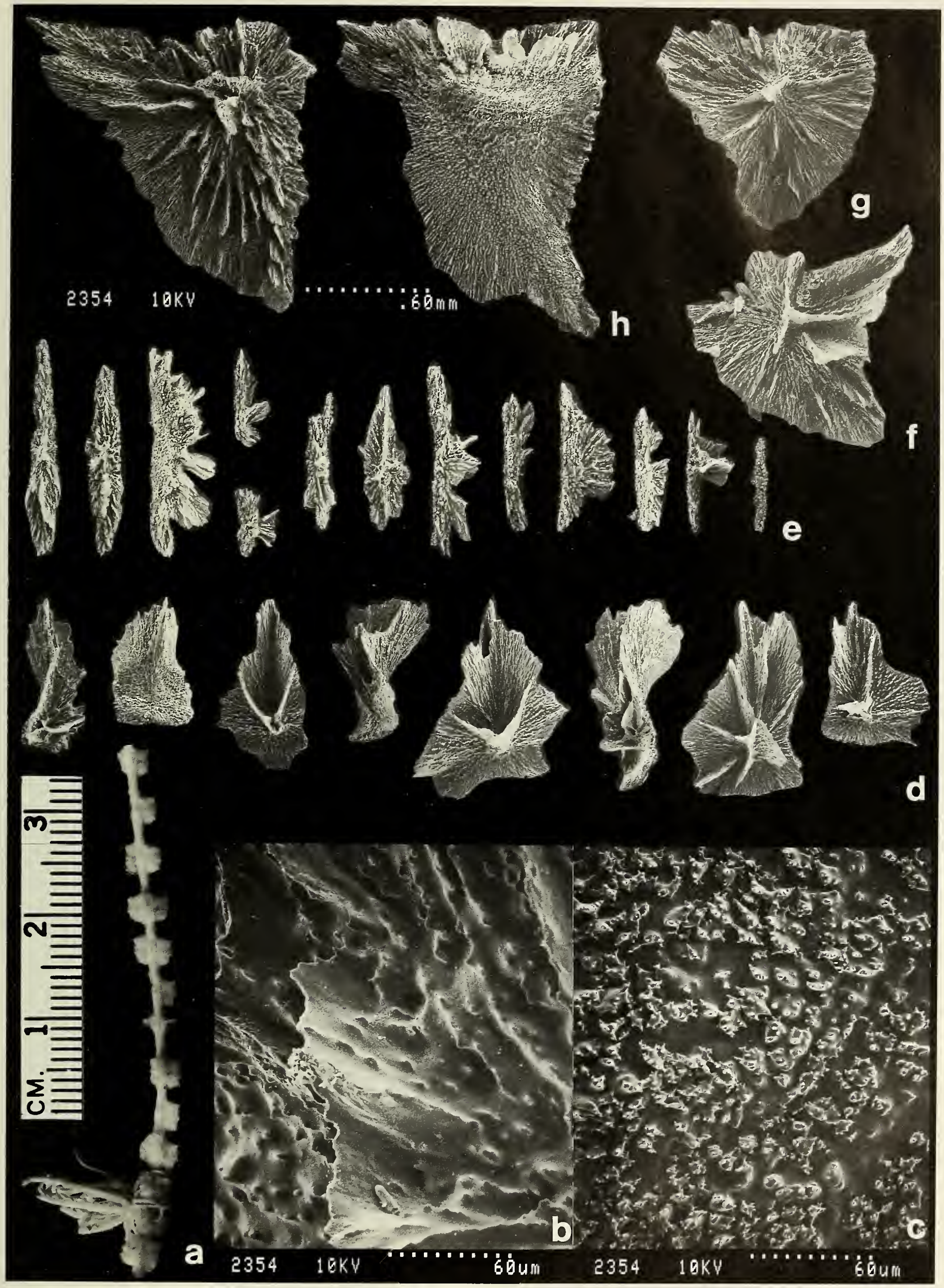

Fig. 1. *Narella ornata* new species. USNM 94617. a, Holotype fragment; b, External sculpture of body scale; c, Internal sculpture of body scale; d, Opercular scales; e, Coenenchymal sclerites; f–h, Body scales. b–h, SEM 2354.

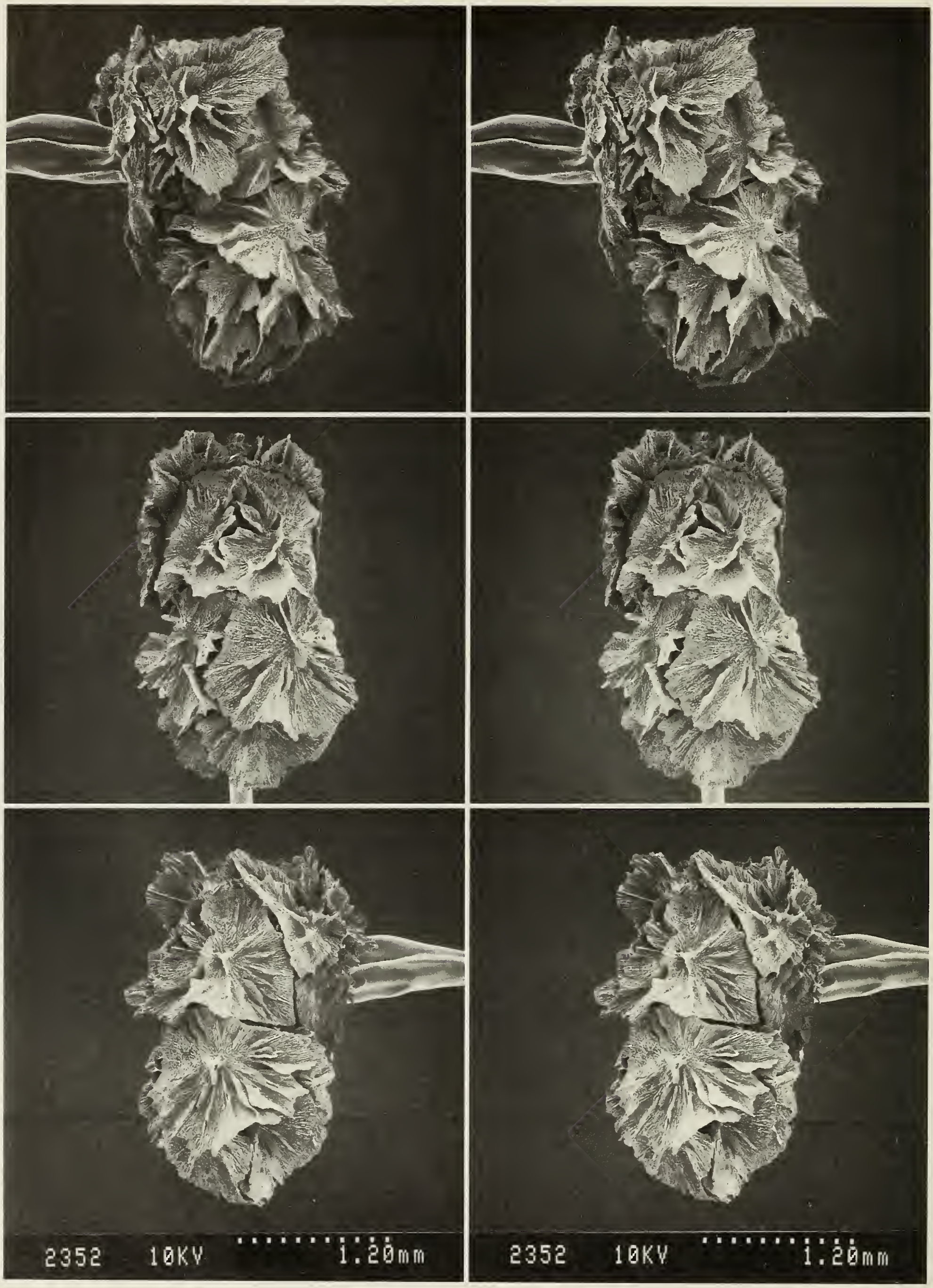

Fig. 2. *Narella ornata* new species. USNM 94617. Isolated polyp in lateral (top), abaxial (middle), and oblique views. SEM 2352, stereo pairs.

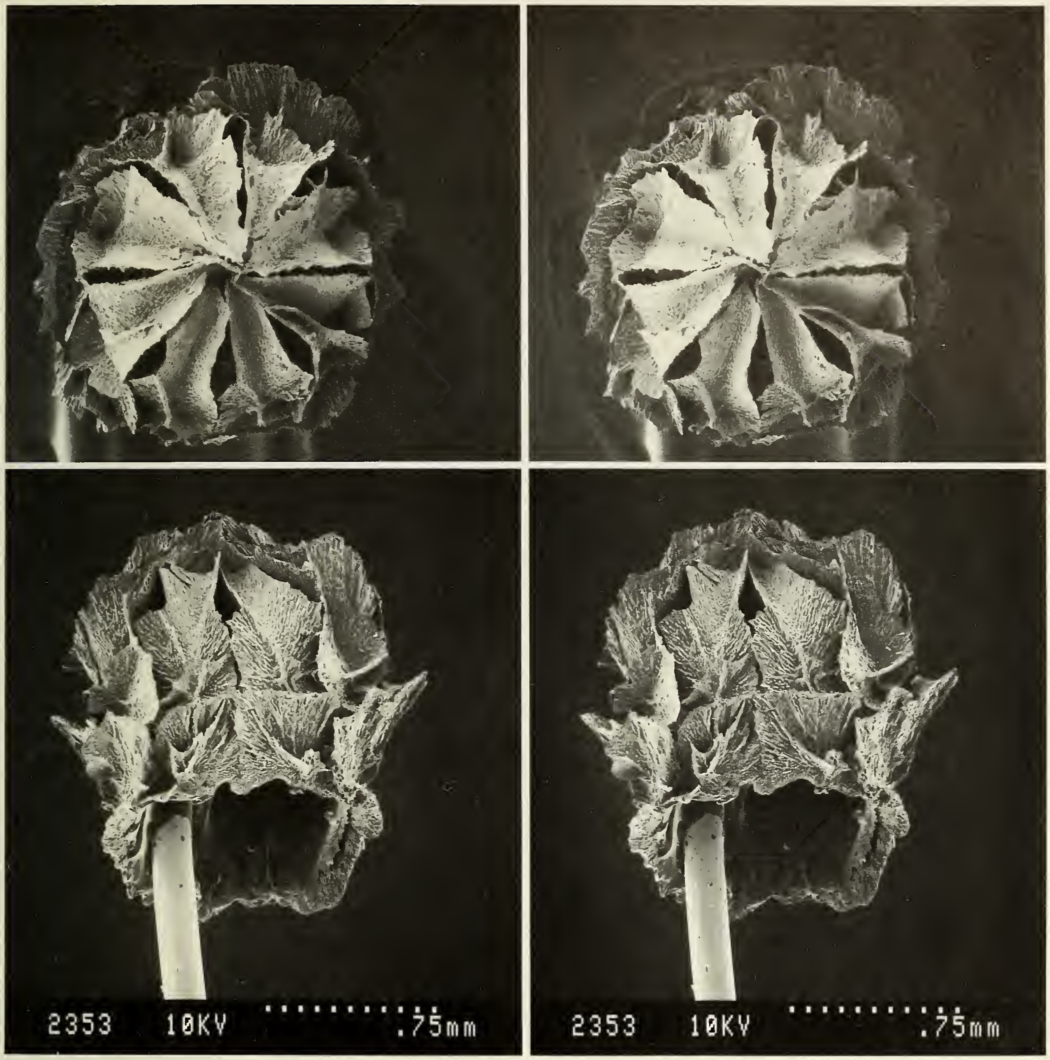

Fig. 3. *Narella ornata* new species. USNM 94617. Buccal portion of polyp showing closed operculum in oral aspect (top) and from the adaxial side (bottom). SEM 2353, stero pairs.

though type specimens and a selection of other material were sent to the U.S. National Museum by Prof. Nutting in 1907 after completion of his investigations, he retained a substantial number of specimens at the State University of Iowa as was his prerogative as collaborating specialist. The specimens still remaining at the University were transferred to the National Museum of Natural History in 1990, but nothing corresponding to the missing gorgonian is included in that material.

As the taxonomic characters of the remnant still extant are so conspicuously unlike those of any species of *Narella* now known, it can be established as a new species on those characters alone, without knowledge of the overall colonial morphology.

Acknowledgments

The scanning electron micrographs accompanying this paper were made by Mr. W. R. Brown, head of the SEM Laboratory, U.S. National Museum of Natural History. The constructive criticism of C. W. Hart, Jr., is acknowledged with thanks. The composite plate of sclerites was mounted and lettered by Ms. Molly Ryan, staff illustrator in the Department of Invertebrate Zoology. I am grateful to Ms. Cynthia Ahearn for her efforts to trace the colony from which the present fragment was cut.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(1):153–165. 1995.

Two new species of the red alga *Chrysymenia* J. Agardh (Rhodymeniales: Rhodymeniaceae) from the tropical western Atlantic

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Abstract.—Two new species of *Chrysymenia, C. littleriana* and *C. nodulosa,* are described from subtidal habitats, and compared to worldwide members of their morphological form-group, and to the other species of the tropical western Atlantic. *Chrysymenia nodulosa,* from the southwest coast of Puerto Rico, is characterized by its terete to compressed axes, opposite or alternate pinnate branching to 2 orders, nodulose swellings on the thallus surface, and spermatangia produced in anticlinal rows. *Chrysymenia littleriana,* from southern Martinique, is characterized by compressed axes, opposite pinnate branching to 5 orders, a lack of nodulose swellings, and spermatangia in periclinal rows. Among the known species of *Chrysymenia, C. bullosa* is recognized to be a *Botryocladia* and a new combination is proposed. Observations suggest that the ontogeny and structure of spermatangia in species of *Chrysymenia* be investigated as taxonomic characters, possibly for subgeneric groupings.

The red algal genus *Chrysymenia* J. Agardh (1842:105; Rhodymeniaceae Harvey, Rhodymeniales Kylin) is known from temperate to tropical seas. Species of this genus are found from the lower intertidal to the subtidal, sparsely distributed but sometimes locally abundant, and usually growing solitarily or few to several in a stand. The genus *Chrysymenia* is characterized by mucilaginous, fleshy thalli composed of simple or branched axes and branches that are terete, compressed, or nearly flattened, and that are usually hollow throughout. Anatomically, the cavities are bounded by large medullary cells and are mucilage-filled. The medullary cells may lack filaments or issue few to many medullary filaments and bear sessile gland cells. The cavities may be filled in varying degrees with medullary filaments, especially at the base of the stipe or in the flattened branches of some species. Outward to the medullary cells is a cortex 1–4 cells thick. Tetrasporangia are cruciately divided and scattered between the cortical cells. Cystocarps are scattered, partially immersed, ostiolate, and project above the cortex. Spermatangia are borne in surface areas of the cortex.

The seventeen presently known species of *Chrysymenia* can be divided into three morphological form-groups. Species of form-group 1 have erect thalli that are terete to moderately compressed: *C. ventricosa* (Lamouroux) J. Agardh (1842), *C. vesiculosa* J. Agardh (1851), *C. enteromorpha* Harvey (1853), *C. halymenioides* Harvey (1853), *C. wrightii* (Harvey) Yamada (1932), and *C. grandis* Okamura (1933). Species of form-group 2, have erect thalli that are flattened and blade-like: *C. agardhii* Harvey (1853), *C. digitata* (Harvey) J. Agardh (1876), *C. planifrons* (Melville) J. Agardh (1876), *C.*

dickieana J. Agardh (1892), *C. lobata* Howe (1914), *C. polyglandulosa* Okamura (1930), and *C. ornata* (J. Agardh) Kylin (1931). Species of form-group 3 are repent, with flattened, lobed thalli: *C. kaernbachii* Grunow (1889), *C. procumbens* Weber van-Bosse (1928), *C. okamurai* Yamada & Segawa (1953), and *C. glebosa* Abbott & Littler (1969). Cribb (1983:67) has suggested that the species of form-group 3 are morphologically similar and may prove to be conspecific. *Chrysymenia bullosa,* originally described from the Archipelago of Madeira (Levring 1974) and recently reported from the Azores (Fredericq et al. 1992), we now recognize, because of its solid stipe, to be a *Botryocladia.* Accordingly we propose the following new combination, ***Botryocladia bullosa*** (Levring) J. Norris & Ballantine, comb. nov. [Basionym: *Chrysymenia bullosa* Levring, Bol. Mus. Municipal Funchal 28(125):80, figs. 13–14, 1974].

Currently seven species of *Chrysymenia* are reported from the tropical western Atlantic: *C. agardhii, C. dickieana, C. enteromorpha, C. halymenioides, C. planifrons, C. ventricosa* (Taylor 1960, Wynne 1986), and *C.* cf. *okamurai* (reported from Belize by Norris & Bucher 1982). Some of these species had originally been members of the genus *Cryptarachne* (Harvey) Kylin (1931: 11, 1956:331; see also Taylor 1960:480), which was separated from *Chrysymenia* on the basis that the thalli of *Chrysymenia* are generally terete (rarely compressed) and have a central cavity lacking internal rhizoids, whereas the thalli of *Cryptarachne* are compressed to flat and possess internal rhizoids. Some of the species included in *Chrysymenia* by Kylin (1931), however, clearly possess medullary rhizoidal filaments. In discussing *Chrysymenia glebosa,* Abbott & Littler (1969) followed Okamura's (1936) opinion that the presence or absence of medullary rhizoidal filaments is a poor taxonomic character, and thus recognized a single genus.

Herein we describe two new western Atlantic species of *Chrysymenia* with type localities in Puerto Rico (Greater Antilles) and Martinique (Lesser Antilles).

Materials and Methods

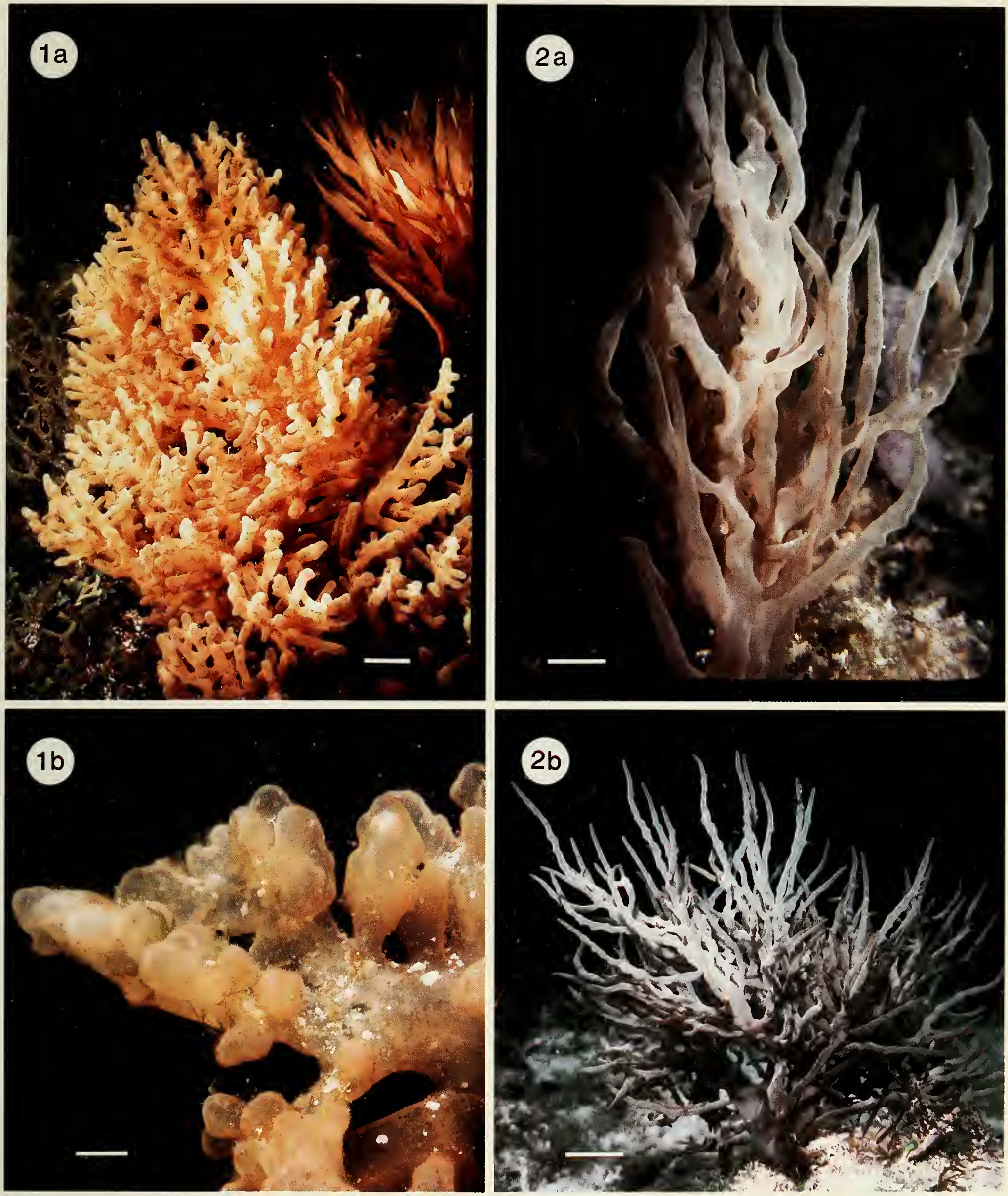
All specimens of *Chrysymenia* were collected by SCUBA diving and liquid-preserved in buffered 5% Formalin-seawater. Hand-cut sections and squash preparations were stained and fixed with 1% acidified aniline blue and mounted in Karo® clear corn syrup, with phenol added as a preservative, on microscope slides (Tsuda & Abbott 1985). Line drawings were prepared with the aid of a camera lucida on an Olympus light microscope. Photomicrographs were taken on a Zeiss Universal microscope using a Zeiss MC-63 with a M-35 camera body and Kodak® TMAX 35 mm B&W film. Specimens, including microscope slides and liquid-preserved material are deposited in the Algal Collection of the U.S. National Herbarium, National Museum of Natural History, Smithsonian Institution (US); duplicate isotype or paratype specimens are deposited in the Algal Herbarium, University of Puerto Rico, Mayagüez (MSM), the University of Michigan Herbarium (MICH), and the Herbarium of Seoul National University (SNU). Herbarium abbreviations follow Holmgren et al. (1990).

Results

Chrysymenia littleriana
J. Norris & Ballantine, sp. nov.
Figs. 1a, b, 3, 6, 10–14

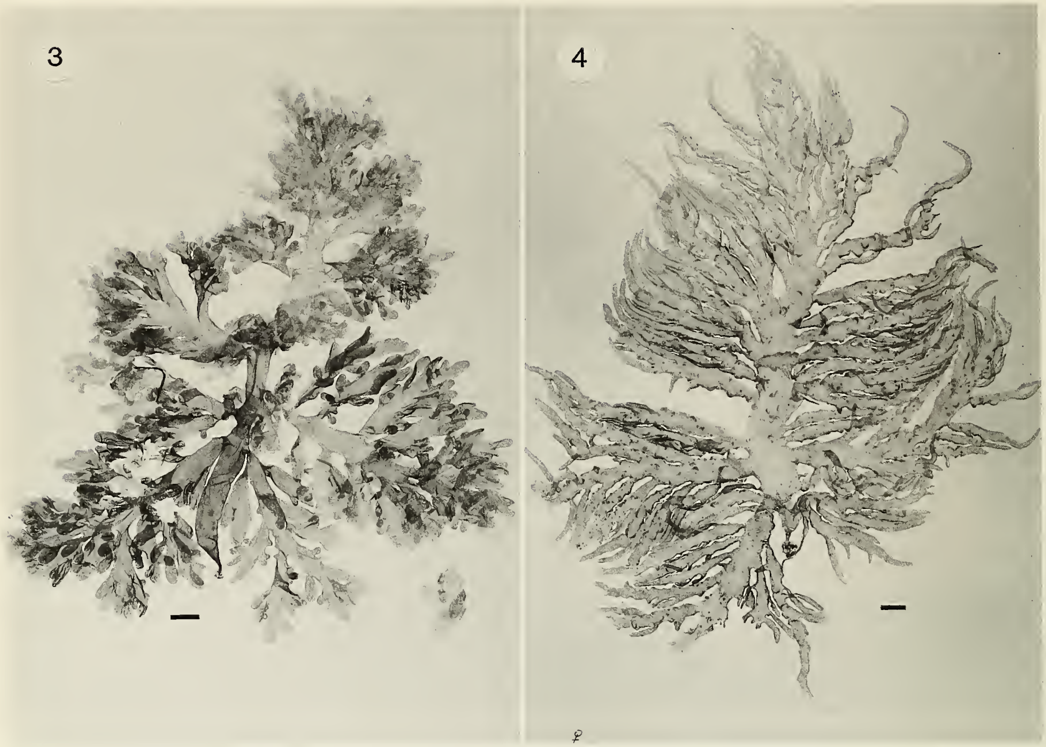
Latin description. — Thalli erecti usque ad 20 cm alti rufi gelatinosissimi, axe principali brevi (3–5 mm alto) tereti, parte basali compresescenti ad 15 mm lato, per hapteron discoideum affixo, usque ad 3–4(–5) ordines ramosi, filamentis lateralibus oppositis irregulariter pinnatis. Rami ad basin plerumque leviter constricti (interdum aconstricti), saccatescentes elongatescentesque, ad apicem inflati plerumque late obtusati usuque ad 10 mm diam.

Axes et rami cavati, cavo mucoso, me-



Figs. 1–2. Underwater photographs of the new species of *Chrysymenia* at their type localities. 1, *C. littleriana,* 15 m depth, Diamond Rock, Martinique: a, habit (scale bar = 20 mm); b, close-up of a branch showing the broadly obtuse apices (scale bar = 30 mm). 2, *C. nodulosa,* 17 m depth, Media Luna Reef, La Parguera, Puerto Rico: a, close-up showing the nodulose swellings on the thallus and tapering apices of the branches (scale bar = 20 mm); b. habit (scale bar = 10 mm).

dulla incolorata cellularum 2 aut 3 stratis composita; stratum intimum medullae cellularum irregulariter rotundatarum vel ovalium, usque ad 500 μm diam.; strata externa medullae cellularum anticlinaliter elongatarum versus exterium decrescentum. Fila rhizoidalia medullosa usque ad 15 μm diam., cellulis medullosis intimis genita, aliquando basaliter inflata, interdum localiter abunda. Cavitas ad basin stipitis



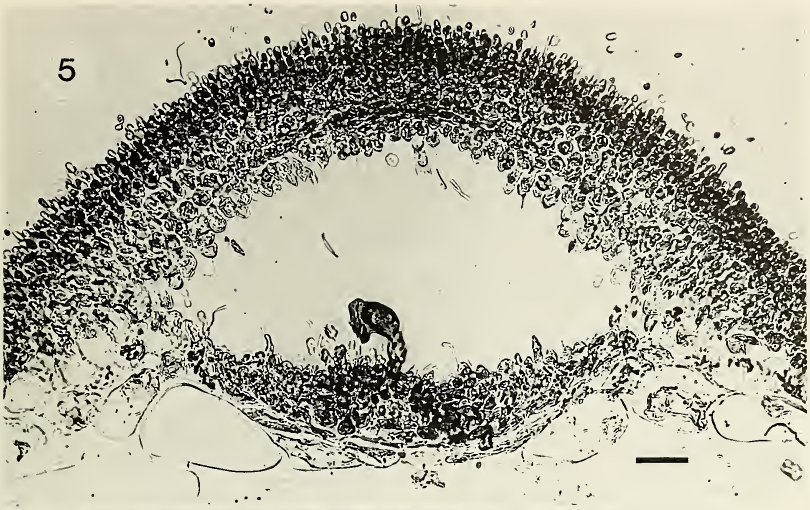
Figs. 3–4. Holotype specimens. 3, *Chrysymenia littleriana,* Alg. Coll. #US-162777 (scale bar = 10 mm); 4, *Chrysymenia nodulosa,* Alg. Coll. #US-162770 (scale bar = 10 mm).

dense filis rhizoidalibus medullosis repleta, filis inter cellulas medullosas at super hapteron crassiparietibus. Cellulae glandulosae interdum ex cellulis medullosis intimis in cavitatem centralem eminentes, pyriformae, usque ad 22–30 μm longae, atrocoloratae 1(–5) in quoque cellula. Cortex tristromaticus, cellulis intimis modice pigmentosis usque ad 25 μm diam., cellulis intermeditis usque ad 15 μm diam., cellulis externis cellulae (1–)2 stratis formatae, cellulis manifeste elongatis, ca. 12 μm longis × 6 μm diam.

Tetrasporangia cruciata elliptica, ca. 25 μm longis × 16 μm diam., ex cellulis corticis intiis orta. Spermatangia in soros superficiales dispositis, rotunda vel ovalia, 2–3 μm lata, in catenas periclinales (1–)2–3(–4) per cellula parentales spermatangiorum efferetia. Cystocarpia prominentia thalliformia, pericarpio crasso, in partibus distabilis thalli dispersa.

Description.—Thalli erect, to 20 cm tall, reddish-mahogany, highly gelatinous, with a short, terete main axis, 3–5 mm long, the basal portion becoming compressed, to 15 mm in diam., attached below by a discoidal holdfast, the thallus branched 3 to 4(–5) orders, with opposite, irregularly pinnately branched lateral branches. Branches at their base usually slightly constricted (occasionally not constricted), becoming saccate and elongated, and terminating in inflated, usually broadly obtuse apices up to 10 mm in diam.

Axes and branches hollow and mucilage-filled with a medulla composed of 2 or 3 layers of colorless cells; innermost layer of cells irregularly roundish to oval, up to 500 μm diam.; outer medullary cells decreasing



Figs. 5–6. Transverse sections through the prominent cystocarps. 5, hemispherical cystocarp of *C. nodulosa,* note the fusion cell (scale bar = 50 μm); 6, dome-shaped cystocarp of *C. littleriana* with mature carposporangia (scale bar = 100 μm).

sharply in size towards the exterior and anticlinally elongated. Medullary rhizoidal filaments up to 15 μm diam., issuing from the innermost medullary cells, occasionally inflated at the origin, sometimes locally abundant. Cavity of the lowermost basal portion densely filled with medullary rhizoidal filaments that also grow around and between the medullary cells, and these are thick-walled above the holdfast. Gland cells occasional on the innermost medullary cells facing into the central cavity, pyriform, to 22 μm by 30 μm, darkly staining, and usually 1(–5) per cell (Fig. 11). Cortex composed of 3 cell layers, an innermost layer of lightly pigmented cells up to 25 μm diam., an intermediate layer of cells up to 15 μm diam., and an outer layer of (1–)2 distinctly elongate cortical cells, averaging 12 μm long by 6 μm in diam.

Tetrasporangia cruciate, elliptical, ca. 25 μm by (12.5–)16 μm, and cut off by inner-

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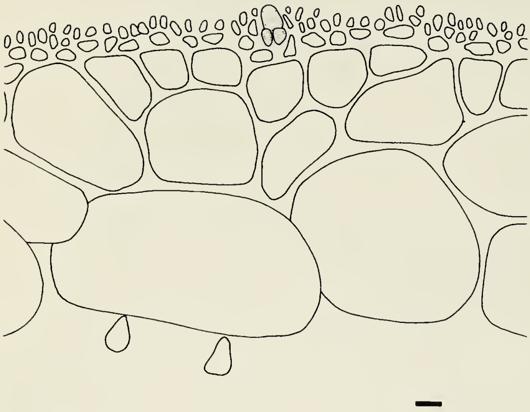

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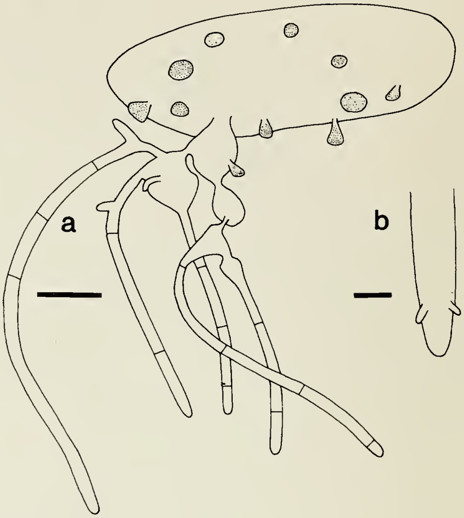

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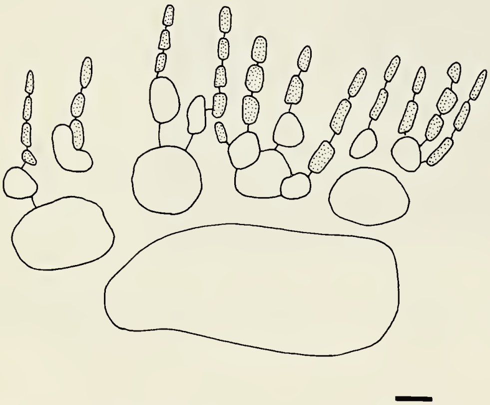

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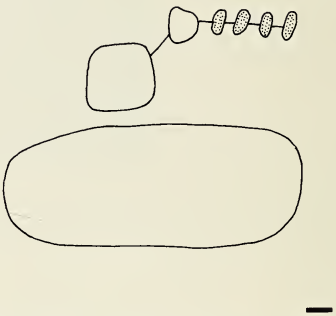
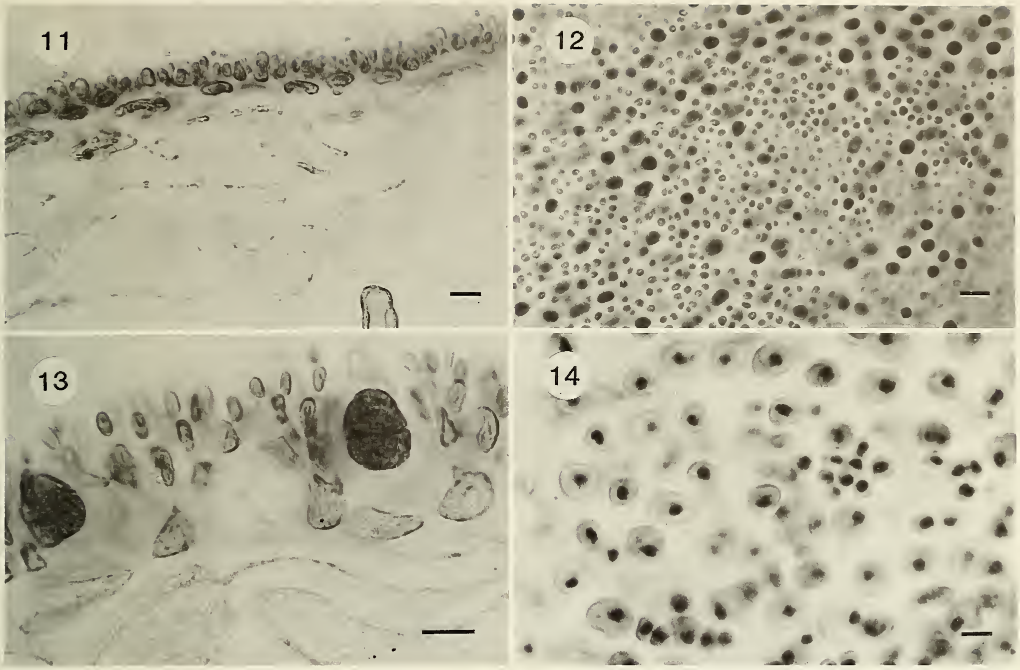


Figs. 7–8. Anatomy of *C. nodulosa.* 7, transection through a tetrasporangial thallus; note the cruciate tetraspore in the outer cortex, and the gland cells borne on large cells of the inner medulla (scale bar = 25 μm); 8a, inner medullary cell from near the base showing numerous gland cells and developing medullary filaments (scale bar = 100 μm); 8b, end of a medullary filament showing two small papillate projections (scale bar = 20 μm).

Figs. 9–10. Transection through spermatangial sori. 9, cortex of *C. nodulosa* showing spermatangial parent cells with one to four spermatia cut off in anticlinal series (scale bar = 15 μm); 10, *C. littleriana* showing spermatangial parent cell with spermatia cut off in periclinal series (scale bar = 15 μm).

most cortical cells (Fig. 13). Spermatangia in sori on thallus surface (Fig. 12). Spermatangial parent cells produce in periclinal chains (1–)2–4 spermatangia, spherical to oval, 2–3 μm in diam. (Figs. 10, 14). Cystocarps prominent, up to 1.2 mm dome-shaped, scattered over the distal portions of the thallus, with a thick pericarp (Fig. 6).



Figs. 11–14. Anatomy of *C. littleriana.* 11, transection showing outer cortex and inner medulla with a single large gland cell (scale bar = 25 μm); 12, surface view of spermatangial sorus (scale bar = 10 μm); 13, transection through a tetrasporangial thallus showing cruciate tetraspores in outer cortex (scale bar = 15 μm); 14, surface view showing spermatia in periclinal rows above the spermatangial parent cell (scale bar = 5 μm).

Holotype.—DML-746 (Alg. Coll. US-162777), including liquid-preserved specimen and accompanying microscope slides; leg. C. Forsyth, B. L. Brooks, M. M. Littler & D. S. Littler, 20 Jul 1986 (Fig. 3).

Type locality.—Attached to rock, ca. 8 m depth, Diamond Rock (14°26′60″N, 61°02′50″W), Martinique, French West Indies, Lesser Antilles.

Paratypes.—All from the type locality, attached to basalt rock, 12–15 m depth, Diamond Rock, DML-17092 (Alg. Coll. US-162662), 21 May 1989, leg. D. S. Littler, M. M. Littler, B. L. Brooks & S. A. Reed, 21 May 1989; and, DML-17223 ♀, ♂, & ⊕ (Alg. Coll. US-162775; MSM; MICH; SNU), leg. B. L. Brooks, S. A. Reed, D. S. Littler & M. M. Littler, 23 May 1989.

Etymology.—*Chrysymenia littleriana* is named for our colleagues, Diane S. Littler and Mark M. Littler (National Museum of Natural History, Smithsonian Institution) in recognition of their phycological contributions and having collected this distinctive alga; in choosing the Latin adjectival,-*iana,* the specific name translates as "the Littlerian *Chrysymenia.*"

Chrysymenia nodulosa
J. Norris & Ballantine, sp. nov.

Figs. 2a, b, 4, 5, 7, 8a, b, 9

Latin description.—Thalli erecti, usque ad 30 cm alti, cinerascentes gelatinosi, stipitibus brevibus, axibus ramisque juventute fere omino teretibus, usque ad 6 mm diam. leviter nodulosis aetate compressescentibus usque ad 12 mm latis, magis nodulosis, ramificatio oppositis aut alternatis, plerumque plano singulari, ramosis lateralibus pinnatis usque ad 2 ordines.

Axes et rami cavatae, medulla incolorata, cellularum plerumque 3 stratis composita, cellulis intimis maximis, cellulis extrinsecus decrescentibus. Cellulae medullosae intimae irregulariter rectangulares, usque ad 300 μm × 600 μm. Fila rhizoidalia medullosa plerumque in partibus veteribus, usque ad 22 μm diam., basaliter tumidis ex cellulis medullosis intimis, plerumque cellulis medullosis aliis, saepe distaliter minute papillosis. Cellulae glandulosae abundantes ex intimis cellulis medullosis in cavitatem centralem eminentibus, pyriformae, usque ad 35 μm longae × 32 μm diam., atrocoloratae, usque ad 25 in quoque cellula. Cortex bi- vel tristromaticus, cellulis parvis; pilis in partibus veteribus corticis adundantibus superficie in sicco corno.

Tetrasporangia cruciata, elliptica, 28–36 μm longa × 14–18 μm diam.; in strato corticali parce dispersa. Spermatangia in soros superficiales dispositis. Spermatangia rotunda vel ovalia 2.2–3.6 μm lata in catenas anticlinales (1–)2–4(–5) per cellulas parentales spermatangiorum efferentia. Cystocarpia prominentia hemirotunda, usque ad ca. 1 mm diam. ad superficiem thalli.

Description.—Thalli erect, up to 30 cm tall above a short stipe, grayish, gelatinous, axes and branches when young almost entirely terete, to 6 mm diameter, and slightly nodulose, becoming compressed, to 12 mm broad, and more nodulose with age and size; branching mostly in a single plane with opposite or alternate, pinnately branched laterals to 2 orders.

Axes and branches internally hollow with a medulla generally of 3 layers of colorless cells which are largest internally and become smaller towards the surface. Innermost medullary cells are irregularly rectangular, up to 300 μm by 600 μm (Fig. 7). Medullary filaments mostly in older portions, to 22 μm in diam. (Figs. 8a, b), inflated at their origin from the innermost medullary cells (Fig. 8a) or occasionally from other medullary cells, and often with small papilla-like projections near distal ends (Fig. 8b). Gland cells (Figs. 7, 8a) are abundant on innermost medullary cells facing into the central cavity, pyriform, to 35 μm long by 32 μm diam., darkly staining, and up to 25 per cell. Cortex composed of 2 or 3 layers of small cells (Fig. 7); hairs abundant in cortex of older portions of thallus, giving the surface a horny texture when dried.

Tetrasporangia cruciate, oval, 28–36 (–38) μm long by 14–18 (–20) μm wide; sparingly scattered in the cortical layer (Fig. 7). Spermatangia in sori on thallus surface. Spermatangial parent cell produces an anticlinal chain of (1–)2–4(–5) spermatangia, spherical to oval, 2.2–3.6 μm (Fig. 9). Cystocarps protruding, hemispherical, to about 1 mm diam. in surface view (Fig. 5).

Holotype.—DLB-3108, cystocarpic (Alg. Coll. US-162770), leg. D. L. Ballantine, 5 May 1988 (Fig. 4).

Type locality.—17 m depth, 1.5 km seaward of Media Luna Reef, La Parguera, Puerto Rico, Greater Antilles.

Isotypes.—DLB-3108, tetrasporangial (Alg. Coll. US-162772; MSM); and DLB-3108, spermatangial (Alg. Coll. US-162771; MSM; and MICH).

Paratypes.—All from Media Luna Reef, La Parguera, leg. D. L. Ballantine: DLB-1837 (MSM), 24 Jan 1985; DLB-2128 (Alg. Coll. US-014407), 2 Nov 1985; DLB-3340 (MSM), 21 Feb 1989; and DLB-3375 (MSM), 26 Apr 1989.

Etymology.—The specific epithet *nodulosa* refers to the small, knobby swellings on the thallus surface, a characteristic unique to this new species of *Chrysymenia*. It is the diminutive of Latin *nodosus* (Stearn 1973), and means "full of little knobs."

Key to the Western Atlantic species of *Chrysymenia*

1. Thallus flat 2
1. Thallus terete to compressed 4
2. Branches of the thallus broad (>2.0 cm), foliose 3
2. Branches of the thallus narrow (<2.0 cm), irregularly branched to 4(–5) orders .... *C. dickieana*

3. Thallus dichotomous to palmately branched, 2.0 to 2.5 cm broad . . . . *C. agardhii*
3. Thallus branching irregularly lobed, >2.5 cm . . . . *C. planifrons*
4. Thallus terete, occasionally compressed at and above the base 5
4. Thallus slightly to moderately compressed throughout 6
5. Branches highly constricted at the base . . . . *C. enteromorpha*
5. Branches not or barely constricted at the base . . . . *C. ventricosa*
6. Branching dichotomous . . . . *C. halymenioides*
6. Branching pinnate 7
7. Thalli with nodulose swellings (more pronounced in older and/or larger thalli) . . . . *C. nodulosa*
7. Thalli without nodulose swellings . . . . *C. littleriana*

Discussion

The genus *Chrysymenia* has close affinities to *Botryocladia* (J. Agardh) Kylin (1931: 17). These genera are separated by the vegetative characters of solid axes and diaphragms in *Botryocladia* and hollow axes without diaphragms in *Chrysymenia.* Brodie & Guiry (1988) pointed out that the degree of stipe development in *Botryocladia* is variable. They speculated that the genus might be an artificial grouping of species, but they retained it with reservations. In our specimens, we observed the short, stiptate regions of the new species to be filled with rhizoidal filaments, in some places very densely. This suggests that the nature and origin of the cells in the stipe and axes may be a useful taxonomic character, i.e., the solid, parenchymatous medulla of the axes in *Botryocladia* vs. the rhizoidal filament-filled cavity of the stipe in *Chrysymenia.*

Chrysymenia littleriana and *C. nodulosa* have some features in common, including the short stipe above a discoidal holdfast, compressed axes, and pinnate branching (Figs. 1–4). These new species are also similar anatomically (Figs. 7, 11), with large medullary cells of *C. littleriana* generally in two layers and those of *C. nodulosa* mostly in three layers. Both species have two or three layers of cortical cells, although the outermost cortical cells in *C. littleriana* are elongate (Fig. 13). They both produce non-aggregated gland cells from inner medullary cells (Figs. 7, 8, 11), although they are much more abundantly produced in *C. nodulosa.* In *C. nodulosa,* the medullary filaments frequently possess very minute, papilla-like projections near their distal ends (Fig. 8b) and the inner medullary cells give rise to internal rhizoids that are inflated at their origin (Fig. 8a). Sometimes the internal rhizoids of *C. littleriana* are also similarly inflated. Transections of both *C. littleriana* and *C. nodulosa* through the terete, stipitate basal region reveal cellular medullary and cortical regions similar to the distal portions of inflated thallus branches; however, the central medulla of this region is densely filled with branching, rhizoidal filaments.

Reproductively the cruciately divided tetrasporangia are oval and cut off by an inner cell of the cortical layer in both new species (Figs. 7, 13); however, they are larger in *C. nodulosa* (28–36 μm by 14–18 μm) than in *C. littleriana* (25 μm by 16 μm). Female *C. nodulosa* and *C. littleriana* are readily recognizable by their hemispherical and dome-shaped cystocarps that project well above the thallus surface (Figs. 5, 6).

Lee (1969:figs. 1A, B, 2A, B) recognized two modes of spermatangial development in the Rhodymeniales: (1) the "separate type," where the parent cells are separate from each other, the parent cell and spermatangia are surrounded by a common gelatinous wall, and the spermatia produced are comparatively large; and (2) the "seriate type," in which the parent cells originate from the same cortical cell in seriate rows and are pit connected to each other, the spermatangia and the parent cell each have an independent cell wall, and the spermatia

Table 1.—Comparison of the new species of *Chrysymenia* with: A.) the morphologically similar species of form-group 1; and B.) the other known species of the tropical Western Atlantic.

	Habitat	Degree of flattening	Branching pattern	Branch constrictions	No. cortical cell layers
A. Form-group 1					
C. enteromorpha (1, 2, 3)	Deep, 15–90 m	Terete	Radial, commonly whorled from distal end of axial segments	+	1
C. grandis (4)	Deep, 30 m	Subcylindrical to slightly compressed	Simple or irregularly branched	No	
C. halymenioides (2, 5)	Deep, 43 m	Sub-terete to compressed	Dichotomous	Slight at most	Several
C. littleriana (3)	5–15 m	Compressed	Oppositely pinnate	Slight at most	3
C. nodulosa (3)	Deep, 17–24 m	Compressed	Alternate to oppositely pinnate	Slight	2 to 3
C. ventricosa (Med.) (6)	Shallow to 130 m	Terete	Alternate to oppositely pinnate	No	Several
C. ventricosa (Carib.) (1, 2)	Deep, to 90 m	Compressed below, terete above	Irregularly alternate to opposite	Slight	Several
C. wrightii (7, 8)	Shallow	Terete	Radial, alternate, opposite or irregular	+	1 to 3
B. Other tropical Western Atlantic species					
C. agardhii (1, 2)	Shallow to deep, to 29 m	Flat	Dichotomous to palmately lobed	No	1 to 2
C. planifrons (1, 2)	Deep, 30 m	Flat	Irregularly lobed	No	1

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1) Børgesen 1920, 2) Taylor 1960, 3) This study, 4) Okamura 1933, 5) Harvey 1853, 6) Kuckuck 1912, 7) Lee 1978, 8) Ben Maiz et al. 1987.

Table 1.—Extended.

No. medullary cell layers	Gland cells	Hollow	Presence of medullary filaments	Distribution	Tetrasporangia	Cystocarps	Spermatangia
1	Scattered or small groups	+	−	Bermuda, North Carolina, Florida, U.S.V.I., Brazil, P.R.	Elliptical, scattered, 28 × 39 μm	Projecting	
	+	+		Japan	Elliptical, 10–15 μm	Small, roundish, not prominent	
4 to 5	+	+		Bermuda, Florida, Jamaica, Netherlands Antilles	Spherical to elliptical	Rounded, conical	
2 to 3	Occasional, mostly solitary, on medullary cells	+	+	Martinique, Guadeloupe	Elliptical, scattered, (12.5–)16 × 25 μm	Conical, projecting to 1.2 mm diam.	Average 2.4 μm diam., spermatangia in periclinal seriate series
3	Abundant on medullary and submedullary cells	+	+	Puerto Rico	Oval, scattered, 28–38 × 14–20 μm	Hemispherical, projecting to 1 mm diam.	Average 2.7 μm diam., spermatangia in anticlinal seriate series
2 to 3	Numerous, scattered	+	+	Morocco, Mediterranean	Elliptical, scattered, 20–26 × 15–19 μm		
2 to 3	Occasional, solitary; oblong	+	+	U.S.V.I., Bermuda, Jamaica, Venezuela	Elliptical, scattered, 20 μm	Hemispherical, projecting	
3 to 5	Aggregated or solitary	+	+	Japan, Korea, Mediterranean	Spherical to elliptical, 38–42 × 48–53 μm	Projecting, 850–950 μm diam.	2.9 × 4 μm, spermatangia in anticlinal seriate series
2	Occasional, scattered	+	+	North Carolina, Florida, Bermuda, U.S.V.I.	Spherical, 27 μm		
1 to 2	Occasional, scattered	+	+	Florida, Puerto Rico, U.S.V.I., Netherlands Antilles			

are comparatively small. The nature and development of spermatangia in *Chrysymenia* have been little studied and are known for only three species (Table 1). Spermatangial production for both new species is the seriate type (Figs. 9, 10), similar to that reported by Lee (1978) for *C. wrightii,* with the outer cortical cells cutting off up to 4 spermatangial parent cells. In *C. nodulosa,* the spermatangia are cut off serially from spermatangial parent cells in anticlinal rows (Fig. 9). In contrast, spermatangia are cut off periclinally in *C. littleriana* (Figs. 10, 14). As spermatangial thalli are discovered and described for other species of *Chrysymenia,* the different kinds (separate vs. seriate, and periclinal vs. anticlinal; Table 1) should be correlated to see if these characters have any taxonomic significance, perhaps for use in subgeneric groupings as has been proposed for *Gracilaria* by Yamamoto (1978).

Chrysymenia nodulosa and *C. littleriana* are unique among Caribbean species of the genus (Table 1), and distinct from all the other species of morphological form-group 1 (as noted in the Introduction). Both new species lack the totally terete thallus with the highly constricted branches as seen in *C. enteromorpha* (Børgesen 1920). They are also easily separated from *C. halymenioides,* which is dichotomously branched.

Chrysymenia nodulosa and *C. littleriana* could be confused with *C. ventricosa* sensu Taylor (1960:460, see e.g., pl. 62:fig. 3). However, on close examination, the two new species are clearly different from it in several respects. *Chrysymenia nodulosa* differs from all known species of *Chrysymenia* (Table I) in having abundant, nodulose projections irregularly scattered across its thallus surface (Figs. 2a, b, 4). It also possesses more elongate and larger tetrasporangia, as well as having branches that are more constricted at their origin than in specimens of *C. ventricosa* (MICH; US). *Chrysymenia littleriana* branches to 3–4(–5) orders vs. 1–3 orders for *C. ventricosa.* The branches of *C. littleriana* are considerably more closely set and have broadly obtuse branch apices, and the tetrasporangia are smaller and more elongate than those of *C. ventricosa.* Furthermore, the distal portions of the thalli are compressed in *C. littleriana* and *C. nodulosa,* whereas they are terete in *C. ventricosa.*

Of the non-western Atlantic species, *Chrysymenia wrightii* superficially resembles *C. nodulosa*; however, *C. wrightii* differs in possessing terete axes and up to five layers of medullary cells (Lee 1978, Ben Maïz et al. 1987). These characters also serve to differentiate *C. littleriana* from *C. wrightii.*

Acknowledgments

We thank S. Fredericq for the Latin descriptions and the photomicrographs of spermatangial preparations, D. S. Littler for the color photo of *Chrysymenia littleriana,* D. H. Nicolson for nomenclatural discussions, R. H. Sims for the type specimen photos, M. J. Wynne (MICH) for a loan of specimens of *C. ventricosa,* and W. Fenical (Chief Scientist) for JN's collaboration on the 1985 and 1986 Lesser Antilles expeditions of OR/V *Cape Florida* (University of Miami) supported by National Science Foundation #CHE-86-20217 and in part by the Smithsonian Institution's Caribbean Coral Reef Ecosystem Program (CCRE contribution number 433), and the Smithsonian Marine Station at Link Port, Fort Pierce, Florida (SMSLP contribution number 366). For reviewing the manuscript we appreciate the comments of N. Aponte, K. E. Bucher, and D. B. Lellinger.

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Applications published in the *Bulletin of Zoological Nomenclature*

The following Applications were published on 20 December 1994 in Vol. 51, Part 4 of the *Bulletin of Zoological Nomenclature.* Comment or advice on 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.	
2888	*Valdivianemertes* Stiasny-Wijnhoff, 1923 (Nemertea): proposed conservation.
2908	*Vejdovskyella* Michaelsen, 1903 (Annelida, Oligochaeta): proposed precedence over *Macrochaetina* Bretscher, 1899.
2896	*Scottia* Brady & Norman, 1889 (Crustacea, Ostracoda): proposed designation of *Scottia pseudobrowniana* Kempf, 1971 as the type species.
2893	*Temnorhynchus* Hope, 1837 (Insecta, Coleoptera): proposed conservation
2865	BRACHYPTERINAE Erichson, 1845 (Insecta, Coleoptera) and BRACHYPTERINAE Zwick, 1973 (Insecta, Plecoptera): proposed removal of homonymy.
2917	*Coproica* Rondani, 1861 and *Ischiolepta* Lioy, 1864 (Insecta, Diptera): proposed conservation of usage by the designation of *Limosina acutangula* Zetterstedt, 1847 as the type species of *Coproica*
2907	*Sphaerocera* Latreille, 1804 and *Borophaga* Enderlein, 1924 (Insecta, Diptera): proposed conservation; *Sphaerocera curvipes* Latreille, 1805 and *Phora flavimana* Meigen, 1830: proposed conservation of the specific names.
2898	*Scomber dentex* Bloch & Schneider, 1801 (currently *Caranx* or *Pseudocaranx dentex*) and *Caranx lugubris* Poey, [1860] (Osteichthyes, Perciformes): proposed conservation of the specific names.
2934	*Bagrus hoevenii* Bleeker, 1846 (currently *Hemibagrus hoevenii;* Osteichthyes, Siluriformes): proposed designation of a neotype.
2877	*Lycognathophis* Boulenger, 1893 (Reptilia, Serpentes): proposed conservation.
2953	*Loris* E. Geoffroy Saint-Hilaire, 1796 (Mammalia, Primates): proposed conservation.

The 122nd Annual Meeting of the Biological Society of Washington will be held on Friday, 12 May 1995, at 12:00 noon in the Waldo Schmitt Room, National Museum of Natural History, Washington, D.C.

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PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY
OF
WASHINGTON

VOLUME 108 NUMBER 2
22 JUNE 1995
ISSN 0006-324X

THE BIOLOGICAL SOCIETY OF WASHINGTON

1994–1995

PROCEEDINGS

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Known office of publication: National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Printed for the Society by Allen Press, Inc., Lawrence, Kansas 66044

Second class postage paid at Washington, D.C., and additional mailing office.

POSTMASTER: Send address changes to PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON, P.O. Box 1897, Lawrence, Kansas 66044.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(2):169–179. 1995.

A new species of *Raricirrus* (Polychaeta: Ctenodrilidae) from wood collected in the Tongue of the Ocean, Virgin Islands

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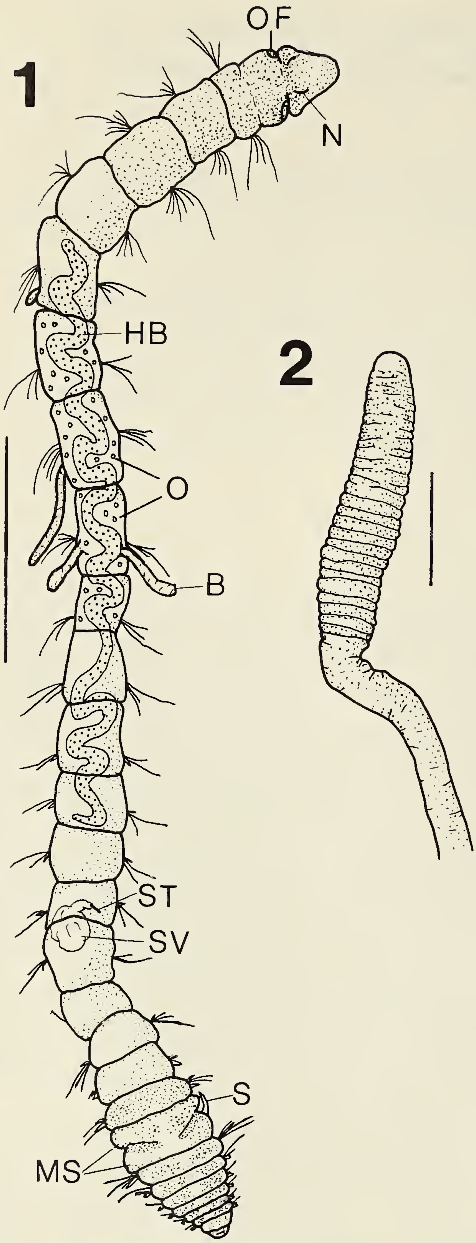
Abstract.—*Raricirrus variabilis* new species (Polychaeta: Ctenodrilidae) is described from the Tongue of the Ocean, St. Croix, Virgin Islands. This deep-sea species was collected from submerged wood at 4000 m and is an apparent organic-enrichment opportunist. Taxonomic differences between the genera *Raricirrus* and *Raphidrilus* are discussed. The life history characteristics of this species are examined.

Woody plant material is rapidly broken down in the deep sea by bivalves belonging to the family Pholadidae (Mollusca), subfamily Xylophagainae. The activities of these pholads have been shown to provide a highly concentrated, tractable source of organic material that supports a community of associated organisms (Turner 1973, 1977, 1981). Many of these associated species survive in the deep sea by specifically finding and exploiting organically enriched sites (Grassle & Morse-Porteous 1987, Smith & Hessler 1987, Desbruyères & Laubier 1988). As part of a long-term study of such wood-associated communities by Dr. Ruth Turner, specimens of an undescribed polychaete belonging to the family Ctenodrilidae were recovered from pholad-riddled wood panels and stray wood ("wild wood") retrieved from the deep-sea floor in the Tongue of the Ocean. This paper describes *Raricirrus variabilis*, new species, and further elucidates the separation of two ctenodrilid genera *Raricirris* and *Raphidrilus.*

Raricirrus variabilis, new species

Material examined.—St. Croix, Virgin Islands: 17°56.63′N, 64°48.6′W, 4000 m. Holotype (MCZ 4008) from wood panel P-13; submerged 17 Dec 1978 (*Alvin* Dive 873), recovered 6 Dec 1980 (*Alvin* Dive 1079). Paratypes (MCZ 4009) 12 specimens from same panel and dates. Paratype (MCZ 4011) one specimen from wood panel P-2; submerged 17 Dec 1978 (*Alvin* Dive 873), recovered 13 Dec 1980 (*Alvin* Dive 1082). Paratypes (MCZ 4010) 6 specimens from wood panel P-12; submerged 17 Dec 1978 (*Alvin* Dive 873), recovered 13 Dec 1980 (*Alvin* Dive 1082). Paratypes (USNM 170552) 8 specimens from wood panel P-5 & P-13 wash material; submerged 17 Dec 1978 (*Alvin* Dive 873), recovered 6 Dec 1980 (*Alvin* Dive 1079). Paratypes (USNM 170553) 4 epitokous specimens from 6 Ft. plank, wild wood; recovered 20 Dec 1978 (*Alvin* Dive 876).

Description.—Benthic form: Body elongate with widened posterior region; anterior and middle body segments longer than wide, posterior segments much wider than long (Fig. 1). Holotype 6.75 mm long, 0.43 mm maximum width (modified segments) with 27 setigers (Table 1, specimen S); paratypes 1.54–7.59 mm long, 0.25–0.61 mm wide, with 18–31 setigers (Table 1). Prostomium conical, eyespots lacking; nuchal organs dorsolateral, appearing as slits or round depressions with what appear to be cilia within. Prostomium with lateral oral folds; pro-



Figs. 1–2. *Raricirrus variabilis,* new species. 1. Dorsal view of holotype (specimen S). B = branchiae, HB = heart body, MS = modified segments, N = nuchal organ, O = oocytes, OF = oral fold, S = enlarged spine, ST = reproductive stylet, SV = seminal vesicle. Scale bar = 1.0 mm. 2. Distal end of branchia (specimen MCZ 4011). Scale bar = 100 μm.

stomium, peristomium and first setiger continuous dorsally, differentiated ventrally. Body of larger specimens brownish gray, prostomium brown posterodorsally, first two setigers and posterior body region gold brown across dorsum; smaller specimens uniformly pale tan to cream color.

Branchial filaments greatly elongate (approximately 60% of total body length) with club-like ends (Fig. 2), emerging posterodorsal to notopodia. Branchial filaments fragile and easily lost or broken (incomplete branchiae on setigers 5, 7 and 8 in holotype), branchial scars on other segments not discernible; anteriormost occurrence observed at setiger 2, posteriormost on last setiger anterior to the modified segments of an epitokous individual. Heart body a reddish brown convoluted tube (Fig. 1) extending for a variable (range shown in parentheses) number of segments (4–11) beginning on setiger 4 (4–6).

Notosetae and neurosetae emerging directly from body wall, lateral in anterior region, becoming ventrolateral elsewhere. Notosetae of three kinds: four to six capillaries finely serrate distally, usually one (1–3) much longer (ca. ⅔ body width) than others; short pectinate setae with narrow, widely spaced teeth (Fig. 3A) beginning in anterior half of body, grading into coarsely pectinate falcigers in the midbody region (Fig. 3B), and coarsely serrate setae (Fig. 3C) posterior to the modified setigers. Neurosetae three to six pectinate falcigers (Fig. 3D) increasing in length posteriorly; 1–2 straight, coarsely serrate setae (similar to those of posterior notopodia) in the setigers posterior to the modified setigers (Fig. 4).

A pair of modified segments present as first two segments of broadened posterior region in all but several smaller (<2.73 mm long) individuals (Table 1). Modified segments distinct dorsally (Fig. 6), with one pair of large, curved notopodial spines emerging anterolaterally from second modified segment (holotype with only a single spine on right side), fitting into deep grooves on posterior ventral surface of first modified

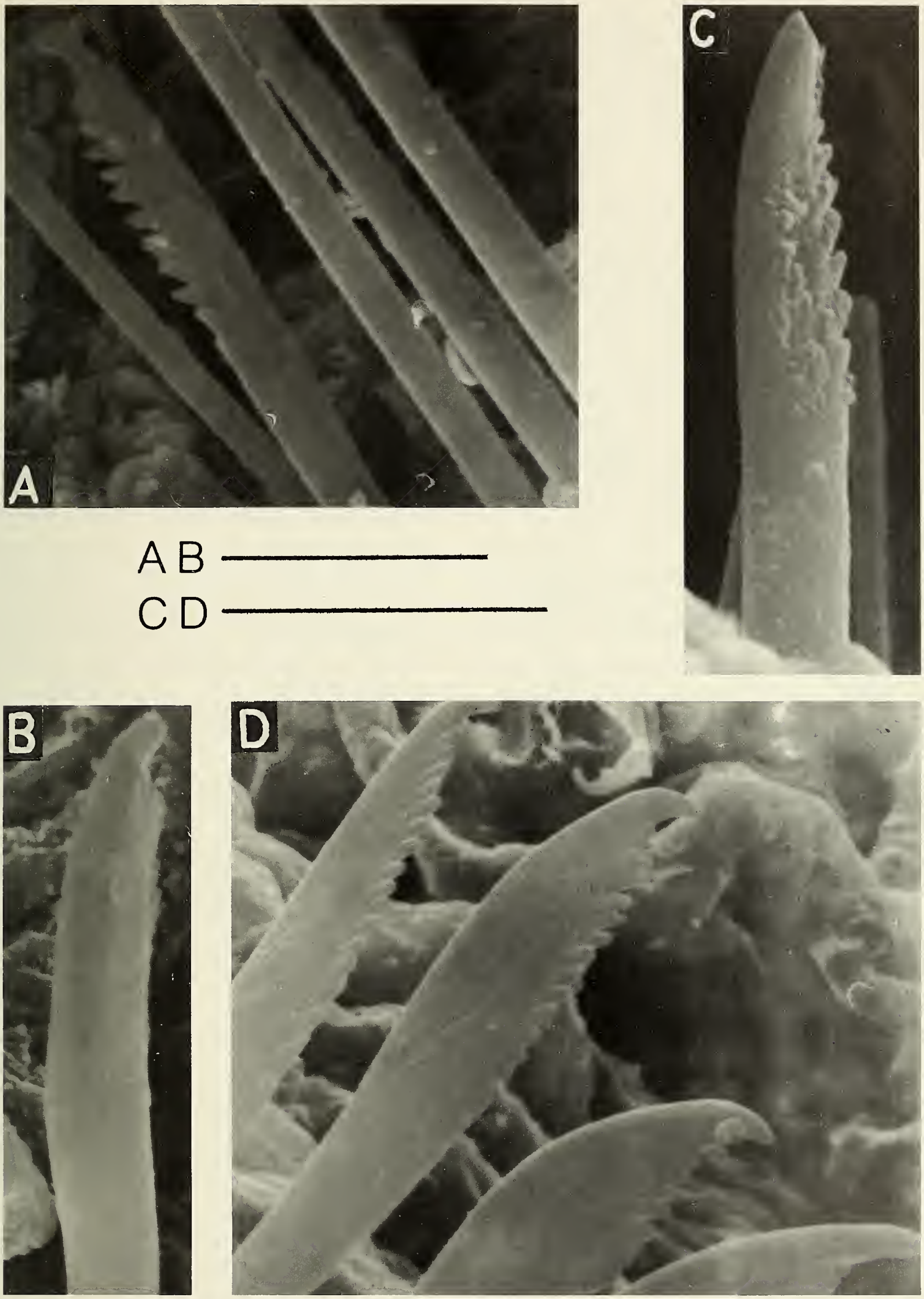
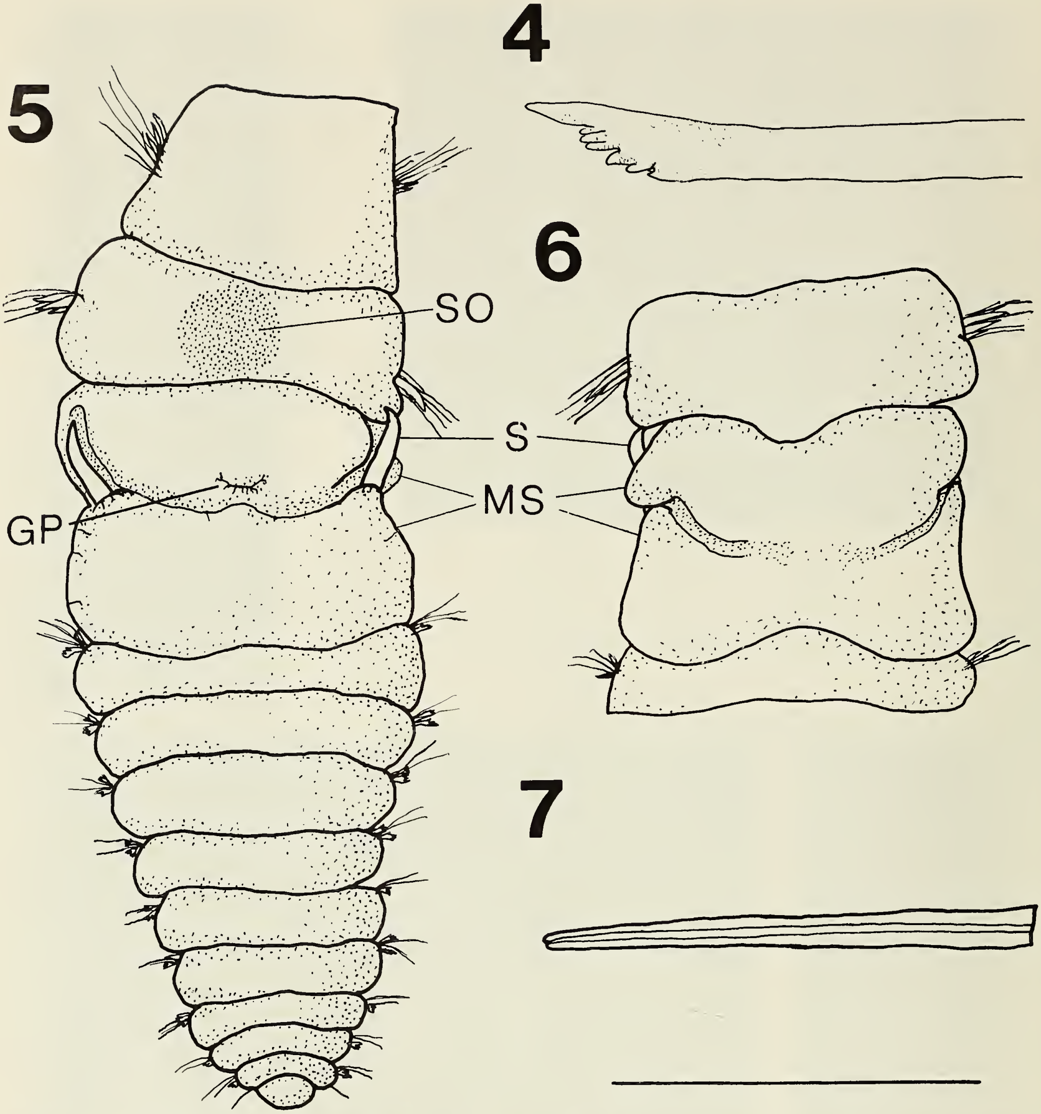


Fig. 3. Setae of *Raricirrus variabilis,* new species. A–C. Notosetae: A. Short pectinate falciger with the bases of several capillary setae from anterior region. B. Coarsely pectinate falciger from midbody region. C. Coarsely serrate falciger from region posterior to the modified segments. D. Pectinate neuropodial falcigers from midbody region. Scale bars = 10 μm.



Figs. 4–7. *Raricirrus variabilis,* new species. 4. Coarsely serrate neuropodial falciger from region posterior to the modified segments. Scale bar = 50 μm. 5. Posterior region of epitokous individual (specimen W), ventral view. GP = genital pore, SO = spherical organ. Scale bar = 500 μm. 6. Modified segments of epitokous individual (specimen W), dorsal view. Scale bar = 500 μm. 7. Reproductive stylet (specimen R). Scale bar = 50 μm.

segment (Fig. 5). Three specimens (including holotype) with a pair of enlarged, straight spines in notopodia of 1–2 setigers anterior to modified segments. Median pore observed on ventral surface of second modified segment (Fig. 5, GP), associated with a medial spherical area within first modified segment or segment immediately anterior (Fig. 5, SO). Spherical structure appeared empty or sometimes contained diffuse, coarse-grained material when examined in squash preparation. Pygidium rounded with dorsoterminal anus.

Oocytes observed scattered in several anterior setigers of several benthic specimens (numerous 10–25 μm diameter oocytes in setigers 5–9 of holotype); these setigers often thin-walled and delicate. Straight cuticular stylet (Fig. 7) with narrow lumen present from five to nine setigers (five in holotype) anterior to modified segments in several specimens, associated with a large sac (seminal vesicle) of what were revealed to be spermatozoa in squash preparation (Fig. 1). Presence and development of modified segments apparently unrelated to presence of either observable oocytes or a stylet and seminal vesicle.

Epitokes.—Specimens 6.67–20.64 mm long, 0.73–2.07 mm wide, 28–35 setigers (Table 1). Midbody region brown-gray, clearly differentiated from light cream colored and much narrower posterior setigers. Capillary setae more numerous in notopodial bundles (5–16) and with a greater number (2–9) of elongate capillaries (ca. ¾ body width) than in benthic specimens. Notopodial falcigers lacking; straight, coarsely serrate setae present posterior to the modified segments. Neurosetae similar to those of benthic individuals but with a greater number of falcigers (maximum of 8–10). Heart body extending through five to eight setigers starting at setigers 8–10. The body cavity of two epitokous specimens (Table 1, specimens U and X) contained numerous oocytes from setigers 6–8 to the first segment anterior to the modified segments. Maximum diameter of these oocytes was approximately 140 μm and each oocyte contained a round germinal vesicle in the nucleus, and was filled with coarse, yolky material.

Other material.—While trends in morphological characters are apparent, Table 1 illustrates the great morphological variability expressed by this species. The anteriormost occurrence of the heart body (character 4) in benthic forms was in setiger 4, usually extending through 9 segments to setiger 12 (from 4–6 to 7–14); in epitokes from 8–10 to 13–16. Modified segments (character 5) were absent in some smaller specimens and present in the region of setigers 18–22 in larger individuals. The number of setigers posterior to the modified segments (character 6) was variable (2–9 in benthic forms, 9–11 in epitokes), but generally ranged from five to seven in larger benthic individuals.

The variability in the distribution of setal types displayed in the benthic form of *Raricirrus variabilis* made the characterization of body regions based on setal characteristics impossible. The greatest number of capillary notosetae (character 7) occurred in the first or second setiger with from four to seven capillaries per setal bundle, from one to three of these capillaries much longer than the rest. Subsequent notopodia possessed from one to five capillaries with a single elongate capillary per setal bundle. The anteriormost occurrence of notopodial pectinate falcigers (character 11) was usually at setigers 3–9, although the first occurrence of such setae was at setigers 10–13 in several specimens. Coarsely serrate notosetae (character 12) were usually present beginning immediately posterior to the modified segments and were absent in most of the smaller individuals (<3.20 mm long) analyzed. Several specimens possessed serrate notosetae in the last setiger anterior to the modified segments.

Similar coarsely serrate neurosetae (character 15) were present in all but three of the smaller individuals and were commonly found only in the posterior setigers. Several specimens had coarsely serrate neurosetae in from one to five setigers anterior to the modified segments. Enlarged, curved spines of the modified segments (character 16) usually occurred either as a single or double pair. Several of the specimens with well developed modified segments either lacked enlarged spines or possessed only a single spine.

Three of the four epitokous individuals examined were much larger than any of the other specimens and possessed a greater number of setigers than any of the benthic individuals examined (Table 1). The heart

Table 1.—Summarizes the morphological characters for 20 specimens of the benthic form and four specimens of the epitokous form of *Raricirrus variabilis*, new species. X = character not present. Holotype = specimen S.

Individual	Character															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	Benthic specimens															
A	20	1.54	0.25	4–7	X	X	4	1	2	1	3	20	3	2	18	X
B	20	1.95	0.27	4–8	X	X	3	1	2	1	1	X	4	2	X	X
C	24	2.18	0.30	4–11	X	X	4	1	2	1	5	X	4	3–4	24	X
D	25	2.23	0.27	4–12	22–23	2	4	2	1	1	3	X	5	3–4	17	1 + 1
E	20	2.30	0.23	4–10	X	X	3	2	1	1	4	X	4	3–4	X	X
F	18	2.50	0.32	4–7	X	X	6	1–2	1	1	3	X	4	3–4	X	X
G	24	2.57	0.32	4–12	20–21	3	4	1–3	2	1	5	24	5	4–5	22	2 + 2
H	23	2.73	0.25	4–14	X	X	4	1–2	1	1	7	X	4	3–4	14	X
I	27	3.20	0.41	4–12	21–22	5	5	3	2	1	8	23	6	4	23	2 + 2
J	27	3.30	0.43	4–12	18–19	7	5	4–5	3	1	13	21	5	4–5	22	X
K	25	3.41	0.30	4–12	21–22	3	6	3–4	2	1	7	23	6	3–4	23	1 + 1
L	25	3.50	0.36	4–11	21–22	3	5	2–3	1	1	6	23	5	4	23	1 + 1
M	27	3.61	0.30	5–12	21–22	5	4	2–3	2	1	9	23	5	4	23	1 + 1
N	31	3.70	0.40	5–11	21–22	9	5	3–4	1	1	6	20	6	4–5	23	1 + 1
O	29	4.43	0.41	4–12	21–22	7	7	4–5	3	1	3	23	5	4–5	20	1 + 1
P	28	4.57	0.48	6–12	20–21	7	7	3–5	2	1	6	22	6	3–6	22	weak 2 + 2
Q	26	4.57	0.34	4–12	20–21	5	6	3	2	1	7	22	6	3–5	22	0 + 0
R	28	5.41	0.52	4–12	20–21	7	6	4–5	3	1	9	23	6	5–6	22	2 + 2
S	27	6.75	0.43	5–12	19–20	6	6	2–3	2	1	11	21	6	4–5	21	0 + 1
T	28	7.59	0.61	4–12	20–21	7	7	2–3	2	1	10	23	6	3–6	19	2 + 2
	Epitokous specimens															
W	28	6.67	0.73	8–13	18–19	9	8	6–8	4	2–4	X	22	8	5–8	22	1 + 1
V	34	14.16	1.16	9–16	23–24	10	16	11–16	8	4–8	X	25	10	8–10	25	1 + 1
U	35	17.11	2.07	9–15	23–24	12	16	12–15	9	5–8	X	25	11	9–11	25	1 + 1
X	32	20.64	1.27	10–14	20–21	11	12	5–11	6	3–5	X	22	10	5–9	19	1 + 1

1 = number of setigers, 2 = length (mm), 3 = width (mm), 4 = heart body location (range of setigers), 5 = location of modified segments, 6 = number of setigers posterior to modified segments, 7 = maximum number of capillaries in notopodia, 8 = number of capillaries in midbody segments, 9 = maximum number of long capillaries, 10 = number of long capillaries in midbody, 11 = first occurrence of pectinate falcigers in notopodia, 12 = first occurrence of coarsely serrate falcigers in notopodia, 13 = maximum number of neuropodial falcigers, 14 = number of neuropodial falcigers in midbody region, 15 = first occurrence of coarsely serrate falcigers in neuropodia, 16 = reproductive spines.

body of the epitokous specimens did not occur until setiger 8–10, extending to setiger 13–16. Modified setigers were present at the same or slightly more posterior setigers than in the benthic form, but the number of setigers posterior to these segments was greater in the epitokous specimens (9–12).

Epitokous individuals possessed a greater number of capillary notosetae along with a greater number of elongate capillaries in the anterior and midbody setigers. Notopodial pectinate falcigers were absent in the epitokous specimens while serrate notosetae were present only in the segments posterior to the modified segments. Coarsely serrate neurosetae were found only posterior to the modified segments with the exception of one epitokous individual with such neurosetae present in the segment immediately anterior to the modified segments.

Remarks.—*Raricirrus variabilis* differs from *R. maculatus* Hartman, 1961, and *R. beryli* Petersen & George, 1991, in the possession of a more anteriorly situated heart body, the presence of pectinate notopodial falcigers in the benthic stage, the presence of a seminal vesicle and reproductive stylet, and the apparent absence of an asexual reproductive mode. *Raricirrus variabilis* and *R. maculatus* share the presence of a modified region with large curved spines in at least some specimens, although that of *R. maculatus* is a apparently single modified segment while that of *R. variabilis* is composed of two segments incompletely separated dorsally. *Raricirrus variabilis* differs from *R. beryli* in lacking the ciliated region anterior to the mouth opening and on the ventral surface of the first two setigers.

Epitokous individuals of *R. maculatus* have not been encountered while a single immature male epitoke of *R. beryli* has been described (Petersen & George 1991). The epitoke of *R. beryli* was smaller (11 mm) than the benthic form, with elongate capillary setae approximately 150% of the body width. The epitokous individuals of *R. variabilis* are (with one exception) much larger (14–20 mm) than the benthic form with the elongate capillary setae only 75% of the body width.

Etymology.—The specific name refers to the variability in the distribution of setal types.

Discussion

The family Ctenodrilidae is now comprised of the subfamilies Ctenodrilinae and Raphidrilinae, each with two described genera. The genera *Ctenodrilus* Claparède, 1863, and *Aphropharynx* Wilfert, 1974, are united within the subfamily Ctenodrilinae by their lack of branchial filaments while the subfamily Raphidrilinae consists of the genera *Raphidrilus* Monticelli, 1910, and *Raricirrus* Hartman, 1961, both possessing branchiae. Morphological differences between *Raricirrus* and *Raphidrilus* are slight, however, and there has been some doubt as to whether their separation is justified (see discussion in Petersen & George 1991).

Based on the descriptions of *Raphidrilus nemasoma,* an analysis of the type material of *Raricirrus maculatus* and the analysis of specimens of *Raricirrus beryli,* Petersen & George (1991) retained separation of *Raphidrilus* and *Raricirrus* and identified several morphological characters that could be useful in differentiating these two genera. These characters include the position and extent of the heart body, the structure of the nuchal organs, the structure of the head region, and the presence of a region with modified setae.

Petersen & George (1991) had used the anteriormost occurrence of the heart body as a distinguishing character for the genera *Raphidrilus* and *Raricirrus.* That of *Raphidrilus nemasoma* has been reported to first appear at setiger 4 while that of the two previously known species of *Raricirrus* does not occur anterior to setiger 8 or 9 (Peterson & George 1991). Unfortunately this generalization does not hold true for *R. variabilis* as the heart body begins at setiger 4 (4–6) in the benthic specimens taken from the wood panels and does not appear until setigers 8–10 in the epitokous individuals from the wild wood. The heart body of polychaetes has been viewed as being of hematopoietic function (Kennedy & Dales 1958) however, more recent work has indicated that this organ could also have a protective function. Vovelle et al. (1995) noted chemical differences in the heart bodies of specimens of *Raricirrus beryli* collected adjacent to and away from the North Sea oil platforms indicating a possible role in the detoxification of hydrocarbons in this polluted environment. While the anteriormost occurrence of the heart body seems to be a valid specific character and may possibly be related to the ability of a species to cope with its environment, it is not useful in the differentiation of genera.

Sokolov (1911) described the nuchal organs of *Raphidrilus* as often-closed slits with short cilia extending from the base of the pit while Petersen & George (1991) described those of *Raricirrus* as bare oval areas surrounded by fields of cilia. The majority of specimens of *R. variabilis* examined possessed slit-like nuchal organs with no visible ciliation of the surrounding prostomial surface when viewed using scanning electron microscopy. Several specimens that were observed under the dissecting microscope had the rims of their nuchal organs widely expanded, exposing what appeared to be a uniformly ciliated surface within. The morphology of the nuchal organs of *R. variabilis* is more similar to that described for the genus *Raphidrilus* than for *Raricirrus*. However, while the ultrastructure of nuchal organs has been utilized in the recognition of possible phylogenetic relationships among polychaete families (Purschke 1986), the use of their gross morphology as a taxonomic character at the generic level is questionable. Nuchal organs may be eversible (Whittle & Zahid 1974) with associated retractor muscles (Purschke 1986) and may vary in morphology at reproductive maturity, perhaps exhibiting sexual dimorphism (Schlötzer-Schrehardt 1987, 1991). This variability in the morphology of nuchal organs within a species as well as a lack of knowledge regarding nuchal organ variability within a family or genus precludes their use (at the light microscope level) in differentiating between these two genera.

Petersen & George (1991) also referred to the shape and arrangement of the head as perhaps being of possible taxonomic significance. The prostomium, peristomium, and first setiger of *Raricirrus beryli* and *R. maculatus* are described by Petersen & George (1991) as forming a single "visual unit" with all these segments united along the dorsal surface. In the figures of Monticelli (1910) and Sokolov (1911) the prostomium and peristomium of *Raphidrilus nemasoma* appear to be united dorsally while the first setigerous segment is clearly separated from these segments. The prostomium, peristomium and first setigerous segment of *R. variabilis* are also united dorsally and this character may be of utility in the separation of *Raphidrilus* and *Raricirrus*. Further analysis of material belonging to the genus *Raphidrilus* would be required to substantiate the use of this morphological character in separation of the two genera.

Raricirrus variabilis is placed within the genus *Raricirrus*, rather than *Raphidrilus*, primarily due to its setal characteristics. *Raphidrilus nemasoma* is described as possessing only capillary notosetae and neurosetae with the exception of several modified segments possessing thick spines (Monticelli 1910, Sokolov 1911). *Raricirrus variabilis*, as well as the other two described species in this genus, possesses both serrate capillaries and coarsely serrate setae in their notopodia. *R. variabilis* differs from the other species in the possession of short, coarsely serrate falcate spines (Fig. 3A) in the anterior notopodia while *R. maculatus* and *R. beryli* both have long, natatory capillaries in their "dispersal" forms (Petersen & George 1991). The finely pectinate falcigers, grading to coarsely serrate forms posteriorly, are characteristic of all three species in the genus.

Based on the analysis of *Raricirrus variabilis,* the generic diagnosis for *Raricirrus* Hartman, 1961 emended by Petersen & George 1991, is further emended as follows: *Raricirrus* Hartman, 1961, emended.

Type species.—Raricirrus maculatus Hartman, 1961, by monotypy and original description.

Diagnosis.—Raphidrilinae with prostomium not obviously delimited from peristomium and setiger 1 dorsally; with or without ventral cilia on peristomium and first few segments; last 6–9 setigers shorter and wider than preceding ones, forming a distinct posterior region. Branchiae simple, filamentous, may be clublike distally. Heart body in variable number of anterior and middle segments. Notosetae serrate capillaries and coarsely serrate forms posteriorly, some species also with short pectinate falcigers; neurosetae falcate and finely pectinate anteriorly, grading to coarsely serrate forms posteriorly; simple curved spines sometimes replacing most or all normal setae in 1 or 2 modified posterior segments of some species. With or without seminal vesicle and reproductive stylet.

Remarks.—Raricirrus variabilis is an example of an opportunist in the deep sea which survives by finding and exploiting organically enriched sites (Grassle & Morse-Porteous 1987). The two previously described species in the genus are also reported from environments with elevated levels of organic carbon being most positively correlated with elevated levels of hydrocarbons. *Raricirrus maculatus* is known from an area close to an industrial waste discharge site in fine sediments that are contaminated with heavy metals and chlorinated hydrocarbons (Hartman 1961, Petersen & George 1991). *Raricirris beryli* was first reported at low densities from a sewage sludge dumping ground and at very high densities in fine sediments with high hydrocarbon concentrations from northern North Sea oilfields (Moore 1991, Petersen & George 1991). *Raricirris beryli* has also been collected by A. Norrevang in shallow (5 m) waters in Skopun Harbor in the Faroes, a harbor without any apparent elevated hydrocarbon input (Petersen 1994 pers. comm.). Based on strong association with high concentrations of certain components of the aromatic fraction of hydrocarbons, Moore (1991) has characterized *R. beryli* as a polychaete indicator species for sediments containing pollution levels of hydrocarbons. The epitokes and/or larvae of *R. variabilis* are most likely attracted to sites in the deep sea with high concentrations of organic material such as decaying wood.

The largest eggs observed in female epitokes (Table 1, specimen U) of *Raricirrus variabilis* were approximately 140 μm in diameter. While any determination of mode of development based on egg size should be done with great caution (Bridges 1993), it is probable that this species has either direct development or a short lecithotrophic larval mode of development. Assuming that these eggs approximate egg size at maturity, their diameter compares favorably with those of the unknown species of *Raphidrilus* (*Raphidrilus nemasoma* (sic)) studied by Qian & Chia (1989). By following the development of newly fertilized eggs, Qian & Chia found that the eggs of *Raphidrilus* sp. developed directly into free-crawling preadults. Similarly the eggs of *R. variabilis* may produce preadults through direct development subsequent to deep-sea dispersal by the epitokous body form. Bridges (1993), for example, has reported a lecithotrophic mode of development for a morph of *Streblospio benedicti* with eggs 100–200 μm in diameter and it is also quite possible, based upon egg diameter, that *R. variabilis* may also have a lecithotrophic mode of development rather than direct development. Additionally, dispersal may also be accomplished by some type of asexual dispersal form similar to that reported for *R. beryli* by Petersen & George (1991).

Two body forms were recognized in *Raricirrus variabilis,* a "normal" benthic form and a form similar to what Petersen & George (1991) identified as an epitokous phase for *R. beryli.* They considered this body form as an epitoke because it was sexually mature with the body usually packed with gametes. The epitokous form of *R. variabilis* was loosely organized with much free movement of the numerous large eggs within the interior of the worms. This may have been an artifact of poor fixation or may be indicative of the transient nature of this life stage with the individuals reduced to little more than egg containers. The epitoke of *R. variabilis* differs from the one immature male epitoke of *R. beryli* described by Petersen & George (1991) in that its capillaries are only 0.75 times the body width while those of *R. beryli* were about 1.5 times body width.

Petersen & George (1991) also described a third body form they referred to as a "dispersal" form which had capillaries 2–4 times the body width but with no obvious gametes. Petersen & George (1991) hypothesized that this dispersal form may disperse, settle and then develop into spawning epitokes. There were no specimens of *R. variabilis* recovered, from the wood panels or the piece of wild wood, that were analogous to the dispersal phase recognized for *R. beryli.*

Many specimens of the two shallow-water species, *R. beryli* and *R. maculata,* examined by Petersen & George (1991) displayed evidence of regeneration subsequent to fragmentation. Both of these species seem to rely on asexual reproduction as a means of exploiting their high organic, high hydrocarbon content, environment. Following colonization of a patch of suitable habitat by some type of dispersal form, asexual reproduction would provide a means of rapid population growth in order to better utilize the available resource (Schroeder & Hermans 1975).

There was no evidence of an asexual reproductive stage for *R. variabilis* (although the possibility exists that temporally restrictive sampling could have missed such an asexual stage if it were a seasonal event). This species seems to have adapted a different reproductive strategy in the exploitation of its patchily distributed resource. Many specimens of the benthic form of *R. variabilis* contained both developing eggs and sperm and were evidently hermaphroditic. Hermaphroditism has often been associated with patchy, unpredictable environments (Petraitis 1991) and may allow *R. variablis* to enhance its exploitation of widely scattered patches of organic material on the deep-sea floor. The benthic form could function as both genders or as the gender which would maximize reproductive success under existing environmental conditions similar to the strategy proposed for *Capitella capitata* by Petraitis (1991).

Once established on a patch of suitable organic resource, the benthic form of *R. variabilis* may engage in sexual reproduction, maximizing its reproductive success through its hermaphrodism. The resultant free-living larvae would increase the population size at the home site although at a reduced rate when compared to the exploitation of a comparable resource in shallower waters. Some of the benthic individuals could develop into the epitokous form, either as a routine percentage of the population as seen in *Dedocaceria caulleryi* Oersted (Gibson & Clark 1976) or perhaps in response to deteriorating resource, as a means of colonizing suitable habitat elsewhere.

Acknowledgments

These polychaetes were collected and dissected from wood panels as part of R. D. Turner's studies of deep-sea wood-boring communities, a project supported by the Office of Naval Research, Contract no. N00014-84-0258 with Harvard University. The SEM pictures were taken with an ABT 55 SEM generously provided by R. Prezant of the Department of Biology, Indiana University of Pennsylvania. An early draft of this manuscript was reviewed and improved by E. Ruff of Ruff Systematics, Solana Beach, California. The manuscript was greatly improved by the suggestions and supporting materials provided by M. Petersen (Zoological Museum, University of Copenhagen) and J. Blake (ENSR Consulting and Engineering, Woods Hole).

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Six copepodid stages of *Ridgewayia klausruetzleri*, a new species of copepod crustacean (Ridgewayiidae: Calanoida) from the barrier reef in Belize, with comments on appendage development

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Abstract.—*Ridgewayia klausruetzleri* from the barrier reef in Belize differs from the five other Atlantic species of *Ridgewayia* in the morphology of the female genital complex and fifth leg of both females and males. Developmental patterns of setation suggest that there are six enditic lobes associated with the syncoxa and basis of maxilla 2, and that the ramal segments are exopodal. The maxilliped has a distomedial lobe on its basis and five endopodal segments, three of which are added proximally from the penultimate segment during the copepodid phase of development. The first through fourth legs exhibit the common, and presumed ancestral, pattern of segmental development. Left and right endopods of the male fifth leg are one-segmented, a condition resulting from developmental convergence for the two rami. The male fifth leg also exhibits setal loss during development of the right endopod and both exopods.

Ridgewayia Thompson & Scott, 1903 along with three other genera of epibenthic, pseudocyclopoidean calanoids, *Brattstromia* Fosshagen (*in* Fosshagen & Iliffe 1991), *Exumella* Fosshagen 1970, and *Placocalanus* Fosshagen, 1970 comprise the copepod family Ridgwayiidae of Wilson (1958). Species of *Ridgewayia* are found around and in crevices and caves in coral reef habitats. Of the nine nominal species of *Ridgewayia,* five are found in the Atlantic Ocean, *R. marki* (Esterly, 1911a), *R. gracilis* Wilson, 1958, *R. shoemakeri* Wilson, 1958, *R. wilsonae* Fosshagen, 1970, and *R. fosshageni* Humes & Smith, 1974. *Ridgewayia typica* Thompson & Scott, 1903, *R. canalis* (Gurney, 1927), *R. krishnaswamyi* Ummerkutty, 1963, and *R. flemingeri* Othman & Greenwood, 1988, are Indo-Pacific.

On 17 July 1989 specimens of a new species of *Ridgewayia* were collected from a solitary swarm of copepods off the northern cay of Tobacco Range in Belize. Tobacco Range (16°54′N, 88°05′W) is a group of four cays about 1 km from the lagoonal side of the barrier reef of Belize. The cays surround a shallow grass flat. The copepod swarm was collected in 3–6 m of water in an area of peat blocks which are fractured and slumped from the northwest shore of the northern cay (MacIntyre et al. 1989). No swarms were observed in June 1988, or subsequently in May 1992 and June 1993. The first description of the copepodid phase of development for a species of *Ridgewayia* is presented here from the six copepodid stages in the swarm.

Methods

The copepods were fixed with 4% formaldehyde in 35% sea water and preserved in 0.5% propylene phenoxytol/4.5% propylene glycol/95.0% fresh water. In the laboratory, specimens were cleared in steps through 50.0% lactic acid/50.0% fresh water to 100% lactic acid and stained by adding a solution of chlorazol black E dissolved in 70.0% ethanol/30.0% fresh water, or treated with a 15% solution of KOH in water and stained.

Prosome and urosome are designated Pr and Ur. First through sixth copepodid stages are designated CI to CVI; CVI is the adult. Thoracic and abdominal somites are numbered according to their appearance 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 increase in age, and decrease in numerical designation, anteriorly.

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 generally follow Huys & Boxshall (1991) except for Mx2 and Mxp; exopod = Re; endopod = Ri; medial lobe of a segment = li, lateral lobe = le. Terminal segments of Mx2 are exopodal. Mxp has at most five endopodal segments.

Ramal segments on the thoracopods (Mxp and P1–5) are numbered by their appearance during development (Hulsemann 1991, Ferrari & Ambler 1992, and here) and not proximal-to-distal as is the usual case for copepod descriptions. On the Mxp 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. On an Mxp with a 5-segmented endopod, the second and first segments are more distal and the third and fourth segments are more proximal (Table 1 and Figs. 3E, 9G, 11F). On P1–5, the distal segment of a ramus is the first segment. The second segment is immediately distal to the basipod. 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 (Figs. 4F, 7B, 9J). The number of setae recorded for the segments follows this same scheme.

Table 1.—Setation of the maxilliped of *Ridgewayia klausruetzleri* for stages CI–CVI; setation of syncoxa and basis (columns 1–6) is complete at CII while setation of endopodal segments 2–5 is not complete until CVI. Lobes of the syncoxa (s1–s4), the basis (b) and its distomedial lobe (l), and the endopodal segments (*n1–n5* numbered by developmental age) are arranged from left, proximally, to right, distally. a = segment not formed.

	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*

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) on P1 (the appendage of thoracic somite 2) consists of the curved basipodal seta,

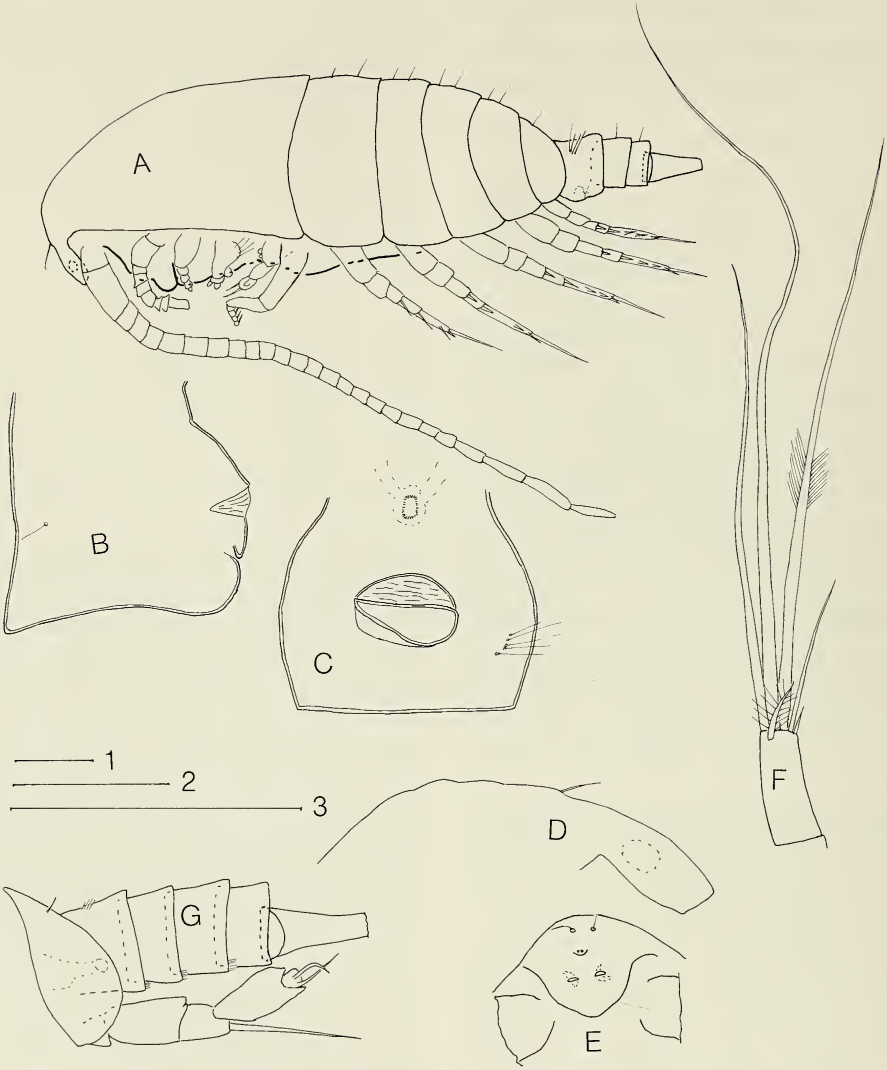

Fig. 1. *Ridgewayia klausruetzleri* n. sp., CVI female: A, animal left lateral; B, genital complex, right lateral; C, genital complex, ventral; D, rostrum right lateral; E, rostrum ventral; F, CR dorsal. CVI male: G, Th 6–7 and abdominal somites. Line 1 = 0.1 mm for A; line 2 = 0.1 mm for G; line 3 = 0.1 mm for B–F.

and distolateral corner of the second endopodal segment. Many setae on P1-5 of *Ridgewayia* narrow abruptly distally; setules usually are present only on the distal section.

Ridgewayia klausruetzleri, new species
Figs. 1–11

Material.—CI—528 specimens; CII—505 specimens; CIII—403 specimens; CIV—319 specimens; CV—636 specimens; CVI—3687 specimens from Tobacco Range (16°54′N, 88°05′W) in Belize are deposited in the National Museum of Natural History, Smithsonian Institution (USNM). An undissected female holotype (USNM 268277), an undissected male allotype (USNM 268278), and one lot of undissected paratypes, 10 females and 10 males (USNM 268279) are in vials of glycerin. The remaining specimens (CI—524, CII—497, CIII—394, CIV—279, CV—596, CVI—3663) comprise a lot of undissected paratypes (USNM 268280) in 0.5% propylene phenoxytol/4.5% propylene glycol/95.0% fresh water.

CVI female.—Length range of 15 specimens 0.84—0.90mm (mean 0.87); average Pr length/Ur length = 3.1.

Pr (Fig. 1A): 6 segments; 1st a complex of 5 cephalic somites plus thoracic somite 1; thoracic somites 2–6 are simple and articulated.

Ur (Fig. 1A): 4 segments; 1st a genital complex of thoracic somite 7 and abdominal somite 2 (Fig. 1B); genital complex slightly asymmetrical, as viewed ventrally (Fig. 1C); several sensilla near left posterolateral corner. Copulatory and oviducal openings separate. Abdominal somites 3, 4, 1 articulated; somite 1 small.

Rostrum (Fig. 1D, E): a short thick plate.

A1 (Fig. 2A-C): 26 articulated segments with 1 + 1, 4 + 1, 2, 2 + 1, 2 + 1, 2 + 1, 2 + 1, 2 + 1, 2 + 1, 2 + 1, 2 + 1, 2 + 1, 2 + 1, 2 + 1, 2 + 1, 2 + 1, 2 + 1, 2, 2, 2 + 1, 1, 1, 2, 2 + 1, 2, 4 + 2 setae + aesthetascs; 13th through 22nd segments with row of small denticles.

A2 (Fig. 4A): coxa with 1 seta; basis with 2 setae. Re 8-segmented with 1, 1, 1, 1, 1, 1, 1, 4 setae. Ri 2-segmented with 1, 15 (7 terminal, 8 subterminal) setae.

Mn (Fig. 4B, C): coxa more heavily sclerotized medially; basis with 4 setae. Re 4-segmented with 1, 1, 1, 3 setae. Ri 1-segmented with 15 setae (11 terminal, 4 subterminal).

Mx1 (Fig. 3A, B): le with 9 setae. Re 1-segmented with 11 setae. Basis with 5 setae; Ri with sets of 4 and 4 medial, and 7 terminal setae. Li 2 and 3 with 5 and 4 setae. Li 1 with 9 apical, 1 anterior setae and 4 posterior setae; denticles on posterior surface.

Mx2 (Fig. 3C): li 1–4 of coxa with 5, 3, 3, 3 setae; li 5 and 6 of basis with 4 and 3 setae. Re indistinctly segmented with 7 setae.

Mxp (Fig. 3D, E): syncoxa with 4 lobes of 1, 2, 4, 3 setae; basis with 5 setae (2 on a distal medial lobe). Ri 5-segmented with 4, 4, 4, 4, 3 setae. Three areas of denticles on coxa and a longitudinal row of denticles on basis.

P1 (Fig. 5A, B): coxa with medial seta; basis with curved, medial seta. Re 3-segmented with 7, 2, 2 setae. All segments with row of denticles toward distal edge; segment 2 with longer denticles at distolateral corner; distolateral margin of segment 3 with a finger-like process with denticles along outer margin and an attenuate process. Ri 3-segmented with 6, 1, 2 setae. Von Vaupel Klein's organ includes setules and seta of basis, and denticles and 2 pores on an attenuate distolateral edge of segment 2.

P2 (Fig. 4D): coxa with medial seta and lateral area of denticles; basis with medial area of denticles. Re 3-segmented with 8, 2, 2 setae; segments 1 and 3 with row of denticles toward distal edge. Ri 3-segmented with 8, 1, 2 setae.

P3 (Fig. 4E): coxa with medial seta and lateral denticles; basis unarmed. Re 3-segmented with 9, 2, 2 setae; posterior face of segments 1 and 3 with denticles toward distal edge. Ri 3-segmented with 8, 1, 2 setae; posterior face of segment 3 with denticles toward distal edge.

P4 (Fig. 4F): coxa with medial seta, and lateral and anterior denticles; basis with lateral seta. Re 3-segmented with 9, 2, 2 setae; posterior face of segments 1 and 3 with denticles toward distal edge. Ri 3-segmented with 7, 1, 2 setae.

P5 (Fig. 5C): coxa unarmed; basis with lateral seta and posterior denticles. Re 3-segmented with 8, 1, 2 setae; segment 1 with denticles on anterior face. Ri 2-segmented with 7, 0 setae.

CR (Fig. 1F): 5 terminal setae of differing lengths, and a small dorsal seta.

CVI male.—Differs from CVI female as follows: length range of 15 specimens 0.77–0.82mm (mean 0.79); average Pr length/Ur length = 3.0.

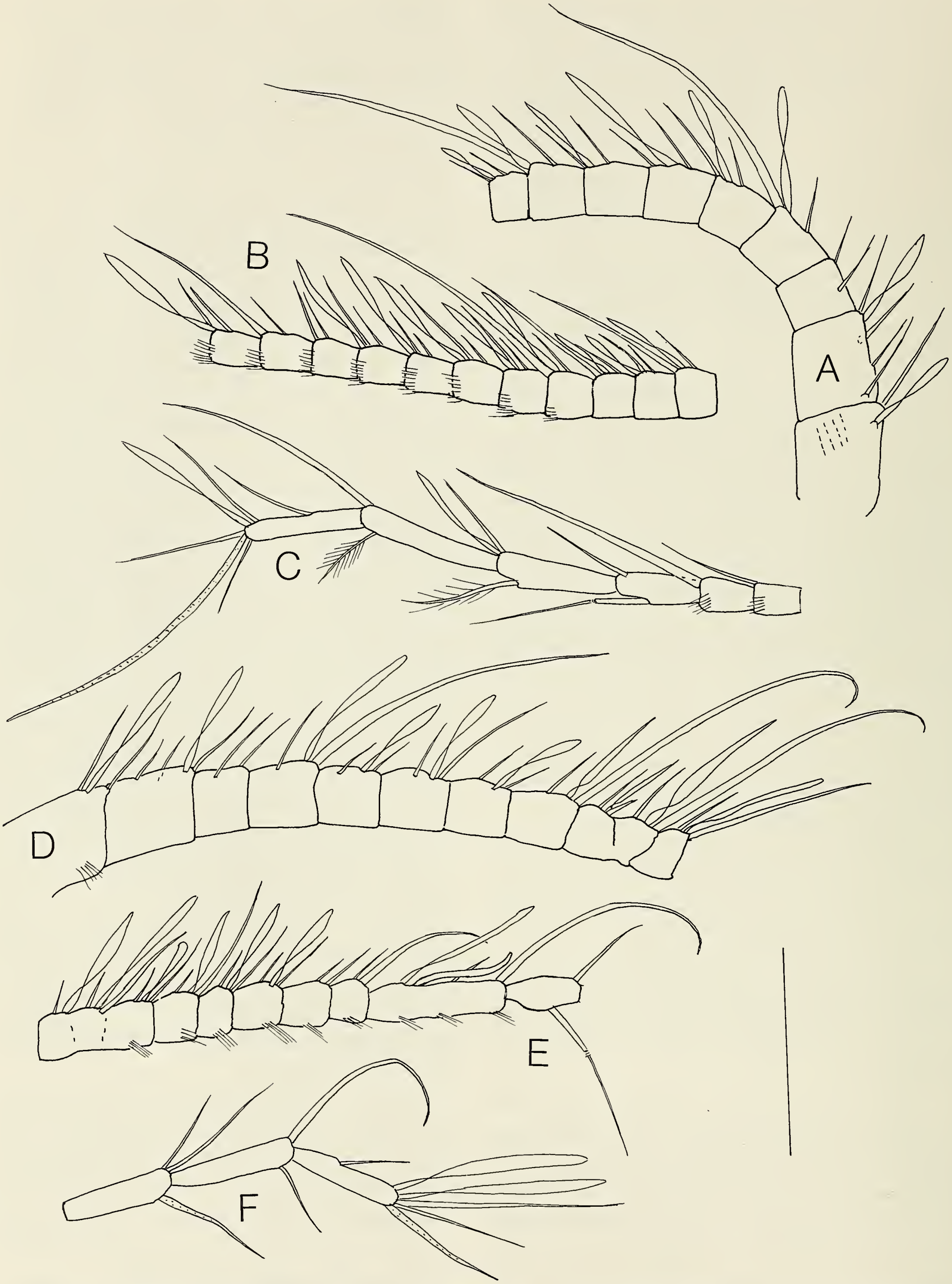

Fig. 2. *Ridgewayia klausruetzleri* n. sp., CVI female: A, A1 articulated segments 1–9; B, A1 articulated segments 10–20; C, A1 articulated segments 21–26. CVI male: D, right A1 articulated segments 1–10; E, right A1 articulated segments 11–18; F, right A1 articulated segments 19–21. Line = 0.1 mm.

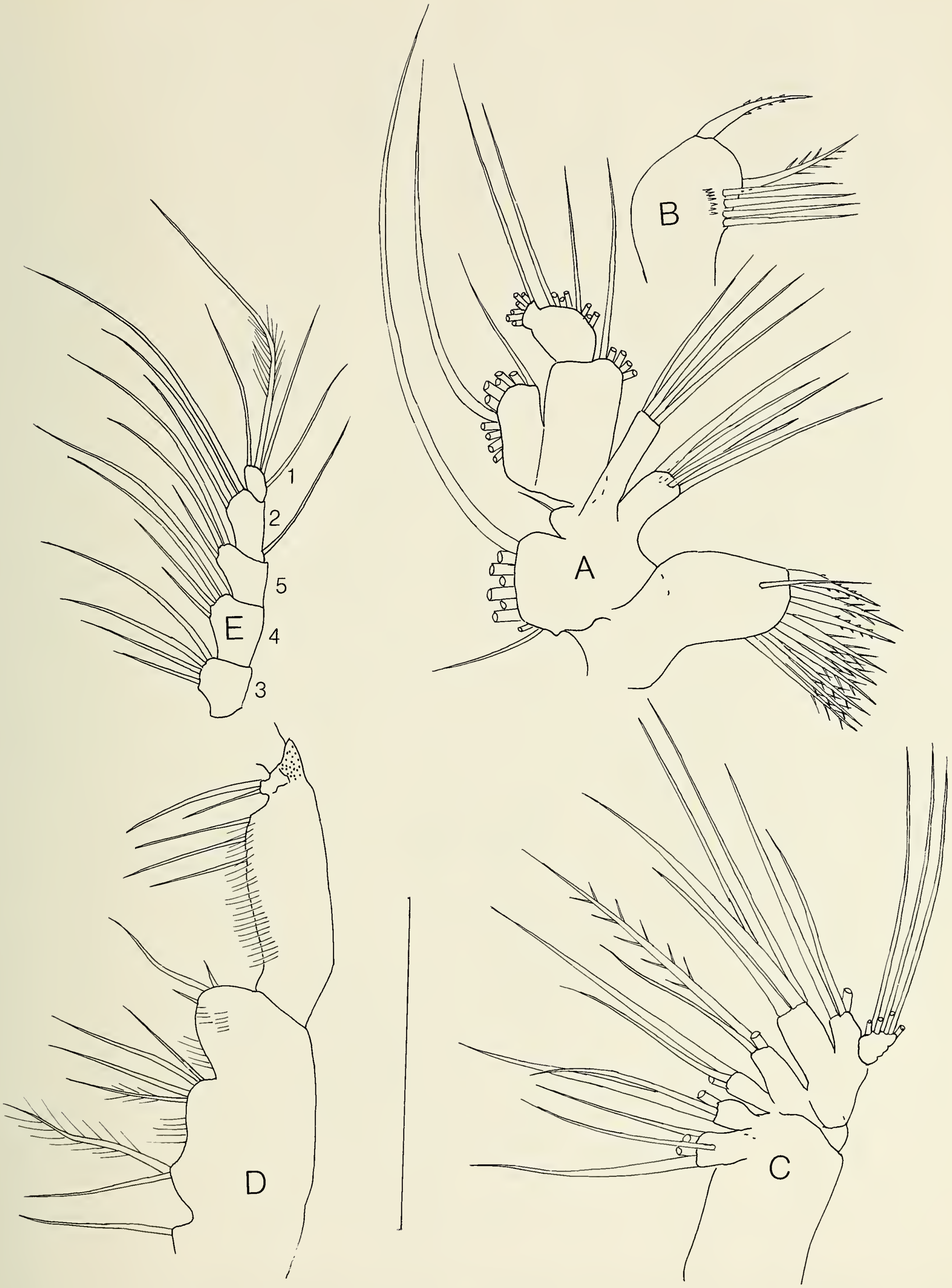

Fig. 3. *Ridgewayia klausruetzleri* n. sp., CVI female: A, Mx1 anterior; B, li1 of Mx1 posterior; C, Mx2 posterior; D, syncoxa and basis of Mxp posterior; E, endopod of Mxp posterior (numbers to the right indicate the appearance of endopodal segments during development). Line = 0.1 mm.

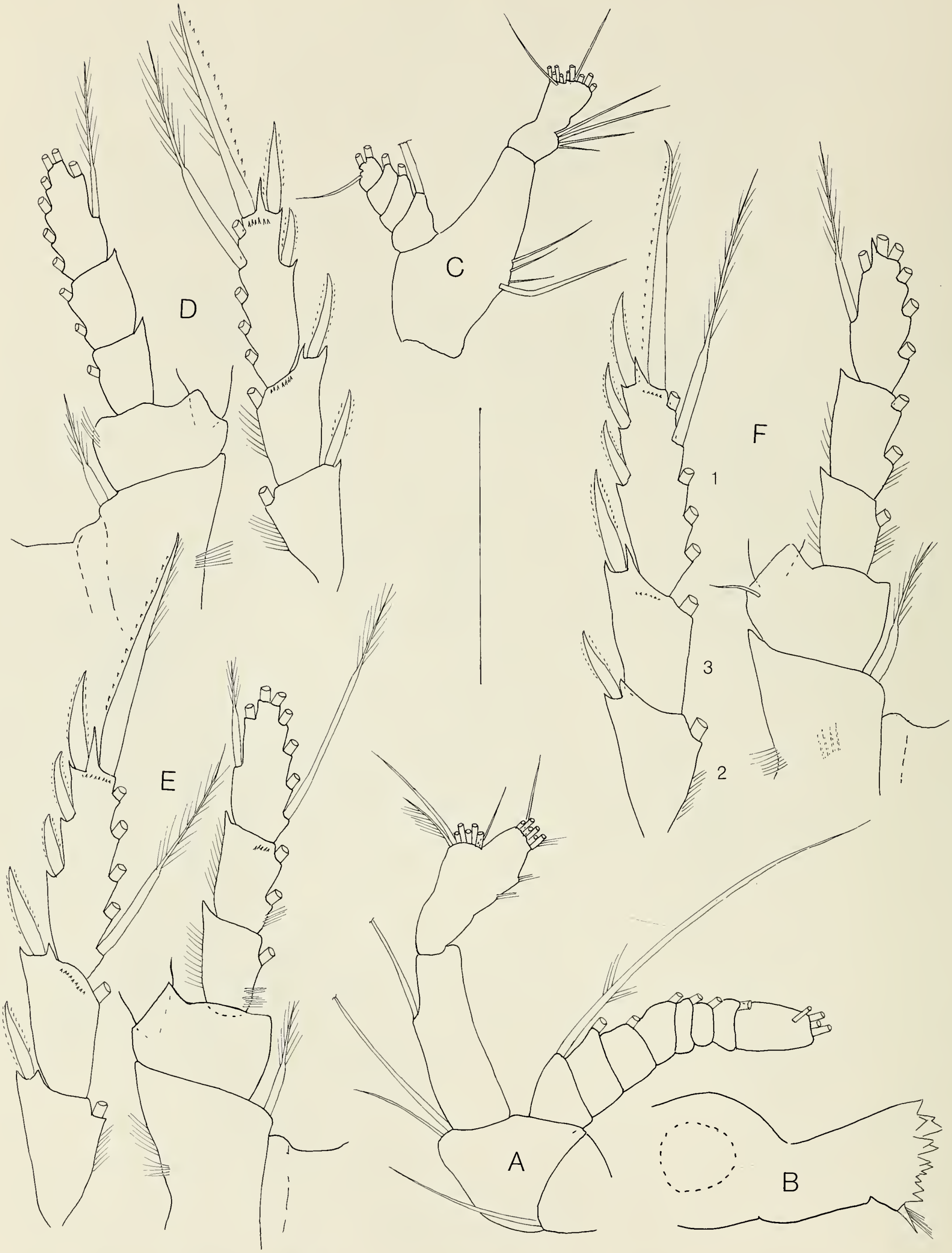

Fig. 4. *Ridgewayia klausruetzleri* n. sp., CVI female: A, A2; B, coxa of Mn; C, palp of Mn; D, P2 posterior, exopod detached; E, P3 posterior, exopod detached; F, P4 posterior, exopod detached (numbers to the right indicate the appearance of exopodal segments during development). Line = 0.1 mm.

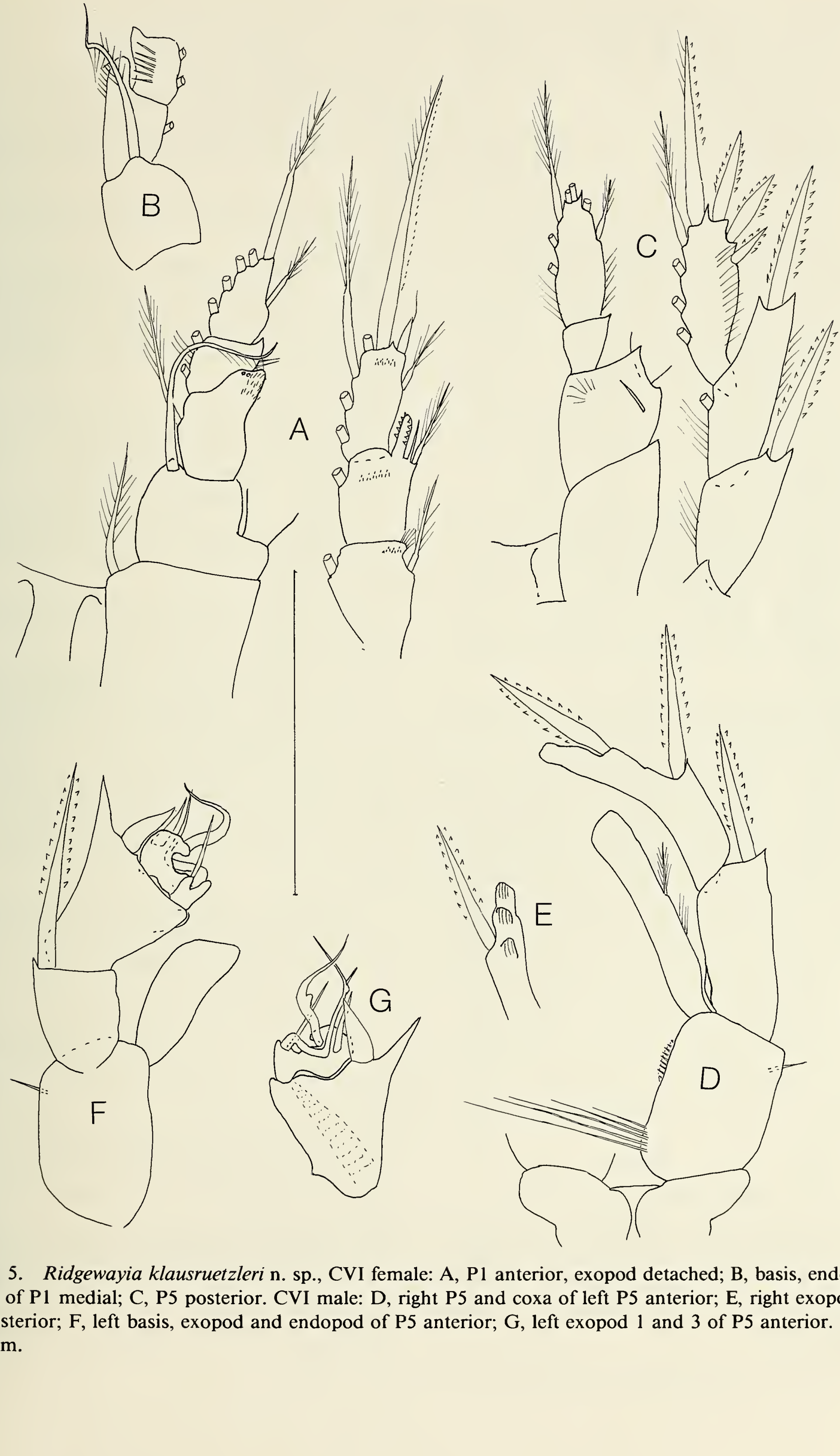

Fig. 5. *Ridgewayia klausruetzleri* n. sp., CVI female: A, P1 anterior, exopod detached; B, basis, endopod 2 and 3 of P1 medial; C, P5 posterior. CVI male: D, right P5 and coxa of left P5 anterior; E, right exopod 1 of P5 posterior; F, left basis, exopod and endopod of P5 anterior; G, left exopod 1 and 3 of P5 anterior. Line = 0.1 mm.

Ur (Fig. 1G): 5 somites; thoracic somite 7 with left lateral genital aperture. Abdominal somites 2, 3, 4, 1 simple and articulated; somite 1 small.

Right A1 (Fig. 2D–F): 21 articulated segments with: 2 + 1, 3 + 1, 2, 2 + 1, 2 + 1, 2 + 1, 2 + 1, 2 + 1, 4 + 2, 2 + 1, 5 + 3, 2 + 1, 2 + 1, 2 + 1, 2, 2, 3 + 1, 2, 2 + 1, 2, 3 + 3 setae + aesthetascs; segments 11–16 with row of denticles and segment 17 with 3 rows. Partly complete arthrodial membrane in segment 9; 2 partly complete ventromedial arthrodial membranes in segment 11; segment 17 probably of 3 fused segments based on 3 rows of denticles. Geniculation between 17th and 18th articulated segments.

P5 (Fig. 5D–G): right coxa unarmed; basis with lateral seta, and long, medial sensilla proximally and short medial denticles distally. Re 2-segmented with 2, 1 setae; 3 ridged pads distally on segment 1. Ri 1-segmented with midlateral seta and denticles.

Left coxa unarmed; basis with lateral seta. Re 3-segmented with 4, 1, 1 setae. Re1 hook-like, articulating at medial corner with 3rd segment; its proximal seta with 3 bends and an extension of its hyaline membrane on convex surface of the 3rd bend; 2nd and 3rd seta simple; 4th seta with 1 bend and an extension of its hyaline membrane on concave surface of the bend. Re2 outer, spine-like seta reaching to distal edge of Re3. Re3 outer, spine-like seta not reaching beyond setae of Re1. Ri 1-segmented, unarmed.

CV female.—Differs from CVI female as follows: length range of 27 specimens 0.73–0.80mm (mean 0.76); average Pr length/Ur length = 3.0.

Ur (Fig. 6A, B): 4 segments; thoracic somite 7 and abdominal somites 2, 3, 1 articulated. Arthrodial membrane between Th7 and Ab2 not as pronounced as those between other somites. Copulatory opening apparently forms at articulation of Th7 and Ab2 (Fig. 6B).

A1 (Fig. 6C): articulating segments 4–14 with 2 + 1, 2, 2 + 1, 2, 2 + 1, 2, 2 + 1, 2, 2, 2, 2 + 1 setae + aesthetascs.

A2 (Fig. 6D): Ri terminal segment with 14 setae (7 terminal, 7 subterminal).

Mx1 (Fig. 6E): Re with 10 setae. Ri with medial sets of 3 and 4 setae, and 6 terminal setae.

Mxp (Fig. 6G): Ri 5-segmented with 4, 3, 3, 3, 2 setae.

P1: Re2 distal margin simple; Re3 (Fig. 6F) distal margin with 2 simple extensions of segment. Ri2 without denticles or pores and elongation of distolateral margin less pronounced.

P5 (Fig. 6H): coxa unarmed; basis with lateral seta. Re 2-segmented with 9, 1, setae. Ri 2-segmented with 6, 0 setae.

CV male.—Differs from CV female as follows: length range of 13 specimens 0.68–0.74mm (mean 0.71); average Pr length/Ur length = 3.0.

Ur (Fig. 6I): pronounced arthrodial membrane between Th7 and Ab2.

P5 (Fig. 6J): right Re 2-segmented with 7, 1 setae. Ri 2-segmented with 4, 0 setae.

Left Re 2-segmented with 7, 1 setae. Ri an unarmed segment.

CIV female.—Differs from CV female as follows: length range of 27 specimens 0.64–0.69mm (mean 0.66); average Pr length/Ur length = 3.1.

Ur (Fig. 7A): 3 segments; thoracic somite 7 and abdominal somites 2, 1 articulated.

A1 (Fig. 8A, B): 25 segments with 1 + 1, 2 + 1, 1, 1 + 1, 1, 1 + 1, 1, 1, 2 + 1, 1, 1, 2 + 1, 2, 1 + 1, 2, 2 + 1, 2, 2, 2 + 1, 1, 1, 2, 2 + 1, 2, 4 + 2 setae + aesthetascs; denticle rows on 13th through 21st segments.

A2 (Fig. 8C): Ri terminal segment with 13 setae (7 terminal, 6 subterminal).

Mn (Fig. 8D): Ri with 3 and 8 setae on segments 1 and 2.

Mx1 (Fig. 8E): basis with 4 setae. Re with 8 setae. Ri with medial sets of 3 and 3 setae, and 5 terminal setae.

Mxp (Fig. 8F): Ri 5-segmented with 4, 2, 2, 2, 1 setae.

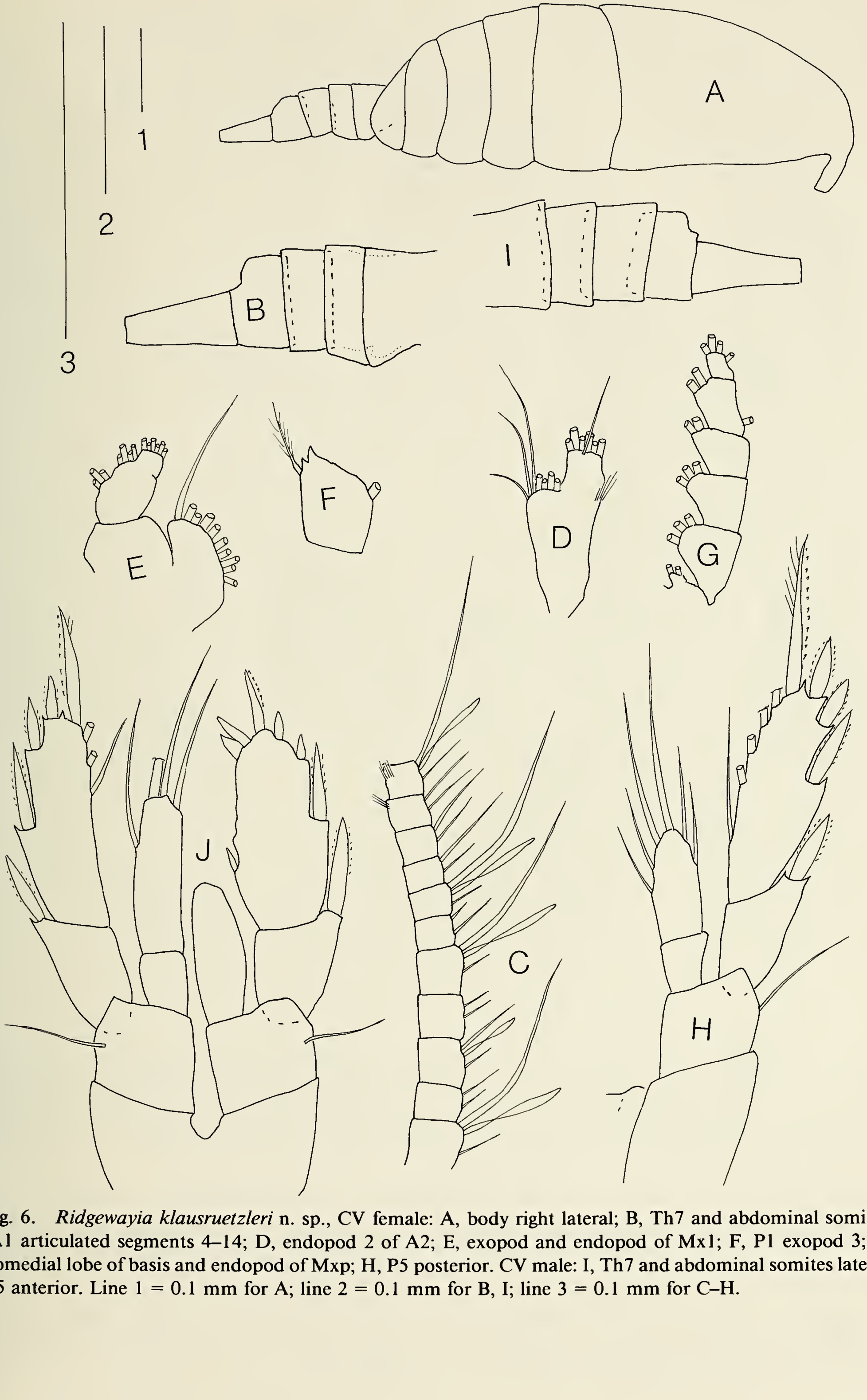

Fig. 6. *Ridgewayia klausruetzleri* n. sp., CV female: A, body right lateral; B, Th7 and abdominal somites; C, A1 articulated segments 4–14; D, endopod 2 of A2; E, exopod and endopod of Mx1; F, P1 exopod 3; G, distomedial lobe of basis and endopod of Mxp; H, P5 posterior. CV male: I, Th7 and abdominal somites lateral; J, P5 anterior. Line 1 = 0.1 mm for A; line 2 = 0.1 mm for B, I; line 3 = 0.1 mm for C–H.

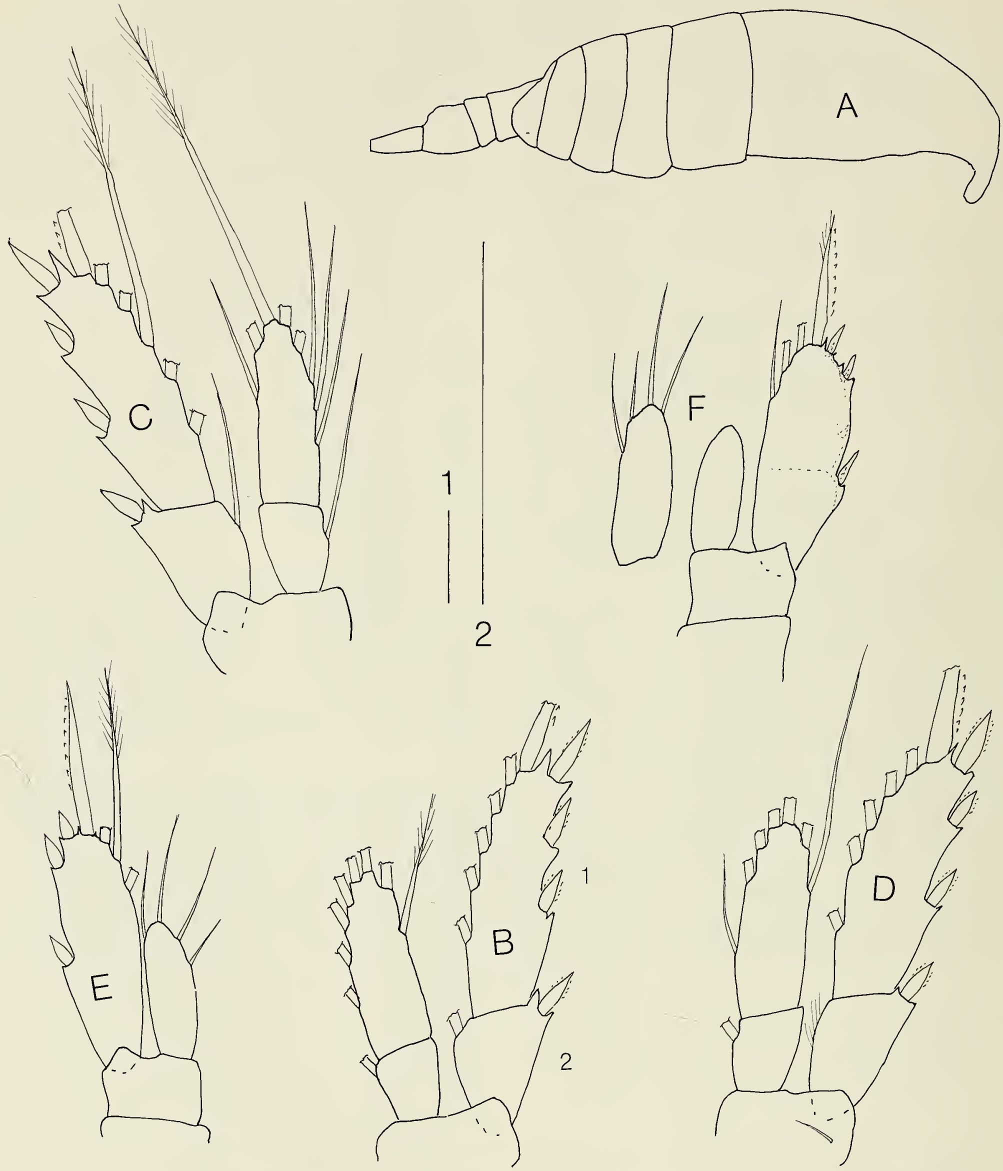

Fig. 7. *Ridgewayia klausruetzleri* n. sp., CIV female: A, body right lateral; B, exopod and endopod of P2 (numbers to the right indicate the appearance of exopodal segments during development); C, exopod and endopod of P3; D, exopod and endopod of P4; E, basis, exopod and endopod of P5. CIV male: F, basis, left exopod and endopod, and right endopod of P5. Setae which were broken and not studied are designated with a wavy-line cutoff. Line 1 = 0.1 mm for A; line 2 = 0.1 mm for B–F.

P1 (Fig. 8G): Re 2-segmented with 8, 2 setae. Ri 2-segmented with 8, 1 setae.

P2 (Fig. 7B): Re 2-segmented with 9, 2 setae. Ri 2-segmented with 8, 1 setae.

P3 (Fig. 7C): Re 2-segmented with 9, 2 setae. Ri 2-segmented with 8, 1 setae.

P4 (Fig. 7D): Re 2-segmented with 9, 1 setae; segment 2 with medial denticles. Ri 2-segmented with 7, 1 setae.

P5 (Fig. 7E): basis unarmed. Re 1-segmented with 7 setae. Ri 1-segmented with 4 seta.

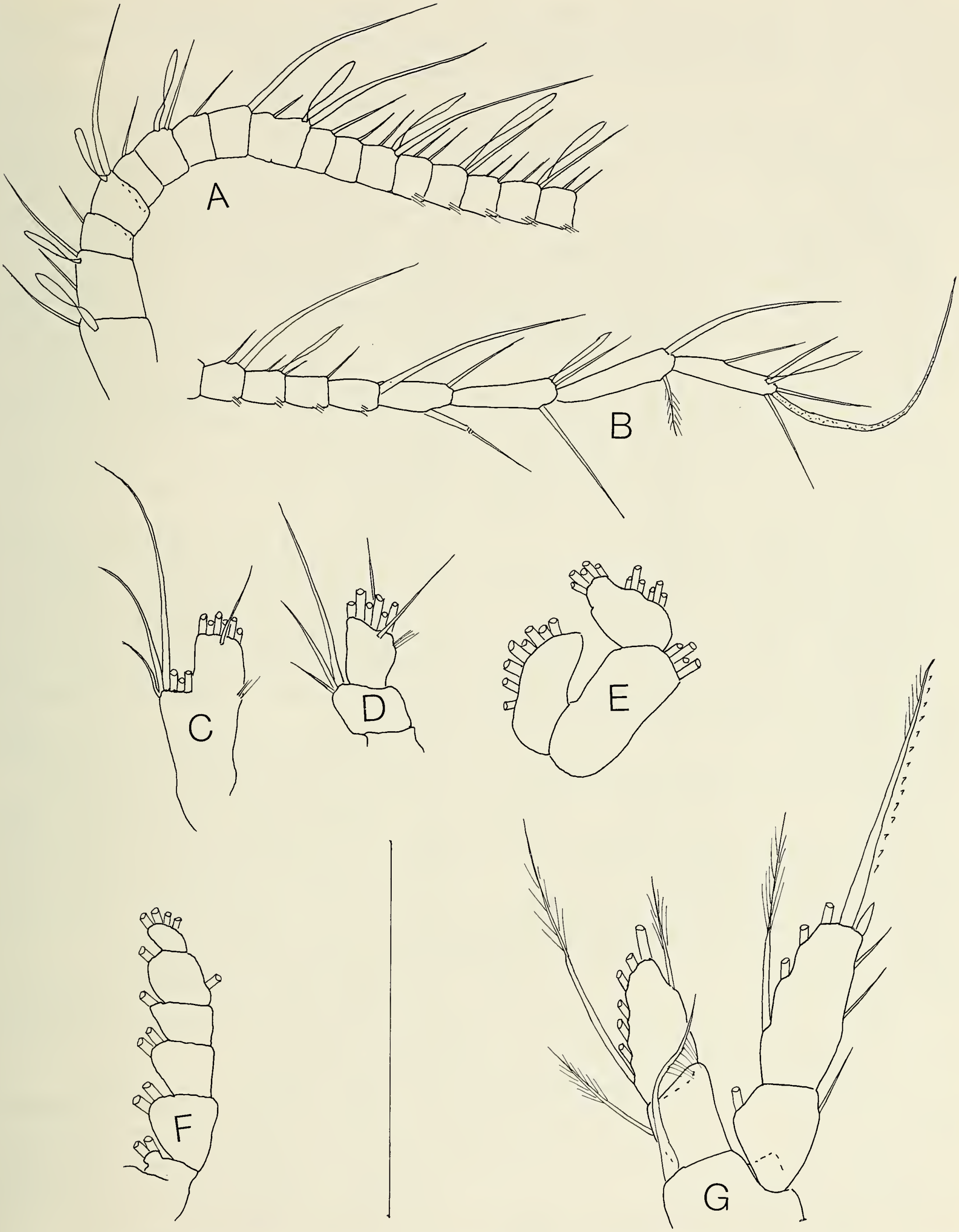

Fig. 8. *Ridgewayia klausruetzleri* n. sp., CIV female: A, A1 articulated segments 1–17; B, A1 articulated segments 18–25; C, endopod 2 of A2; D, endopod of Mn; E, basis, exopod and endopod of Mx1; F, distomedial lobe of basis and endopod of Mxp; G, exopod and endopod of P1. Line = 0.1 mm.

CIV male.—Differs from CIV female as follows: length range of 13 specimens 0.62–0.65mm (mean 0.64); average Pr length/Ur length = 3.0.

P5 (Fig. 7F): right basis unarmed. Re 1-segmented with 7 setae. Ri 1-segmented with 4 setae.

Left basis unarmed. Re 1-segmented with 7 setae. Ri 1-segmented without setae.

CIII.—Differs from CIV female as follows: length range of 25 specimens 0.50–0.58mm (mean 0.54; average Pr length/UR length = 3.4.

Ur (Fig. 9A): 2 segments; thoracic somite 7 and abdominal somite 1 articulated.

A1 (Fig. 9B, C): 24 articulated segments with 1, 1 + 1, 1, 1 + 1, 0, 1, 0, 1 + 1, 0, 1, 1, 1, 1 + 1, 1, 1, 1, 1, 2 + 1, 1, 1, 2, 2 + 1, 2, 4 + 2 setae + aesthetascs.

A2 (Fig. 9D): Ri terminal segment with 11 setae (6 terminal, 5 subterminal).

Mn (Fig. 9E): Ri2 with 7 apical setae.

Mx1 (Fig. 9F): le with 8 setae. Ri 2-segmented; Ri1 with medial groups of 2 and 3 setae. Li1 with 7 apical setae, 1 reduced in length.

Mxp (Fig. 9G): Ri 4-segmented with 4, 2, 1, 1 setae.

P1 (Fig. 9H): proximal 3 setae of Ri1 and seta of Ri2 reduced in size.

P2: proximal, medial seta of Re1 and medial seta of Re2 reduced in size. Proximal, medial 2 setae of Ri1 and medial seta of Ri2 reduced in size.

P3 (Fig. 9I): Re 2-segmented with 7, 1 setae. Ri 2-segmented with 7, 1 setae.

P4 (Fig. 9J): coxa and basis unarmed. Re 1-segmented with 7 setae. Ri 1-segmented with 6 setae.

P5 (Fig. 9K): ventrally-directed bud with 2 medial and 3 apical setae.

CII.—Differs from CIII as follows: length range of 25 specimens 0.44–0.47mm (mean 0.46); average Pr length/Ur length = 2.9.

Pr (Fig. 10A): 5 segments; 1st a complex of 5 cephalic somites plus thoracic somite 1; thoracic somites 2–5 simple and articulated.

Ur (Fig. 10A): 2 segments; thoracic somite 6, with lateral lobes, and abdominal somite 1 articulated.

A1 (Fig. 10B, C): 17 articulated segments with 1, 2 + 2, 0, 1, 0, 1 + 1, 0, 1, 0, 1, 1 + 1, 1, 1, 1, 2 + 1, 2, 4 + 2 setae + aesthetascs; denticles on segments 12 and 13.

A2 (Fig. 10D): Ri terminal segment with 10 (6 terminal, 4 subterminal) setae.

Mx1 (Fig. 10E): le with 5 setae. Re 1-segmented with 7 setae. Basis with 3 setae. Ri1 with medial sets of 2 and 2 setae. Li1 with 2 posterior setae; li2 with 4 setae.

Mx2 (Fig. 10F): li 5 and 6 of basis with 3 and 1 setae. Re indistinctly segmented with 6 setae.

Mxp (Fig. 10G): Ri 3-segmented with 4, 1, 1 setae.

P1 (Fig. 10H): Re 2-segmented with 8, 1 setae. Ri 2-segmented with 7, 1 setae.

P2 (Fig. 10I): Re 2-segmented with 7, 1 setae. Ri 2-segmented with 7, 1 setae.

P3 (Fig. 10J): coxa unarmed. Re 1-segmented with 7 setae. Ri 1-segmented with 6 setae.

P4 (Fig. 10K): ventrally-directed bud with 2 medial, 1 lateral, and 2 apical setae.

CI.—Differs from CII as follows: length range of 25 specimens 0.36–0.40mm (mean 0.38); average Pr length/Ur length = 2.6.

Pr (Fig. 11A): 4 segments; articulation between thoracic somites 3 and 4 not as distinct as between other segments.

Ur (Fig. 11A): 2 segments; thoracic somite 5, with lateral lobes, and abdominal somite 1 articulated.

Rostrum absent

A1 (Fig. 11B): 10 articulated segments with 3, 1 + 1, 1, 1 + 1, 0, 1, 1, 2 + 1, 2, 4 + 2 setae + aesthetascs; denticles absent.

A2 (Fig. 11C): Ri terminal segment with 8 (5 terminal, 3 subterminal) setae.

Mn (Fig. 11D): Ri2 with 5 setae.

Mx1 (Fig. 11E): le with 4 setae. Ri with medial groups of 2 and 1 setae. Li2 with 2 setae.

Mxp (Fig. 11F): syncoxa with 4 lobes of 0, 1, 2, 2 setae; basis with 3 (1 on a distal

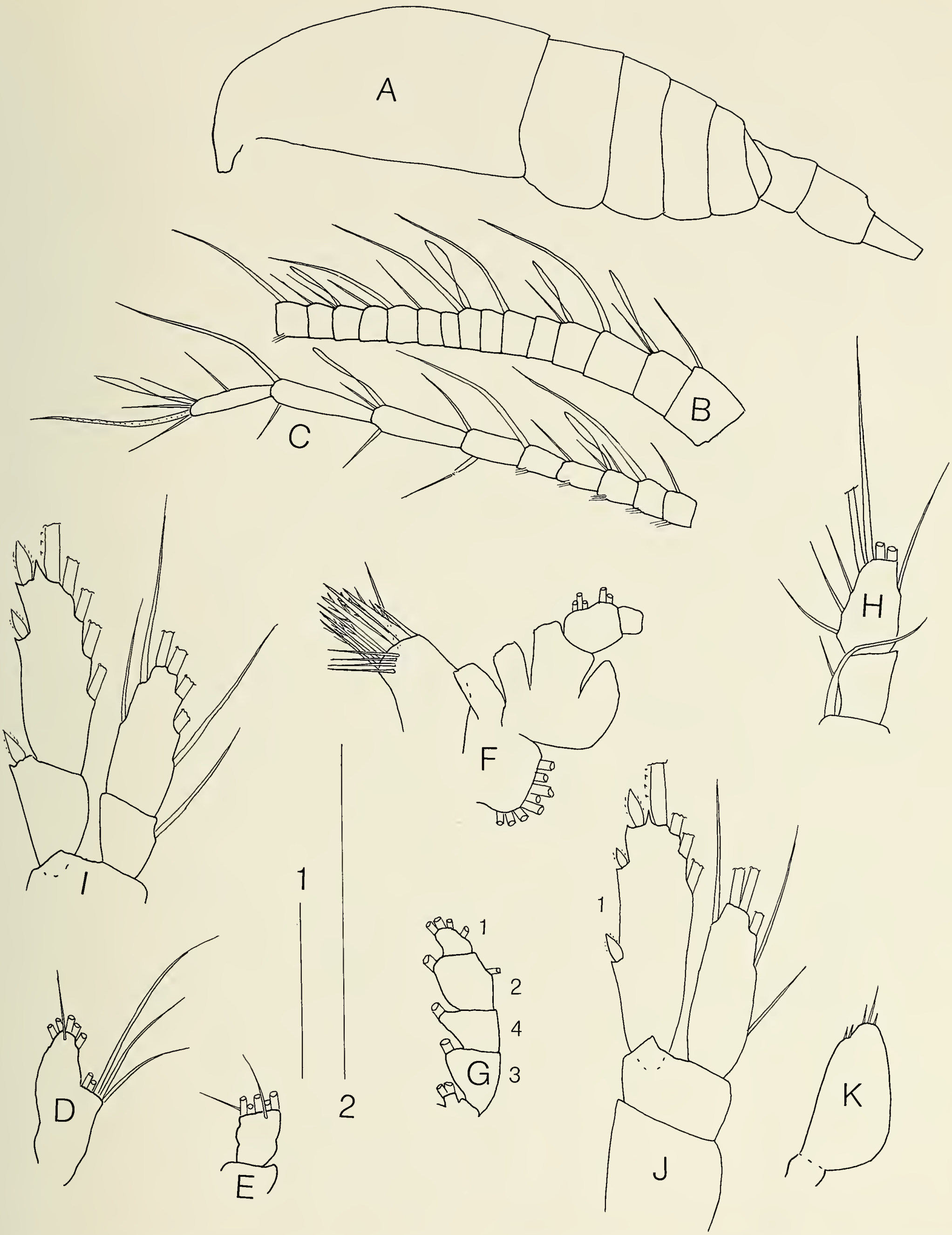

Fig. 9. *Ridgewayia klausruetzleri* n. sp., CIII: A, body left lateral; B, A1 free segments 1–15; C, A1 free segments 16–24; D, endopod 2 of A2; E, endopod 2 of Mn; F, Mx1; G, distomedial lobe of basis and endopod of Mxp (numbers to the right indicate the appearance of endopodal segments during development); H, endopod of P1; I, exopod and endopod of P3; J, exopod and endopod of P4 (number to the left indicates the appearance of exopodal segment during development); K, P5. Setae which were broken and not studied are designated with a wavy-line cutoff. Line 1 = 0.1 mm for A; line 2 = 0.1 mm for B–K.

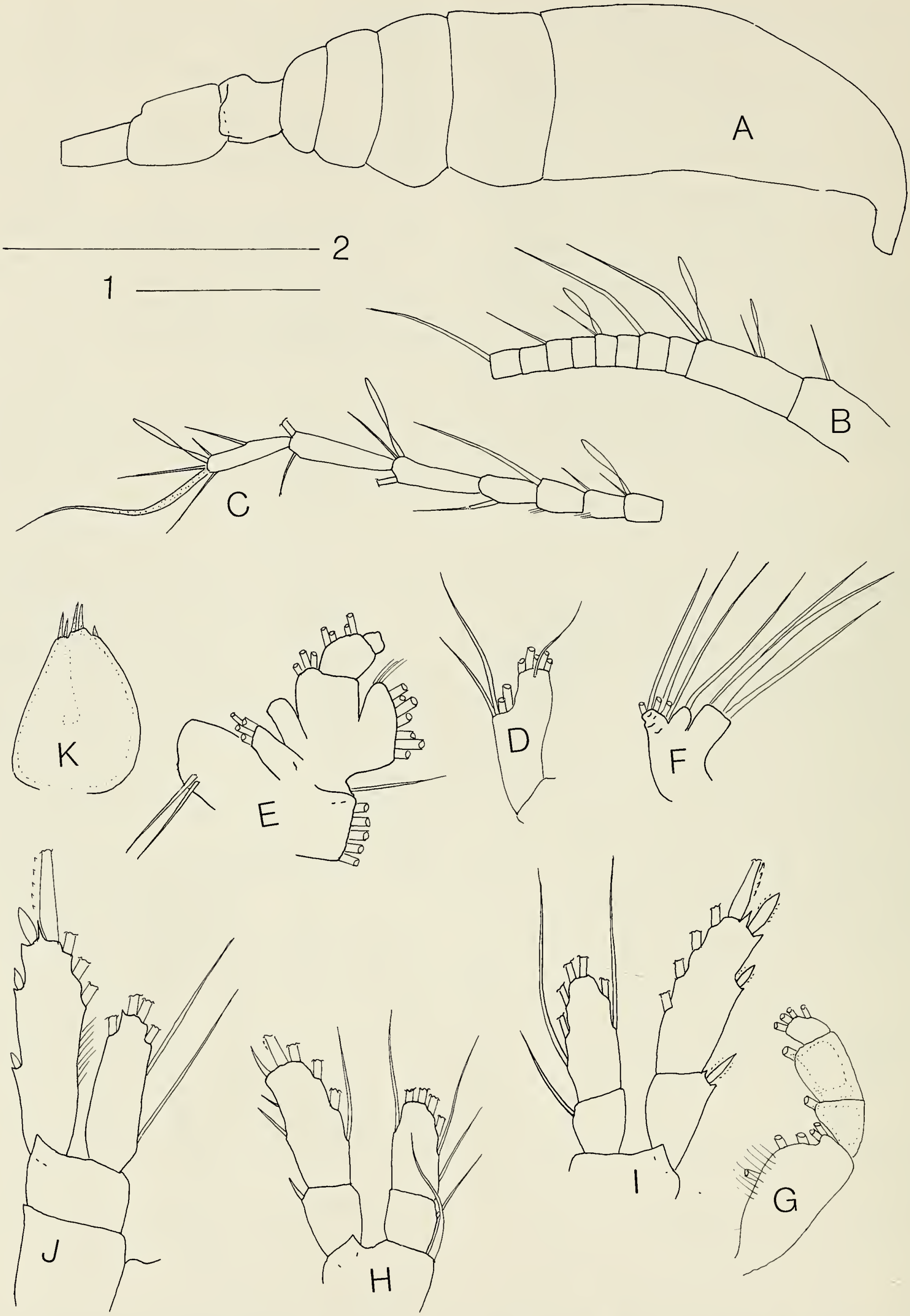

Fig. 10. *Ridgewayia klausruetzleri* n. sp., CII: A, body right lateral; B, A1 articulated segments 1–10; C, A1 articulated segments 11–17; D, endopod 2 of A2; E, Mx1; F, distal lobes of basis and exopod of Mx2; G, basis and endopod of Mxp; H, exopod and endopod of P1; I, exopod and endopod of P2; J, P3; K, P4. Setae which were broken and not studied are designated with a wavy-line cutoff. Line 1 = 0.1 mm for A; line 2 = 0.1 mm for B–K.

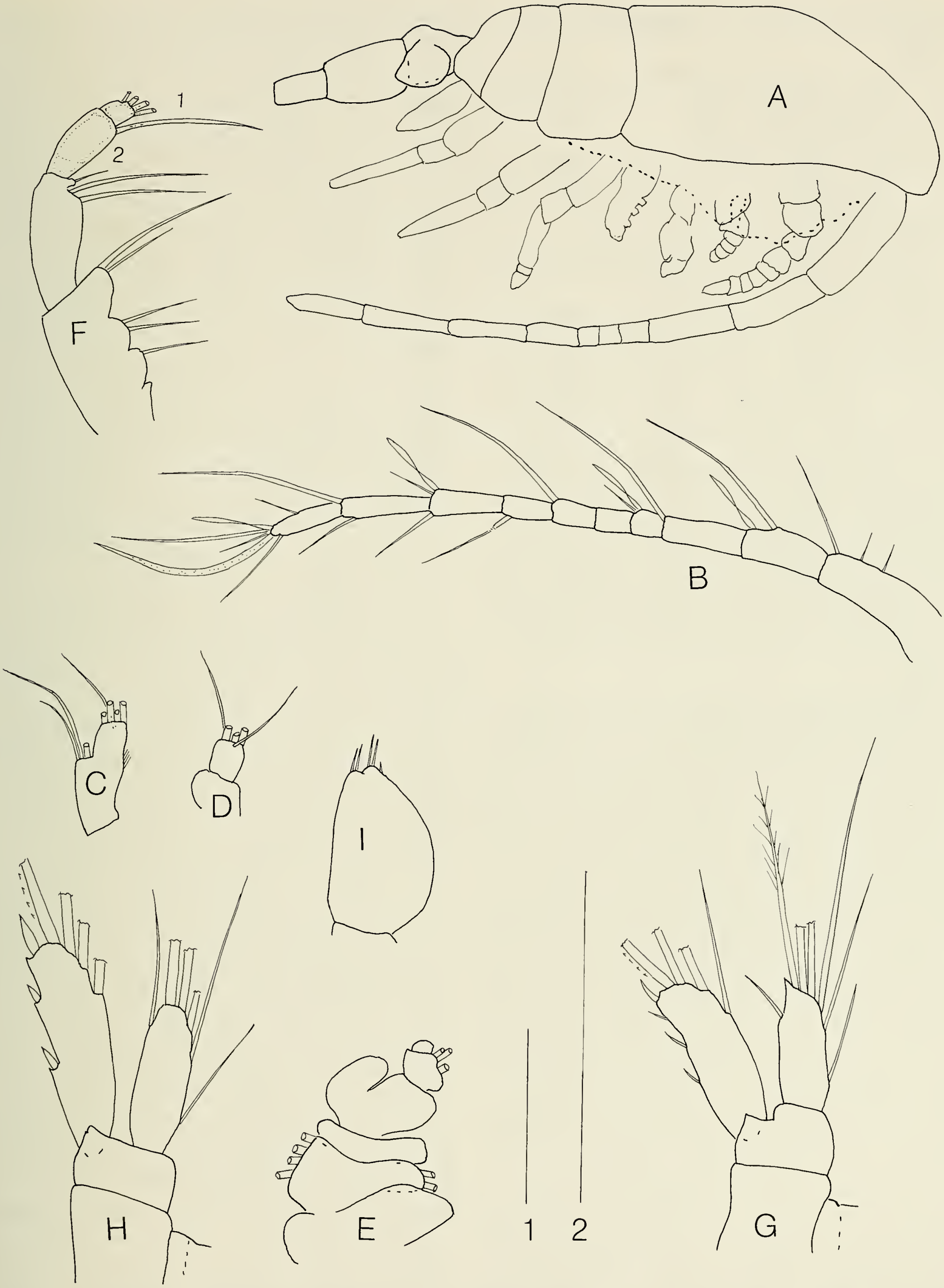

Fig. 11. *Ridgewayia klausruetzleri* n. sp., CI: A, animal right lateral; B, A1; C, endopod 2 of A2; D, endopod 2 of Mn; E, Mx1; F, Mxp (numbers to the right indicate the appearance of endopodal segments during development); G, P1; H, P2; I, P3. Setae which were broken and not studied are designated with a wavy-line cutoff. Line 1 = 0.1 mm for A; line 2 = 0.1 mm for B–I.

medial lobe) setae. Ri 2-segmented with 4, 1 setae.

P1 (Fig. 11G): coxa and basis unarmed. Re 1-segmented with 8 setae. Ri 1-segmented with 7 setae.

P2 (Fig. 11H): coxa and basis unarmed. Re 1-segmented with 7 setae. Ri 1-segmented with 6 setae.

P3 (Fig. 11I): ventrally-directed bud with 2 medial and 3 apical setae.

Remarks.—The six Atlantic species of *Ridgewayia* can be divided into two groups. In the first group, of *R. klausruetzleri, R. marki, R. shoemakeri,* and *R. fosshageni,* the endopod of the male left P5 is a relatively simple, unarmed segment. In the second group, of *R. wilsonae* and *R. gracilis,* this segment is divided into several finger-like extensions. Females of the second group can be separated from each other by the number of setae on the endopod of the female P5, six on *R. wilsonae* or seven on *R. gracilis.*

Among males in the first group, the external spine-like seta on the third (middle) exopodal segment of the left P5 of *R. shoemakeri* and *R. fosshageni* extends beyond the setal elements of the first (distal) segment; in *R. klausruetzleri* and *R. marki,* as redescribed by Yeatman (1969), this seta does not extend beyond the smallest of these elements. An examination of specimens of *R. marki* deposited in the National Museum of Natural History by Dr. Harry Yeatman (USNM 190873) shows that *R. marki* can be separated from *R. klausruetzleri* by the following characters. *Ridgewayia klausruetzleri* is smaller (length range of adult females 0.84–0.90mm, males 0.77–0.82mm) than *R. marki* (females 0.98–1.05mm, males 0.90–1.03mm). The copulatory pore is located more anteriorly on the female genital complex of *R. klausruetzleri* (compare Figs. 1B, C with 12A, B). The distomedial corner of the second (proximal) endopodal segment of the female P5 is not as pronounced as that of *R. marki* (compare Figs. 5C with 12C). The external, spine-like seta of the third (middle) exopodal segment of *R. klausruetzleri* reaches slightly beyond the second seta of the first (distal) segment, while in *R. marki* this spine reaches to the edge of the distal spine-like seta of the first segment. The right basis of the male P5 of *R. klausruetzleri* has a set of long sensilla proximally and a set of short denticles distally; males of *R. marki* (compare Figs. 5F and 12D) have a pad-like thickening distally but no proximal sensilla. The right endopodal seta is located on the distal half of the outer margin in *R. klausruetzleri* but on the proximal half in *R. marki.* The external, spine-like seta on the second (proximal) segment of the left exopod of *R. klausruetzleri* reaches to the end of the well-developed outer tip of the third (middle) segment; in *R. marki* this spine reaches beyond the poorly developed tip (Fig. 12D).

Ecological notes.—No other calanoid copepods were collected in the swarm of copepodids of *R. klausruetzleri*; no nauplii were present. The copepods appeared colorless in the water, but after capture all stages appeared red in direct sunlight. Examination of live specimens with a dissecting microscope indicated that pigment was concentrated at margins of body somites. This color pattern is not apparent in preserved specimens today. Number (and percentage) of each copepodid stage of *R. klausruetzleri* in the swarm were as follows: CI—528 (8%); CII—505 (8%); CIII—403 (7%); CIV—319 (5%); CV—636 (11%); CVI—3687 (61%). This aggregation like other calanoid swarms (Kimoto et al. 1988) includes CI, and contrasts with swarms of the cyclopoid copepod *Dioithona oculata* (Farran, 1913) which seldom include this stage (Ambler et al. 1991). Percentage of females in the last three stages was CIV—68%; CV—68%; CVI—74%; females and males of the CIV and CV cannot be determined without dissection so percentages for those stages were estimated from a subsample of 40 specimens.

Identities and homologies.—Ferrari & Steinberg (1993) have noted for *Scopalatum*

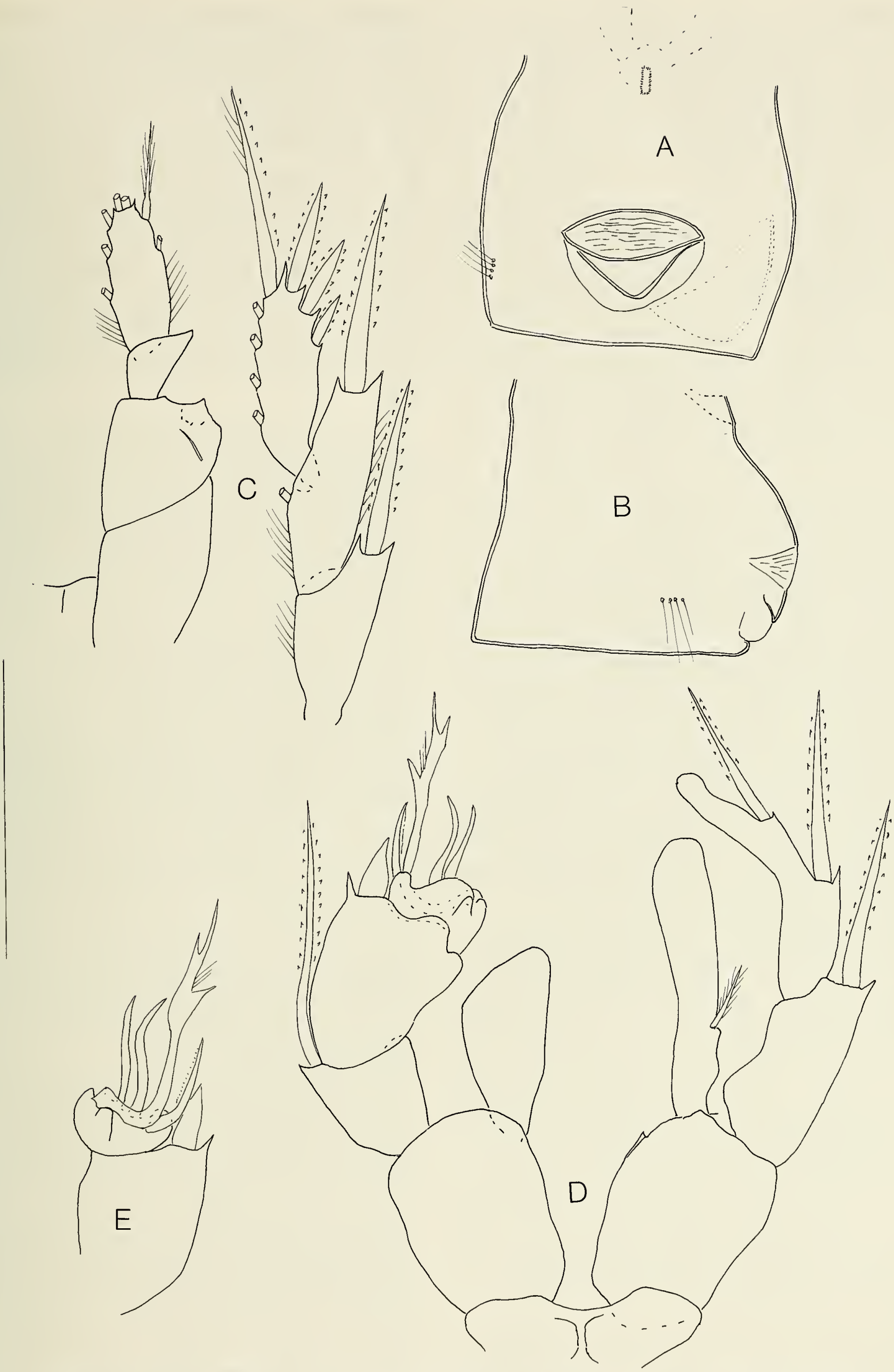

Fig. 12. *Ridgewayia marki* (Esterly, 1911a), CVI female: A, genital complex ventral; B, genital complex lateral; C, P5 posterior, exopod detached. CVI male: D, P5 posterior; E, left exopod 1 and 3 of P5 anterior. Line 1 = 0.1 mm.

vorax (Esterly, 1911b) that the setation of the distal part of maxilla 2 is complete by CII. This early completion of setation is similar to the setal development of the exopods of antenna 2 and mandible, but it is unlike any known endopodal pattern for anterior copepod appendages. Thus the distal part of maxilla 2 is considered an exopod. The setation of *R. klausruetzleri* develops similarly. The sixth lobe of maxilla 2 is considered a lobe of the basis and not an endopodal segment (Huys & Boxshall 1991). It is not an endopodal segment because its setation is complete at CII; it is not an exopodal segment because, like the other enditic lobes, it bears more than 1 seta.

New endopodal segments of the maxilliped (segments 3–5) are formed within the penultimate segment (Figs. 10G & 11F); the antepenultimate segments of CII, CIII, and CIV are the new ones. The distomedial lobe of the basis, which is antepenultimate at CI, adds its last seta at CII. This early completion of setation proceeds identically to that of the syncoxal lobes and non-ramal segments of other appendages, and suggests that this lobe is part of the basis (Von Vaupel Klein 1982) and not a sixth endopodal segment (Huys & Boxshall 1991).

Each new endopodal segment of the maxilliped initially possesses a single seta (Table 1), but setae also are added to non-terminal segments (including the new segments) at CIV, CV, and CVI so that there are two kinds of setae on the new segments: one seta formed as the segment is formed and several setae added after the segment has formed. On the remaining thoracopods, the inner seta of the second (proximal) exopodal segment of thoracopods 2–5 (swimming legs 1–4) is the only seta added after segmentation.

Segmentation of P1–4 appears to follow the common pattern of development which is presumed to be ancestral for copepods (Ferrari 1988). P1 and P2 develop similarly. Although the morphology of the last naupliar stage is unknown, P1 and P2 are reorganized appendages with 1-segmented rami at CI; these rami gain a second segment at CII, after which there is no further segmentation until CV. P3 develops serially and similarly, but one stage out of register with P1 and P2. It is a bud at CI, is reorganized at CII, and adds its second segment at CIII. P4 develops serially, but one stage out of register with P3; it is a bud at CII, is reorganized at CIII, and adds its second segment at CIV. P1–4 add their third ramal segments simultaneously during the molt to CV.

The number of outer setae on the third (middle) exopodal segment of P1 in species of *Ridgewayia* has been interpreted as one or three elements (Wilson 1958, Humes & Smith 1974, Yeatman 1969). Most copepods have one external seta on the third (middle) exopodal segment. *Ridgewayia klausruetzleri* has one seta (an articulating element whose thick base narrows abruptly; this morphology is identical to that of the other setae on the swimming leg segments); the two structures medial to the seta do not articulate and instead are complex attenuations of the segment. This interpretation is clearer at CV because generally there is no change in the number of setae from CV to CVI. In CV *R. klausruetzleri* there is one abruptly narrowing seta and two simple attenuations of the segment (Fig. 6F); the latter two presumably will become the complex attenuations of CVI.

The left and right endopods of the male P5 are one-segmented, but they develop by different patterns. At CIV the left endopod is an unarmed segment; neither segments nor setae are added during later development. At CIV the right endopod is one-segmented with four setae. A second, unarmed segment is added proximally at CV and there is no change in setation. At CVI the endopod is again one-segmented and just one seta is present. The development of the other three setae and the arthrodial membrane between the two segments present at CV presumably is repressed.

Setae also are lost during the exopodal development of male P5. Both the left and right exopods are two-segmented with seven and one setae at CV. At CVI five setae are lost from the first (distal) segment of the right exopod. Two are lost from the first (distal) segment of the left exopod as one seta becomes associated with the new, third (middle) segment.

Etymology.—This species honors Dr. Klaus Ruetzler for his continued support of, and contributions to coral reef research.

Acknowledgments

Dr. Mark Grygier, Silver Spring, Maryland, and five reviewers improved this article. This is contribution number 440 of the Caribbean Coral Reef Ecosystems Program.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(2):201–206. 1995.

Sinoniscus cavernicolus, a new genus and species of terrestrial isopod crustacean from a cave in China (Styloniscidae: Oniscidea)

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Abstract.—This is the first Oniscidea or terrestrial isopod crustacean recorded from a cave in the Peoples Republic of China. The cave where the new species of a new genus of Styloniscinae of Styloniscidae was collected is located near Guilin in Guangxi Province. The species is blind, pigmentless and well adapted to live in a cave.

Kwon & Taiti (1993) in their review and comprehensive account of 49 species of Oniscidea from southern China included no species of Styloniscidae (or of related Trichoniscidae) and no oniscidean specifically from a cave. This is the first record of a troglobitic oniscidean from China. The new genus is in Styloniscinae of Styloniscidae. The specialized oniscidean can be added to Kwon & Taiti's 23 "endemic species" from China (pg. 80). Kwon & Taiti described two blind Philosciidae, neither from a cave—*Papuaphiloscia granulata* and *P. arcangelii.*

Sinoniscus, new genus

Diagnosis.—Blind. Pigmentless. Frontal line distinct; supra-antennal line medially rounded (Fig. 1B). Three flagellar articles; middle article almost two times as long as proximal article; tiny apical article tipped with several long setae. Pereopods without marked sexual dimorphism. Pleon narrower than pereon with all neopleurons laterally appressed. Endopod of pleopod 1 with strong muscular attachment (Fig. 1E). Female with exopods of pleopods of segment 1 and of segment 2 of pleon firmly attached in single scale-like structure fitting across width of each segment (Figs. 3A,B).

Derivation and gender of name. —"Sino-" is a prefix for Chinese to which "-oniscus" is attached referring to an oniscidean from China. Masculine.

Type species.—*Sinoniscus cavernicolus,* new species. Type by original designation.

Affinities.—The new genus is in Styloniscidae because it has conspicuous, strong muscles connected to upper part of endopod of male pleopod 1 (Cf 1E and Vandel 1952: 11, fig. 6). The genital apophysis, although quite narrow, has a tiny apical cone or projection. The left mandible has 2 penicillate setae and the right has only one. The characters above are those on which Vandel (1952:95) defined Styloniscidae. However, Vandel stated that Styloniscidae had a "tête de type trichoniscien," or a head of the trichoniscid type. Vandel (1960:137) stated that in trichoniscids "la ligne frontale n'est pas différenciée (disparition probablement du à une regréssion)." The cephalon of the type of the new genus clearly has a well defined frontal line (Fig. 1B). The presence might represent the primitive state and perhaps it is regressed in contemporary forms, however, more knowledge about the shape of the cephalon of already known species must be obtained since most species of Styloniscidea (and of related Trichoniscidae) are described only on differences in morphology of mouth parts and male pleopods.

The new genus is in Styloniscinae of Styloniscidae because the dorsum is smooth and all neopleurons are appressed laterally on the pleon. All other characters of the new genus are more closely related to species of *Styloniscus* as described by Vandel (1952) who reviewed many species of that genus.

Remarks.—Schmalfuss (1989:21), after presenting a cladogram of family and higher than family clads of Oniscidea, stated that he could not find any characters which could be used to keep Styloniscoidea and Trichoniscoidea distinct. The superfamilies are separated essentially on the same characters as are the nominate families so species of Styloniscidae are closely related to those in Trichoniscidae. Most genera of trichoniscids with species adapted to cave life are in Vandel's (1960) Première Division (now Tribe) of Trichoniscinae. However, *Sinoniscus* (without reference to the muscles of the male pleopods or to the frontal line on the cephalon) fits most closely into Vandel's 'Deuxième Division' with exception that the elongate shaft (tige) projecting from the endopod of male pleopod 1 is not plumose as stated in Vandel's definition of the Deuxième Division (pp. 138, 151).

Sinoniscus is not related to the blind, monotypic *Thailandoniscus* Dalens (1989), a cave adapted styloniscid inhabiting water in caves in Thailand, as comparisons of the cephalons and male pleopods 2, among other things, immediately suggest. The new species described here was found on the mud floor of the cave. Dalens (1989:6) stated that the difference between Trichoniscidae and Styloniscidae is "d'ordre quantitatif et non qualitatif" and the families are distinguished solely "sur l'appareil mâle." Trichoniscidae contains about 86 valid genera and Styloniscidae contains about 11 valid genera. Five genera of Trichoniscidae based on only blind species were discussed by Schultz (1994). The two families must be reevaluated to determine if they can be merged into a monophyletic unit.

Sinoniscus cavernicolus, new species
Figs. 1–3

Description.—About two and one half times longer than broad, dorsum smooth. Anterolateral lobes large (Fig. 1B). Antenna 1 with article 3 longest and tipped with seven aesthetacs, apical one longest. Antenna 2 relatively short with long seta on distal peduncular segment. Right mandible with well developed molar; one seta and lacinia mobilis tipped with tiny teeth between molar and incisor. Incisor with two large, strong outer teeth with inner smaller teeth. Left mandible with well developed molar with two setae on lacinia mobilis; incisor with few teeth. Exopod of maxilla 1 with four outer teeth, one medial tooth and three inner short unnotched teeth; inner margin with tiny, plumose seta (Fig. 1O). Endopod of maxilla 1 tipped with three compound sensory setae, apical one knobed. Maxilla 2 narrows apically with rounded sensory edge, fringe of setae on medial margin. Maxilliped with palp of two segments; first short and broad; second with rounded outer margin ending in point, inner or medial margin straight with several paired setae and one large seta with accompanying shorter seta near apex. Endite narrows apically with large apical spine medial to short, setose apical segment. Exopod of maxilliped about one third length of maxilliped proper with rounded apex and setae filled indentation on outer margin.

All pereopods about same length and with simple setae on inner margins; all with scale-like setae on outer margin of propodus and carpus and scale of setae apically on outer margin of carpus and merus; hair-like setae distally on propodus and proximally on dactylus of each pereopod; each dactylus with single claw and brush-like dactylar organ. Male pereopod I with short dactylus, propodus with two inner setae and scale-like setae on outer edge; carpus with one especially long seta with three other long

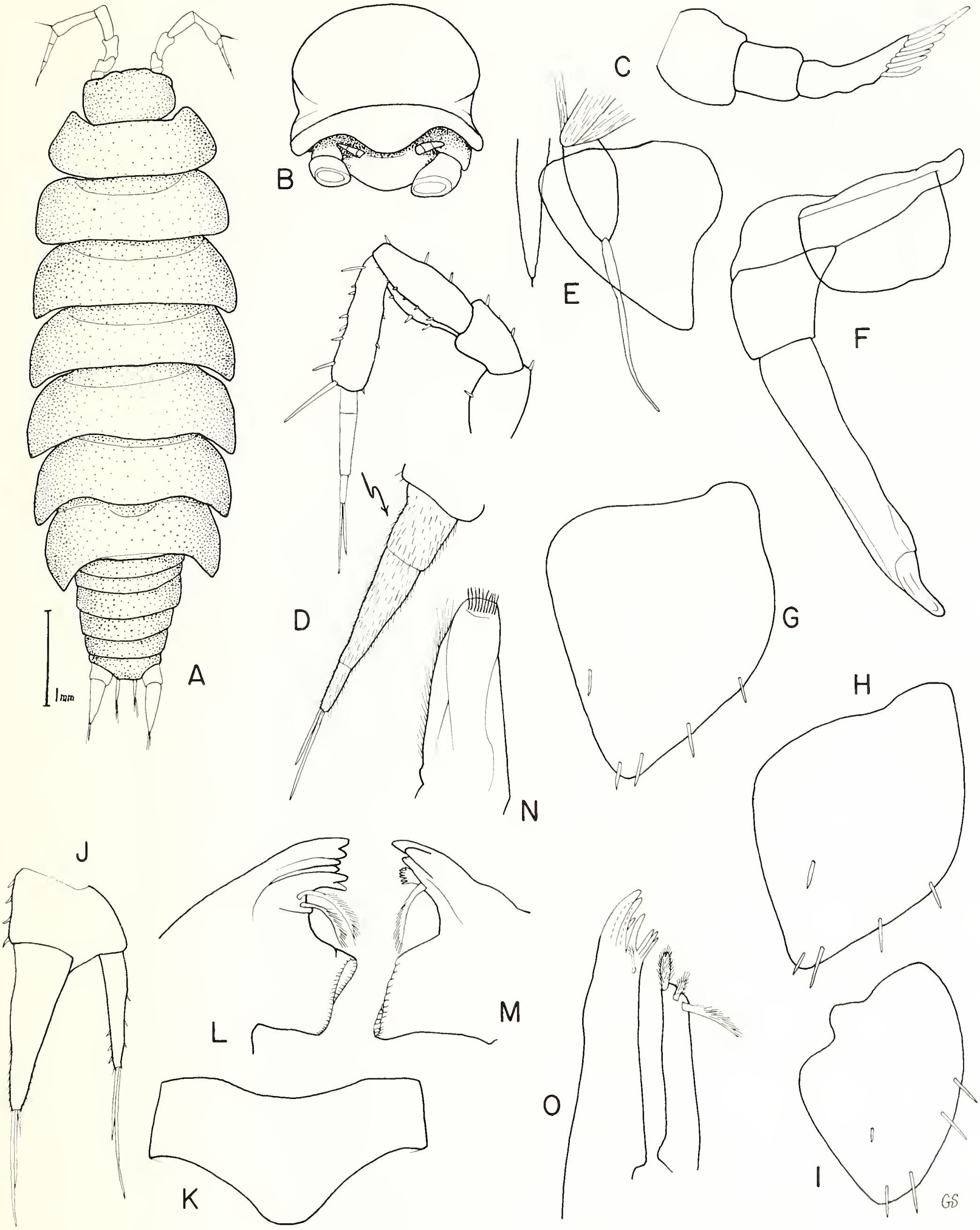

Fig. 1. *Sinoniscus cavernicolus,* new genus, new species: A, Holotype male 6.5 mm long; B, Frontal view cephalon; C, Antenna 1; D, Antenna 2 with detail of flagellum; E–I, Male pleopods 1–5 respectively; J, Uropod; K, Pleotelson; L, Left mandible; M, Right mandible; N, Maxilla 2; O, Maxilla 1.

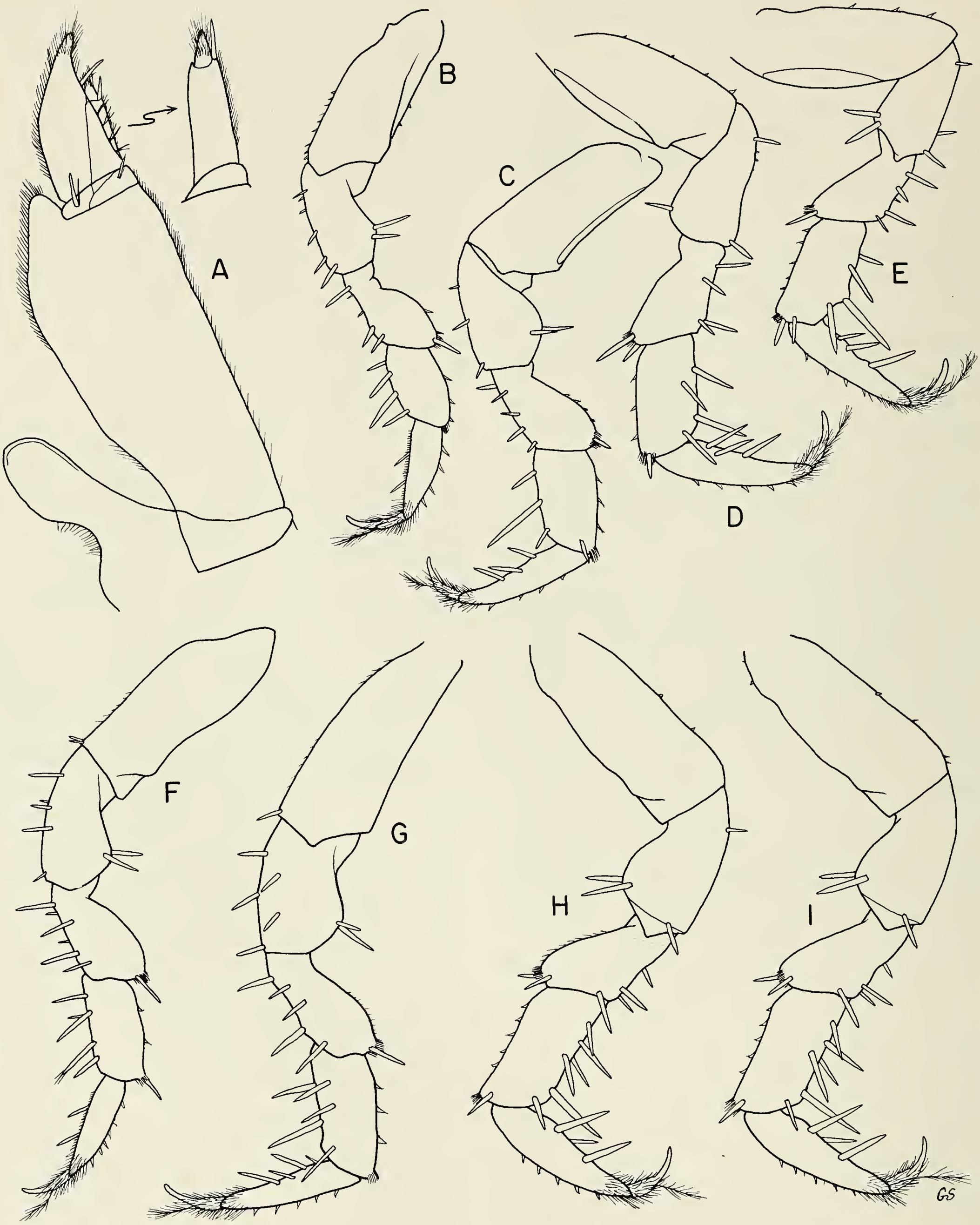

Fig. 2. *Sinoniscus cavernicolus*: A, Maxilliped with detail of endite; B–E, Male pereopods I, II, VI and VII respectively; F–I, Female pereopods I, II, VI and VII respectively.

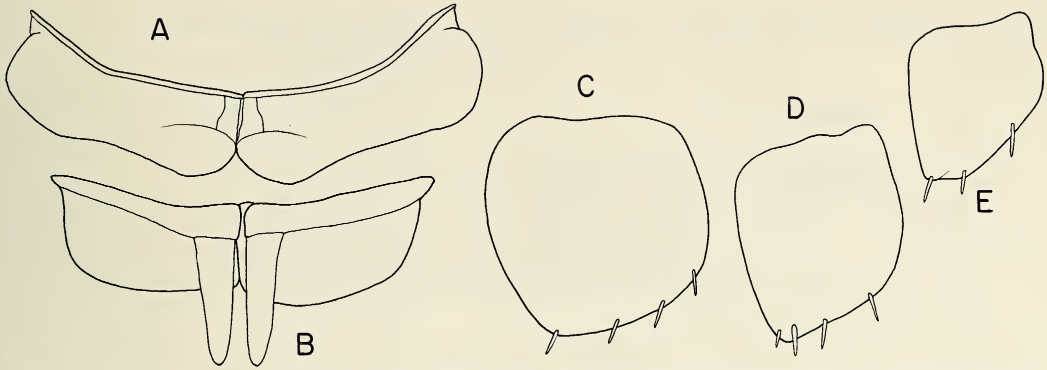

Fig. 3. *Sinoniscus cavernicolus,* allotype female: A, B, Pleopods underside segments 1 and 2 respectively; C–E, Exopod pleopods 3–5 respectively.

setae on inner margin; few setae on inner margin of merus and ischium. Male pereopod II with three long setae on inner margin of propodus; three, one very long, on inner margin of carpus; other segments with few setae on inner margins. Male pereopod VI with three long setae on inner margin; four on carpus; few on other segments. Male pereopod VII with three long setae on inner margin; carpus with six long setae, two on outer apical margin; few on other segments.

Narrow pleon with neopleurons not developed. Exopod of male pleopod 1 simple with pointed posterolateral border; endopod small tipped apically with long, nonplumose shaft, shaft about twice as long as basal segment (Fig. 1E). Exopod of male pleopod 2 small, about one and one half times as wide as long; endopod elongate with short proximal segment and second elongate segment about four times as long as proximal segment; second segment narrows apically, apex rounded (Fig. 1F). Male pleopods 3 to 5 simple, with marginal setae and one seta on face of exopod. Pleotelson, short, with rounded posterior border, no marginal scales or setae. Uropod with conical rami each extending beyond posterior point of pleotelson, both tipped with two long setae.

Pereopods of female much like those of male (Figs. 2F–I). Pleopods 1 in single elongate structure medially split into two lobes. Pleopods 2 with exopods and endopods narrow, elongate and medially located. Exopods of pleopods 3 to 5 of female much like those of male (Figs. 3A–E).

Materials examined.—Nine specimens (3 males and 6 nongravid females).

Measurements.—Males 6.5 to 6.8 mm long; females 6.8 to 7.2 mm long.

Type locality.—A cave at Taiping Yau, Lin Chuan County (just north of Guilin; Reed Flute Cave, a tourist cave, is nearby), Guangxi Province, Peoples Republic of China. Collected 1 Aug 1993 by D. A. Hubbard.

Ecology.—The species was taken from highly organic mud sediment on the floor of the cave.

Distribution.—Known only from the type locality.

Derivation of name.—The Latin *caverna* means "cave" and *-colus* means "dwelling in" so cavernicolus refers to its cave dwelling life style.

Deposition of types.—Holotype male, allotype female and paratypes (1 male and 3 females), Institute of Zoology, Academia Sinica, No. 940925; paratypes, 1 male 2 females. National Museum of Natural History, USNM 267281, Washington, D.C.

Acknowledgment

The author would like to thank Dr. John R. Holsinger of Old Dominion University, Norfolk, Virginia, for sending him the Onis-

cidea collected in the Peoples Republic of China.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(2):207–211. 1995.

Sphaerolana karenae, a new species of hypogean isopod crustacean from Nuevo Leon, Mexico

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Abstract.—*Sphaerolana karenae* is described from two localities in Nuevo León, Mexico. It is the third known species of *Sphaerolana* Cole & Minckley, 1970 and differs from the two previously known species in having three rather than two pleonites visible dorsally, in having the telson pointed rather than rounded, and in having only one rather than two retinacula on the endite of the maxilliped.

Resumen.—*Sphaerolana karenae* es descrita de dos localidades de Nuevo Léon, México. Esta especie es la tercera conocida para *Sphaerolana* Cole & Minckley, 1970 y difiere de las dos especies previamente conocidas en poseer tres pleonitos dorsalmente visibles en vez de dos, el telson termina en punta más que redondeada, y además, de tener solamente un retinaculum y no dos sobre el endito del maxilipedio.

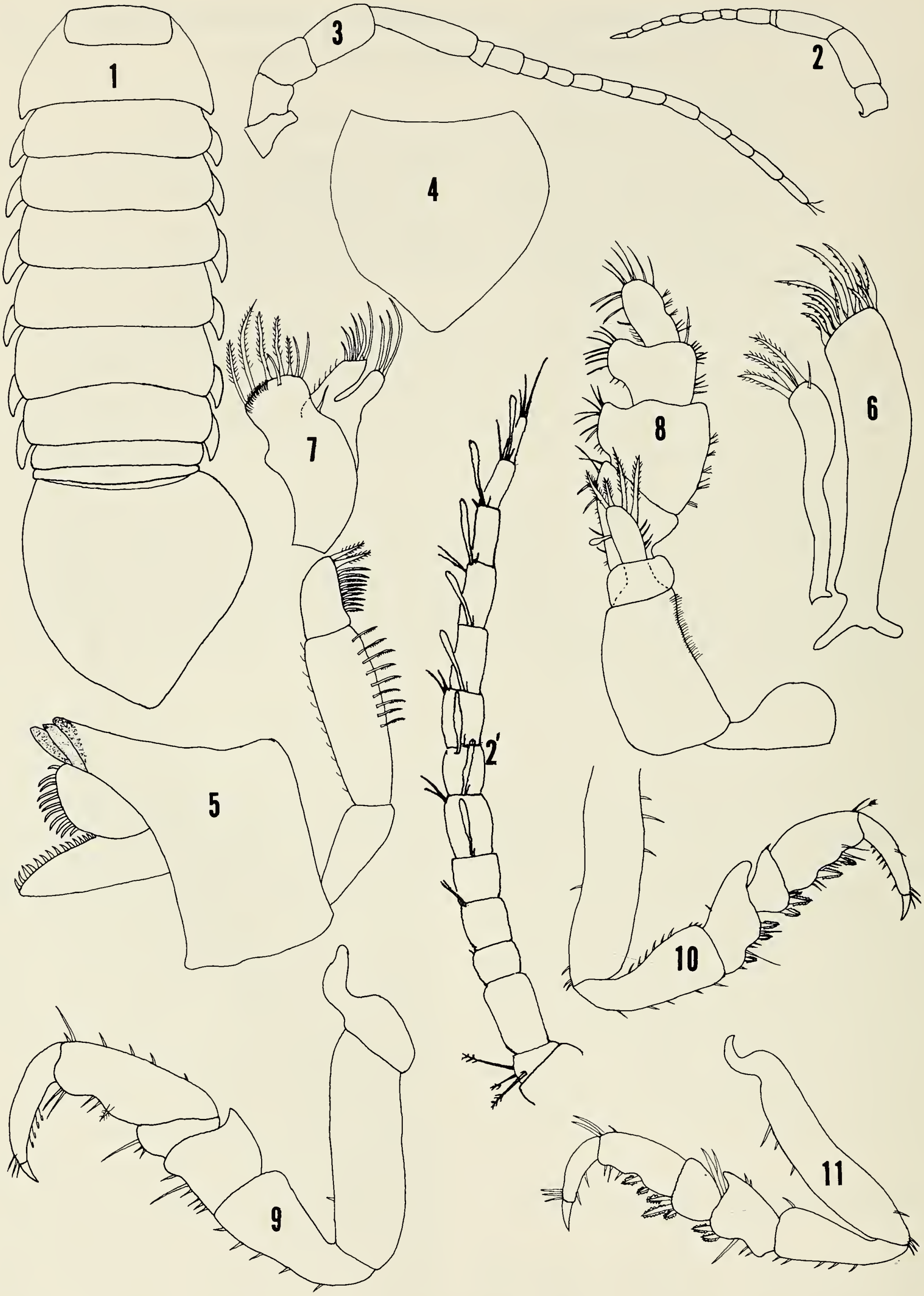
In 1970 Cole & Minckley described the very distinctive troglobitic isopod genus *Sphaerolana*, from the Cuatro Ciénegas basin of central Coahuila state, Mexico. The two species included, *C. interstitialis* (type species) and *C. affinis*, were characterized by their ability to roll into a ball, pleons with only 2 free pleonites, and uropods with tiny rami inserted in a lateral notch of the protopod. We describe herein a third species from the neighboring state to the southeast, Nuevo Léon.

Sphaerolana karenae, new species
Figs. 1–23

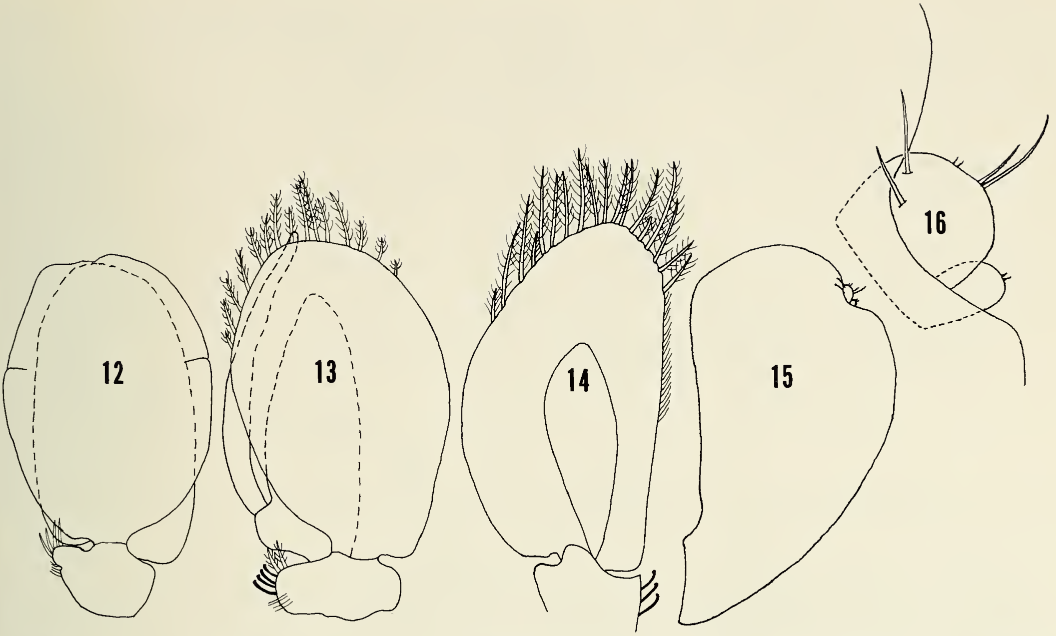
Sphaerolana affinis.—Reddell, 1981:87–88 [Misidentification provided Reddell by T. E. Bowman.]

Material.—Holotype ♂, UANL (Universidad Autónoma de Nuevo León) CCRICI001, and 3 paratypes, UNALCCRIC002, from small spring adjacent to Pilón River, Montemorelos, Nuevo León, Mexico, about 25°27′N, 99°48′W, 20 Jun 1988 and 17 May 1990, leg. M. Valdéz-Marroquin and C. Rodríguez-Almaraz.—3 paratypes on wood in mine below Cueva de la Boca, Santiago, Nuevo Léon, about 25°27′N, 100°06′W, 22 May 1971, leg. S. Peck, deposited in National Museum of Natural History, USNM 139138.

Description.—Length of holotype 7 mm, of largest paratype from USNM 139138 9.7 mm. Head almost 2× as wide as long, without rostrum; frontal lamina about as wide as long; clypeus 4.2× as wide as long. Pleon with 3 free pleonites; pleonite 1 longest; pleonite 3 very short and inconspicuous. Pleotelson about as wide as long, expanded laterally anteriorly, ending in rounded point. Antenna-1 peduncle 3-segmented; flagellum 9–13-segmented; single esthete on 5th through subapical segments. Antenna-2 pe-



Figs. 1–11. *Sphaerolana karenae,* ♂ from Montemorelos (except 2′): 1, Habitus, dorsal; 2, Antenna 1; 2′, Antenna 1, ♂ from Santiago; 3, Antenna 2; 4, Telson; 5, Right Mandible; 6, Maxilla 1; 7, Maxilla 2; 8, Maxilleped; 9, Pereopod 1; 10, Pereopod 2; 11, Pereopod 3.



Figs. 12–16. 12–14, *Sphaerolana karenae* from Montemorelos: 12 pleopod 3, ♂; 13, Pleopod 2, ♂; 14, Pleopod 1, ♂. 15–16, *Sphaerolana karenae* from Santiago: 15, Left uropod, dorsal; 16, Rami of left uropod, dorsal.

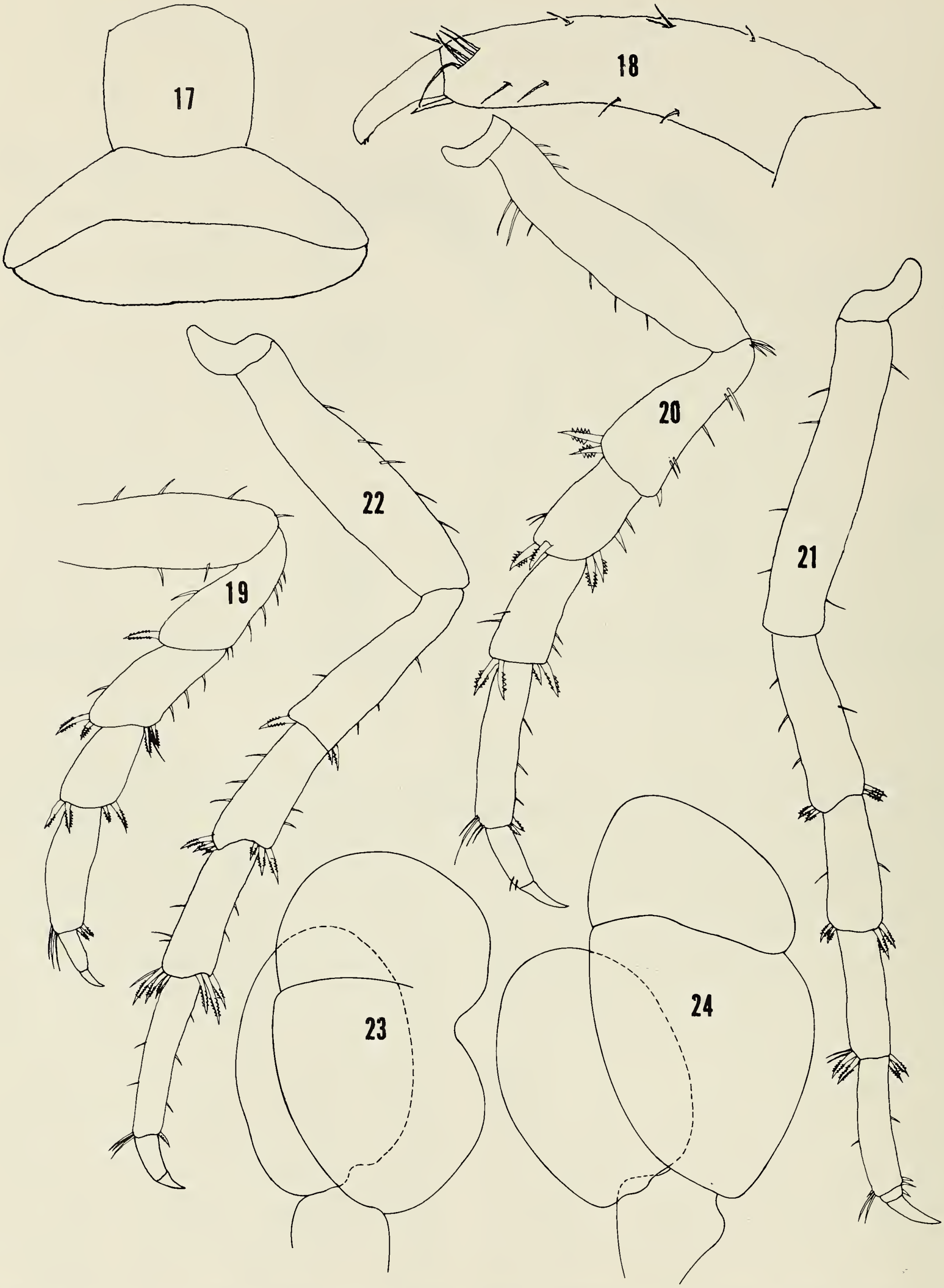
duncle 5-segmented, segment 5 longest; flagellum 12–15-segmented, reaching pereonite 4 when reflexed. Right mandible spine-row process with 11 spines; molar with 15 curved spines; palp segment 2 with 9 pectinate lateral setae and setules along entire medial margin; segment 3 with 11 pectinate setae on lateral margin, distal 2 stouter than others. Maxilla-1 proximal endite with 3 long plumose setae and 2 shorter naked setae; distal endite with 11 stout dentate spines. Maxilla-2 proximal endite medially pubescent, with 5 long plumose setae and 4 shorter setae; distal endite bilobed, inner lobe with 6 setae, outer lobe with 3 setae. Maxilliped endite with single retinaculum, 4 stout plumose setae, and 4 setules; palp segments 3 and 4 produced medially into weak lobes, outer margin of segment 4 with a stout seta, segment 5 with 9 long setae and numerous setules.

Pereopods 1–3 with longer dactyls than those of pereopods 4–7. Pereopod 1 dactyl with a few short setae on anterior and posterior margins. Merus, carpus and propus with 3,3,2 stout toothed spines in pereopod 2; 2,3,2 spines in pereopod 3.

Pleopod 1 protopod with 3 retinacula; exopod elongate, armed with 18 terminal and subterminal plumose marginal setae and row of setules on medial margin. Pleopod 2 protopod with 4 retinacula, 2 plumose setae, and 4 setules; exopod with 15 terminal and subterminal plumose marginal setae; appendix masculina reaching beyond endopod to tip of exopod. Pleopods 3–5 rami unarmed; exopods with partial transverse sutures. Pleopod 3 protopod with 4 setae and 5 setules; rami subequal. Uropod protopod with straight medial margin and broadly rounded apex; rami inserted in notch near apex.

Etymology.—Named for the first author's daughter Ana Karen.

Comparisons.—Table 1 compares taxonomic characters of the three known species



Figs. 17–24. 17–18, *Sphaerolana karenae* from Santiago: 17, Buccal area; 18, Right pereopod 1, dactyl. 19–24, *Sphaerolana karenae* from Montemorelos: 19, Right pereopod 4; 20, Right pereopod 5; 21, Right pereopod 6; 22, Right pereopod 7; 23, Right pleopod 4; 24, Right pleopod 5.

Table 1.—Comparison of species of *Sphaerolana.*

	interstitialis	*affinis*	*karenae*
No. of pleonites demarcated dorsally	2	2	2
Telson apex	broadly rounded	broadly rounded	rounded point
Pleotelson L/W	0.90–0.95	1.1–1.2	0.96
Up protopod: $\frac{\text{length to notch}}{\text{length to apex}}$	0.74	0.88	0.85
A-1 flagellar segs.	10–17	10	8–12
A-1 reaches	pereonite 3	pereonite 4	pereonite 4
A-2 flagellar segs.	15	16	12
Md lacinia teeth	9–16	?	11
Md molar teeth	10–14	?	15
Mxp retinacula	2	2	1
Body length (mm)	up to 17.1	up to 22.1	up to 9.7

of *Sphaerolana. Sphaerolana karenae* is easily distinguished from its two congeners by its three free pleonites, pointed pleotelson, and single retinaculum on the maxilliped endite.

Cole & Minckley's 1970 diagnosis of *Sphaerolana* must be emended by changing the third sentence to read, "Pleonites 1–2 or 1–3 present, visible dorsally; no evidence of either pleonites 3–5 or 4–5″.

Acknowledgments

Part of this work was carried out in Washington by the first author during his tenure of a Short-term Visitor Award from the Smithsonian Institution's Office of Fellowships and Grants. We give thanks to Professor Ernesto Campos for his general comments and a critical review of the manuscript.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(2):212–219. 1995.

Natatolana nukumbutho, a new species (Crustacea: Isopoda: Cirolanidae) from deep water off Suva, Fiji

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Abstract.—*Natatolana nukumbutho,* a new species, is described from specimens taken by baited trap at a depth of 470 m, off Suva, Viti Livu, Fiji. The species is characterized by having acute posterolateral margins on pleonites 3 and 4, entire sutures on all coxae, the appendix masculina slender and shorter than the endopod, and by the spine details of the pleotelson and uropods.

The marine isopod fauna of Fiji is poorly known, with only a few records in the recent literature (e.g., Bruce 1984, 1995a; Bruce & Harrison-Nelson 1988, Kensley 1979). This present contribution adds one more species to the few already known from the area.

Specimens are deposited at the Zoological Museum, University of Copenhagen (ZMUC), and one pair of paratypes at the Australian Museum, Sydney, Australia. Abbreviations: BL—body length; CPS—circumplumose setae; PMS—plumose marginal setae; PS—plumose setae.

Taxonomy

Family Cirolanidae Dana

Genus *Natatolana* Bruce, 1981

Remarks.—The cirolanid isopod genus *Natatolana* is one of the largest of the family with over 60 named species, and numerous undescribed species. It has been recorded from all the world oceans, from shallow water, rarely intertidal, to depths in excess of 2000 meters (Bruce 1986, Brusca et al. 1995). There are, however, no records of the genus from the central South Pacific, and very little collected material exists from this region. The description of the new species below establishes the presence of the genus in the central South Pacific Ocean.

Natatolana nukumbutho, new species

Figs. 1–4

Material examined.—Holotype: ♂ (12.3 mm), off Lauthala Bay, Suva, Fiji, 18°13′S, 178°29′E, 23 Jan 1981, 470 m, in baited trap, coll. Institute of Marine Resources, University of the South Pacific (ZMUC CRU-580).

Paratypes: 2 ♂♂ (11.4, 13.2 [dissected] mm), 11 ♀ (non-ovig 12.2, 13.8, 14.0, 14.0, 14.2, 14.5, 15.5, 16.0, 16.5, 16.8, 17.0 mm), same data as holotype (ZMUC CRU-581, 582; 1 ♂, 1 ♀ AM P43423).

Description.—Male: Body about 2.8 times as long as greatest width; maximum width at pereonites 4–6. Cephalon with submarginal anterior suture, entire anterior and dorsal interocular sutures present, dorsal suture medially weak. Eyes large, rectangular, 1.8 times as long as wide; ocelli distinct, 12–13 horizontally, 8–9 vertically. Pereonite 1 with 2 fine lateral sutures, dorsal suture not extending to posterior margin of pereonite; coxae all with entire carina, posterolateral angles of coxae 6 and 7 acute. Pleon 14.3% BL, pleonites 2–4 each with lateral longitudinal suture; pleonite 1 lateral margins not produced, those of 3 and 4 produced and acute, dorsal and ventral margins of pleonite 4 both convex. Pleotelson slightly longer than pleon, about 16.7% BL, 80%

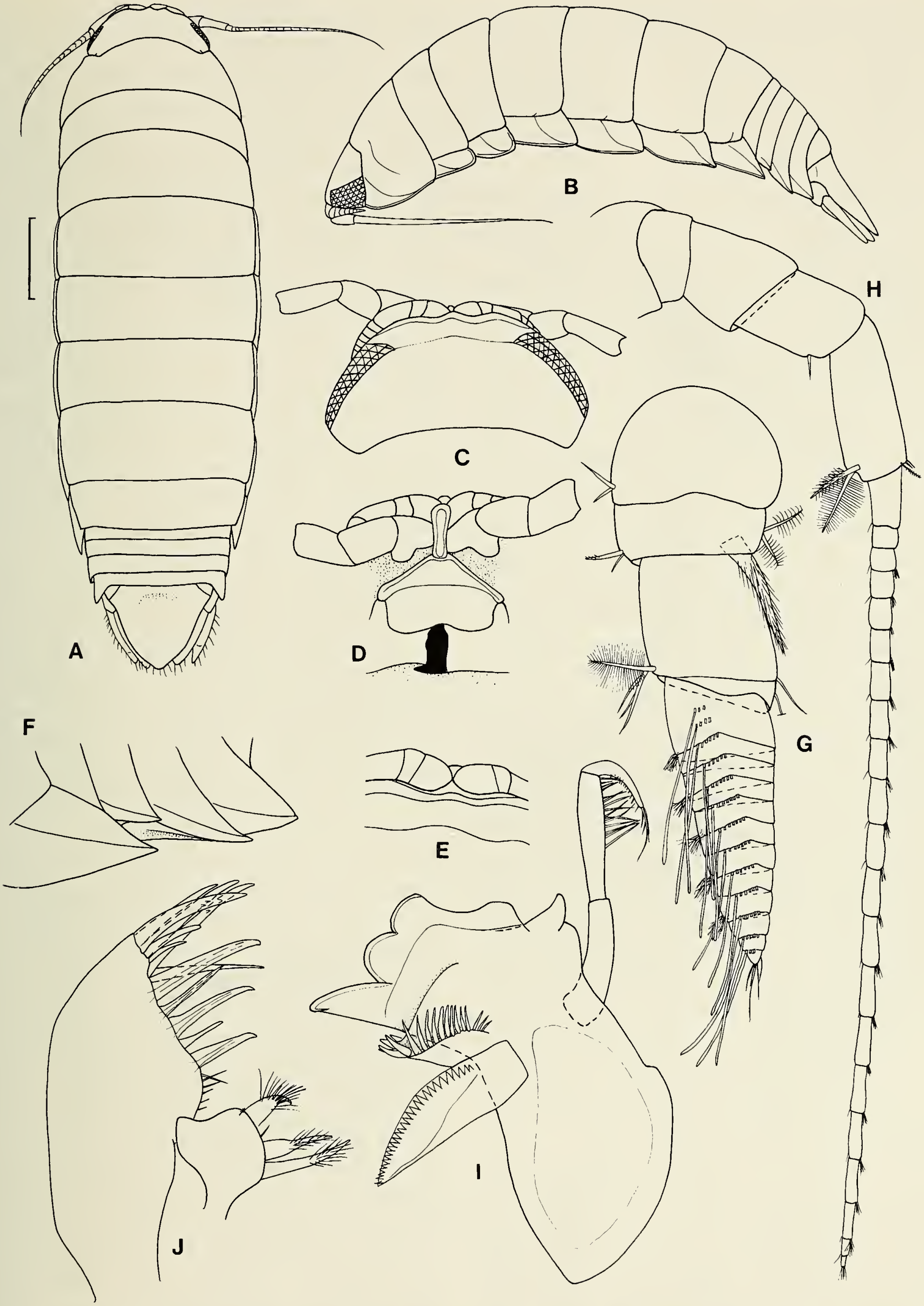

Fig. 1. *Natatolana nukumbutho,* new species. A–E holotype, remainder ♂ paratype 13.2 mm. A, dorsal view; B, lateral view; C, cephalon, dorsal view; D, frons: E, detail of anterior cephalic sutures; F, pleonites, lateral view; G, antennule; H, antenna; I, left mandible; J, maxillule. Scale 2.0 mm.

as long as greatest width, shield shaped, with indistinct narrow and shallow anterodorsal depression which lacks a median notch; posterior margin 12 spines set among PMS, with single seta anterior to anterior-most spine; apex not produced.

Antennule peduncle article 2 about half (0.57) as long as 1, article 3 longest, articles 1 and 2 combined 1.3 times as long as article 3; article 2 with prominent stout broad based pappose seta at ventrodistal margin, nearly as long as and extending near to distal margin of article 3; article 3 with 1 plumose sensory and 3 simple setae at anterodistal angle; flagellum slightly shorter (0.9) than peduncle, with 12 articles, extending to posterior margin of eye, proximal article longest. Antenna peduncle articles 1 and 2 short, their combined length slightly less (0.88) than article 3, article 5 1.6 times as long as article 4, posterodistal angle with 2 densely plumose sensory setae; flagellum with 21 articles, extending to pereonite 4.

Frontal lamina 3.4 times as long as basal width, ventrally flat, lateral margins weakly concave, anterior margin rounded, slightly wider than posterior margin. Mandible spine row with 15 spines; molar process with lateral fold, with about 28 spines along anterior margin. Maxillule as for others of the genus. Maxilla lateral lobe with 5 setae, middle lobe with about 17 in 2 ranks, 10 ventral and 7 dorsal, medial lobe with about 13 CP and distally 3 simple spines. Maxilliped palp articles 2–5 with both margins setose, those of lateral margins being longer than those of medial margins; endite with 2 coupling hooks and 6 long CPS.

Pereopods 1–3 without conspicuously elongate spines on posterior margins. Pereopod 1 basis with cluster of about 8 long slender simple setae at posterodistal angle, anterior margin 10 widely spaced long slender simple setae; ischium anterodistal margin with about 15 long slender simple setae, distomedial lateral margin with row of 7 simple setae, posterior margin with 9 stiff simple setae; merus anterodistal lobe with prominent apical spine and lateral row of about 14 long setae medially with about 5 setae, posterior margin sinuate, with 10 spines (2 of which are medial); carpus with 1 small and 1 large acute spines at posterodistal angle; propodus about 3 times as long as wide, with 4 acute spines on palm becoming progressively larger distally, prominent unornamented blunt spine opposing dactylus, anterodistal angle with cluster of 3 stiff setae, further medial cluster of setae at posterodistal margin; dactylus slender, about 0.75 as long as propodus and about 5.2 times as long as basal width. Pereopod 2 with more numerous, larger and more robust spines than pereopod 1 except for propodal palm which has only 2 small acute spines; ischium anterodistal margin without spines, posterodistal margin with 3 acute spines; merus anterodistal margin with 7 stiff setae and 6 stout spines, distally with further 3 long slender simple setae; carpus posterodistal margin with 2 long acute and 4 short acute spines. Pereopods 5–7 similar in morphology, pereopod 4 intermediate between 3 and 5. Pereopod 7 basis broad, about half as wide as long, anterior margin proximal three-quarters straight, with continuous PS, posterior margin nearly straight, without setae, medial carina with PS along entire length, distal angle with about 20 long PS and laterally a further 6 shorter PS; ischium posterior margin with 5 evenly spaced single acute spines and about 16 long PS, spines at distal angle, anterodistal angle with 2 larger acute and 4 small biserrate spines, mediodistal margin with 2 acute spines; merus posterior margin with 2 short acute spines and 5 slender finely serrate setae, anterodistal angle with 2 spines and 2 setae, posterodistal angle with cluster of about 9 spines and 5 slender finely serrate setae; carpus posterior margin with 2 short acute spines and a large cluster of about 4 long and short spines and 3 finely serrate setae at distal angle, anterodistal angle with cluster of about 10 long acute spines several of which are finely biserrate; propodus poste-

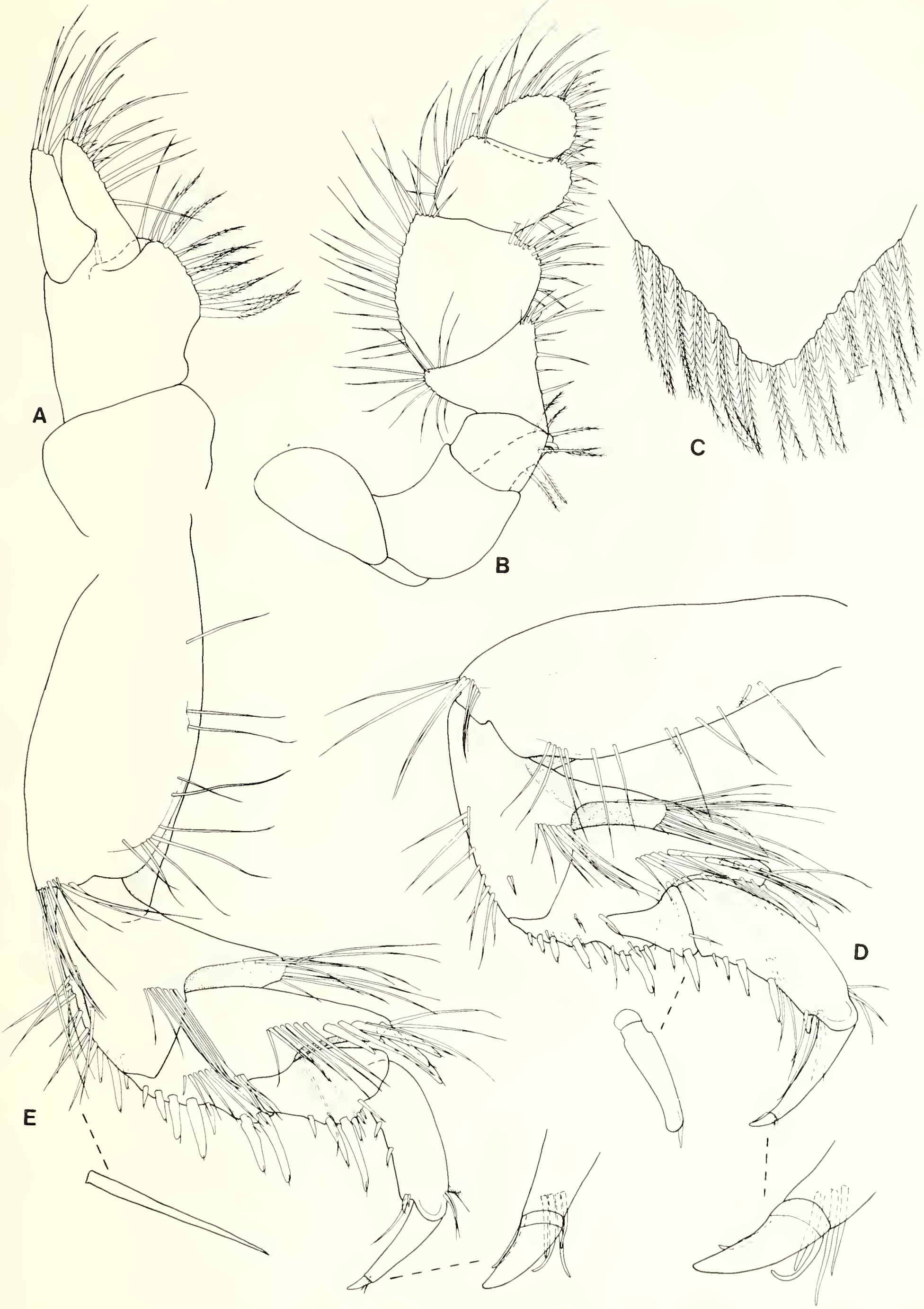

Fig. 2. *Natatolana nukumbutho,* new species. Figures of ♂ paratype 13.2 mm, except C, holotype. A, maxilla; B, maxilliped; C, pleotelson posterior margin; D, pereopod 1; E, pereopod 2.

Fig. 3. *Natatolana nukumbutho,* new species. All figures of ♂ paratype 13.2 mm. A, pereopod 7; B, uropod.

rior margin with 1 and 2 short acute evenly spaced spines on posterior margin, with 3 spines opposing dactylus.

Penial processes absent; position of penial openings and vasa deferenta not discernable.

Pleopod 1 exopod with about 77 PMS, lateral and medial margins evenly rounded; slender spine present at sub-basal proximolateral angle; endopod with about 30 PMS, 0.64 as wide as exopod, medial margin straight; peduncle with 5 coupling hooks.

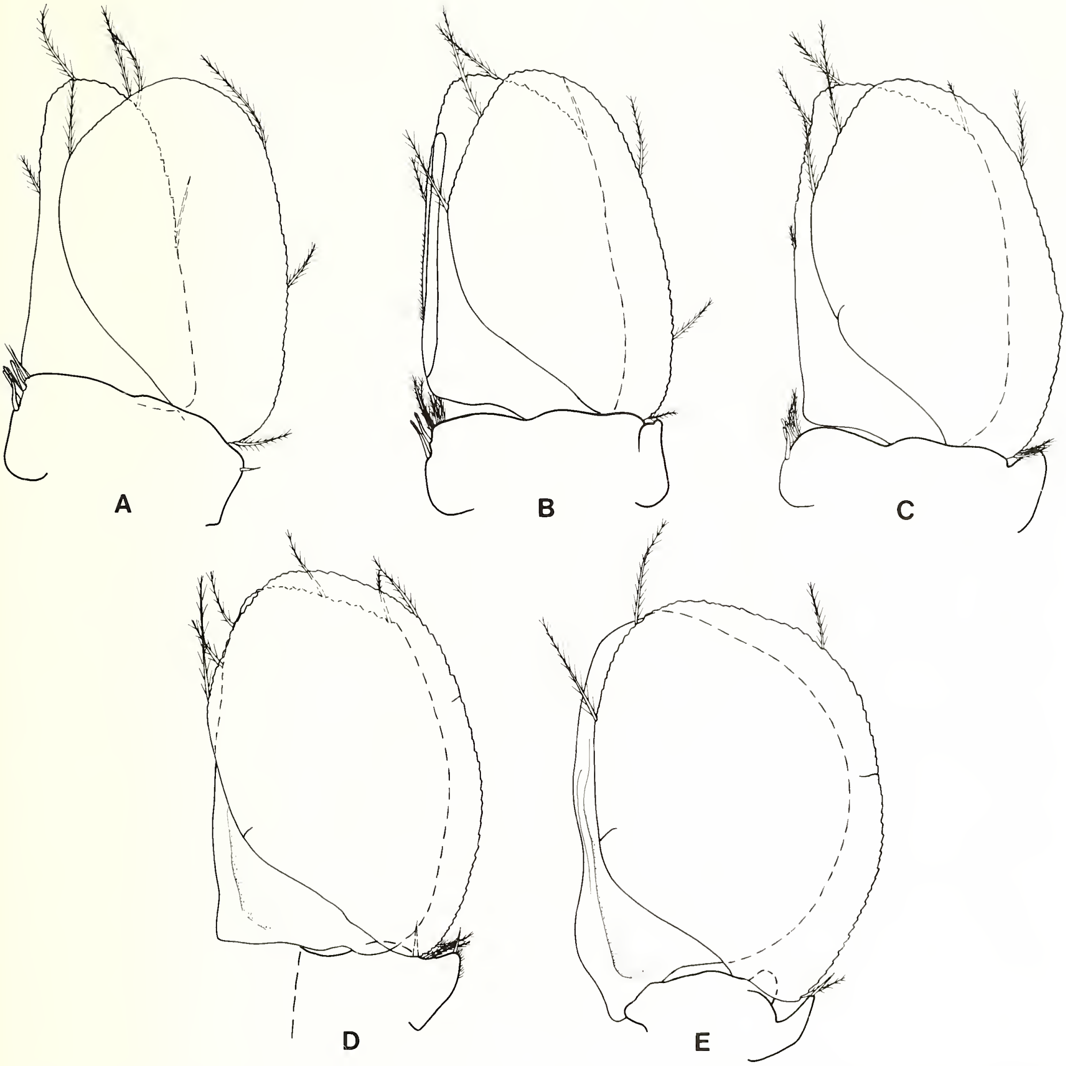

Fig. 4. *Natatolana nukumbutho,* new species. All figures of ♂ paratype 13.2 mm. A–E, pleopods 1–5 respectively.

Pleopod 2 exopod and endopod with about 79 and 29 PMS respectively, peduncle with 4 coupling hooks; appendix masculina straight, slender, about 15 times as long as basal width, 0.7 times as long as endopod, not reaching distal margin of endopod, apex narrowly rounded. Pleopods 3 and 4 similar to each other, exopod suture only laterally distinct. Pleopod 3 exopod and endopod with about 65 and 26 PMS respectively, peduncle with 4 coupling hooks. Pleopod 4 exopod and endopod with about 69 and 25 PMS respectively. Pleopod 5 exopod and endopod with about 67 and 0 PMS respectively, exopod suture fine, entire, peduncle without coupling hooks. Uropod exopod 3.7 times as long as greatest width, about 0.9 length of endopod; exopod lateral margin with 7 spines and 27 PMS, medial margin with 4 spines and continuous long PMS; endopod about 2.5 times as long as greatest width, lateral margin weakly convex, with

4 spines and about 14 PMS on distal two thirds of margin; medial margin posterior two thirds nearly straight, with 5 spines becoming progressively shorter distally except for apical spine, and continuous PMS; peduncle distolateral angle with 1 spine, ventrolateral margin with 2 spines.

Female: Similar to the male except for the primary sexual characters.

Variation.—Pleotelson and uropod spine counts ($n = 14$): telson: 6 + 5 and 6 + 6 each 43%, 5 + 5 occurring only once; uropod exopod (medial margin/lateral margin): $^{4}/_{7}$–71.5%, $^{4}/_{8}$–28.5%; uropod endopod (medical margin/lateral margin):$^{4}/_{5}$–78.6%, $^{4}/_{4}$–21.3%. The larger specimens had the higher number of spines.

Color.—Pale brown with pink tinges in alcohol; chromatophores not apparent.

Size.—Males 11.2 to 13.4 mm, non-ovigerous females 12.2 to 17.0 mm.

Remarks.—Bruce (1986) provided a key to the species groups of *Natatolana* that occur in Australian waters. *Natatolana nukumbutho* does not key to any of those groups, but the cephalic, pleonal and pereopodal morphology is most similar to that of the *Natatolana valida*-group of species. It differs from species of that group, and therefore from all other species of *Natatolana,* in having the following combination of characters: all coxae with entire sutures, pleonite 3 acute but less strongly produced and not extending posterior to the posterior margin of pleonite 5, pleonite 4 less acute (but not rounded as in the *Natatolana woodjonesi*-group) and the appendix masculina distinctly shorter than the endopod. The spination of the pleotelson and uropods can be used to confirm the identity of the species.

Excluding those recorded from Australian waters, only three species of *Natatolana* are known from tropical Pacific and Japan: *Natatolana curta* (Richardson, 1910), *Natatolana japonensis* (Richardson, 1904) and *Natatolana miyamotoi* Nunomura, 1991. The first two species are easily distinguished, *N. curta* having a broadly rounded telson and uropodal endopod, while *N. japonensis* the posterior margin of the pleotelson acutely angled. The description and figures given for *Natatolana miyamotoi* are not of sufficient accuracy or detail to allow interpretation at species level, except that the appendix masculina clearly reaches the distal margin of the ramus. A fourth species, *Natatolana albicaudata* (Stebbing, 1900), is also known from Papua New Guinea, the Philippines and Japan as well as Australia (Bruce 1986, 1995b). That species is readily distinguished by having a broadly rounded pleotelson and the posterolateral margins of pleonite three not being acute and produced.

The position of the genital opening could not be discerned or located by tracing the vasa deferentia, the internal structure of the specimens appearing somewhat decomposed.

Distribution.—Known only from off Suva, Fiji, collected at a depth of 490 m.

Etymology.—The epithet is the name of the nearby Nukumbutho Island and reef pass, and is to be treated as a noun in apposition.

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A new species of the shrimp genus *Chorocaris* Martin & Hessler, 1990 (Crustacea: Decapoda: Bresiliidae) from hydrothermal vent fields along the Mid-Atlantic Ridge

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Abstract. —A new species of the caridean genus *Chorocaris* Martin & Hessler, *C. fortunata,* is described from the Lucky Strike hydrothermal vent field along the Mid-Atlantic Ridge in the vicinity of the Azores. The new species differs from the two previously known members of the genus in having an acute conical prominence on the lower angle of the orbit (antennal spine); this spine and the rostrum extend further anteriorly than the anteriormost border of the pterygostomial and ventrolateral region of the carapace. Additional differences include a more stout cheliped, narrower scaphognathite, longer chela on the second pereiopod, and a much smaller size at maturity.

The caridean shrimp genus *Chorocaris* was established by Martin & Hessler (1990) to accommodate *C. vandoverae,* a small shrimp collected at hydrothermal vent sites in the Mariana Back-Arc Basin, western Pacific. In addition to *C. vandoverae,* Martin & Hessler (1990) also transferred one Atlantic species of vent shrimp, *Rimicaris chacei* Williams & Rona, 1986, to *Chorocaris.* Thus, prior to the current paper there were two recognized species in the genus, with a biogeographically interesting distribution, one known from vent sites in the western Pacific, the other from vents along the Mid-Atlantic Ridge.

In June 1993, collections were made using the submarine DSRV *Alvin* at several vent sites along the Mid-Atlantic Ridge near the Azores. Among the species collected on this cruise were several specimens of a small new species of *Chorocaris,* which we describe herein.

Materials and Methods

Shrimp were collected during a series of dives on the American Lucky Strike Cruise (DSRV *Alvin* and R/V *Atlantis II,* Chief Scientist C. Langmuire, May 27–June 4, 1993, Lucky Strike hydrothermal field, 37°17′N, 32°16′W, 1624–1700 m depth). Although additional specimens from other dives exist in the collections of various researchers (e.g. C. L. Van Dover, currently at the Duke University Marine Laboratory, Beaufort, North Carolina), all specimens used in this report came from DSRV *Alvin* Dive 2607, 2 Jun 1993, 1624 m. In addition to the new species, *Chorocaris chacei* was also present at this site. The material, all of which has been deposited in the Natural History Museum of Los Angeles Count (LACM), with the exception of 5 paratypes sent to the Muséum national d'Histoire naturelle, Paris, and to the University of Lisbon, Portugal, consisted of 71 individuals ranging in size from 3.8 mm to 9.4 mm in carapace length (CL) and from 12.0 mm to 33.1 mm total length (TL).

Chorocaris fortunata, new species
Figs. 1–3

Holotype.—Female, ovigerous, CL 9.7 mm, TL 30.2 mm. LACM 93-45.1. DSRV *Alvin* Dive 2607, Vent Site 3 (Sintra Site), Lucky Strike hydrothermal vent, 1624 m, 2 Jun 1993, Azores (37°17.6′N, 32°16.5′W).

Paratypes.—70 specimens (including 17 ovigerous), LACM 93-45.1 (21 specimens) and LACM 93-45.3 (49 specimens, ten of which were later removed for depositing in the French and Portugese institutions). Same collection data as for holotype. One specimen, CL 8.5 mm, Lucky Strike vent field, 14 Sep 1992 (not included in range of sizes given below).

Additional material (non-paratypic).—2 specimens from a collection of 10 individuals ranging in size from approximately TL 27 mm to 18 mm; 2 of the 10 specimens were ovigerous. Broken Spur vent site, DSRV *Alvin* Dive 2624, approximately 29°10′N, 43°10′W, 26 Jun 1993, 3044 m (Dr. Eve Southward, Marine Biological Association of the United Kingdom, Citadel Hill, Plymouth, England, pers. comm.).

Diagnosis.—*Chorocaris* Martin & Hessler, 1990, with acute, conical suborbital tooth (antennal spine) that, together with blunt rostrum, extends anteriorly beyond the anteriormost extension of the carapace. Chelipeds short, robust, propodus inflated. Second pereiopod with dactylus almost half length of propodus.

Description.—Size of the 71 specimens examined by us ranged from CL 3.8 to 9.4 mm and TL 12.0 to 33.1 mm; average CL 6.5 mm, average TL 21.4 mm. Of these 71 specimens, 17 were ovigerous females (including the holotype), the smallest of which was CL 6.4 mm and TL 20.2 mm, and the largest of which was the holotype.

Carapace (Fig. 1a, b, f) smooth to lightly punctate, with scattered short setae especially anteriorly along midline. Rostrum broadly tapering, exceeding eyestalks and slightly exceeding postorbital prominences. Suborbital prominence (antennal spine) acute, tapering, sometimes conical toward tip, clearly exceeding anteriormost extension of ventrolateral border of carapace.

Eyes lacking pigment, eyestalks flattened-cylindrical, cuticular covering thin and soft, extending posteriorly and slightly laterally beneath carapace, joined medially, with slight indentation where 2 stalks meet.

Stylocerite of antennule (Fig. 1c) acute, extending anteriorly to approximately distal tip of first penducle article. Antennal scale (scaphocerite) (Fig. 1e) oval, almost exactly twice as long as wide, with slight longitudinal dorsal ridge and with acute tooth at approximately ⅘ length along lateral border.

Mandible (Fig. 2a, b) with 6 small teeth along cutting border and blunt posterior tooth separated from cutting teeth. Palp 2-segmented. Maxillae (Fig. 2c–f) as illustrated; first maxilla with row of even sized teeth along inner face of distalmost endite; second maxilla with 3 endites. Maxillipeds (Fig. 2g–n) similar to what has been described for other species in the genus (*C. vandoverae,* Martin & Hessler 1990; *C. chacei,* Williams & Rona 1986). Third maxilliped composed of 3 long segments (and 2 shorter ones, not illustrated), the first of which is thin and strap-like, the distalmost of which has a terminal constriction possibly indicative of former segment line (Martin & Hessler 1990).

First pereiopods (primary chelipeds) (Fig. 3a–d) short, stout. Propodus inflated and thicker than dactylus. Dactylus and propodus each with row of small, corneous denticles along cutting border, and with row of longer setae along the distal outer face,

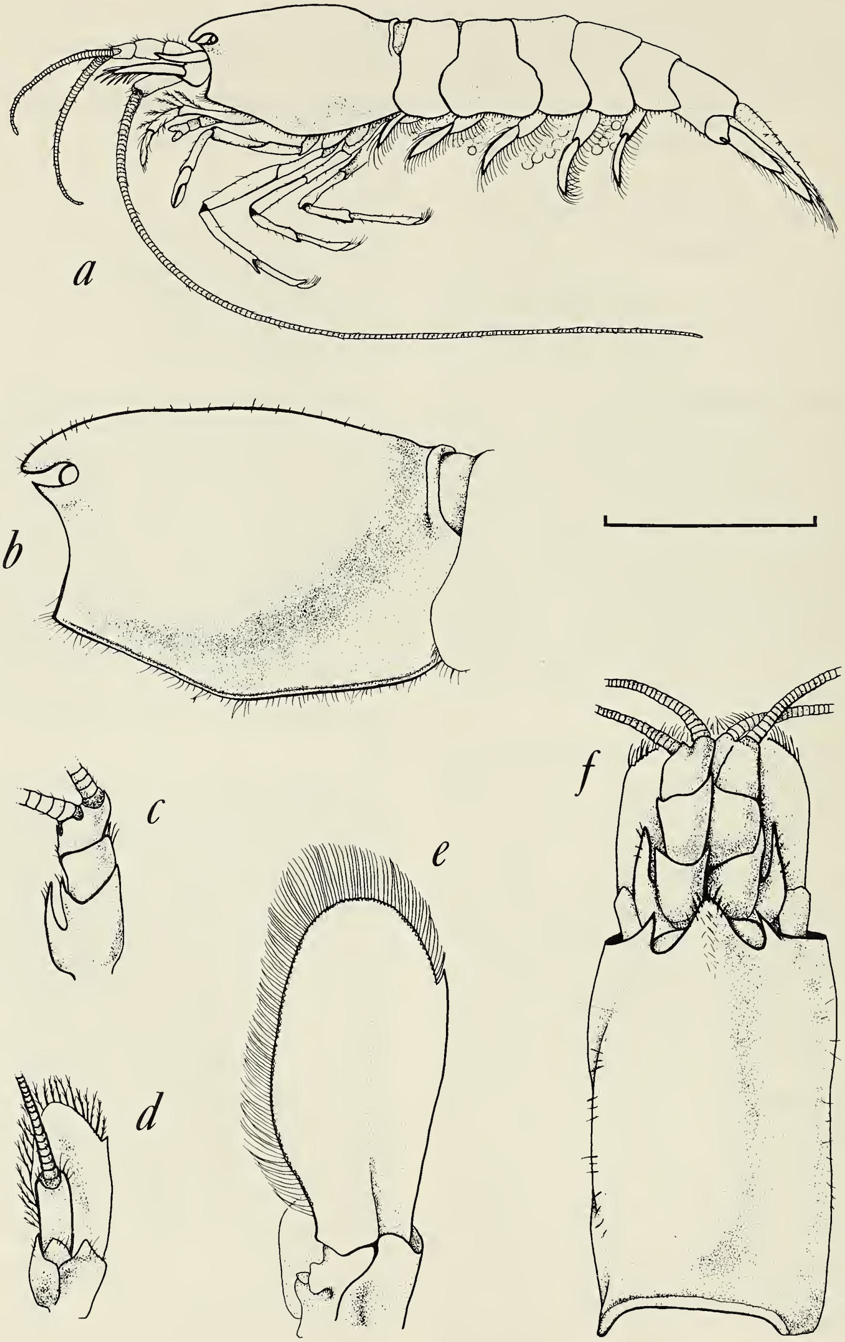

Fig. 1. *Chorocaris fortunata,* female holotype. a, lateral view, major cheliped missing (regenerating, visible as small bud posterior to third maxilliped); b, carapace and extremity of eyestalk; c, base of first antenna, ventral view; d, base of second antenna and antennal scale (scaphocerite), ventral view; e, dorsal view of scaphocerite; f, dorsal view of carapace, eyes, and bases of antennae. Scale bar = 10 mm (a), 5 mm (b–d, f), and 2.4 mm (e).

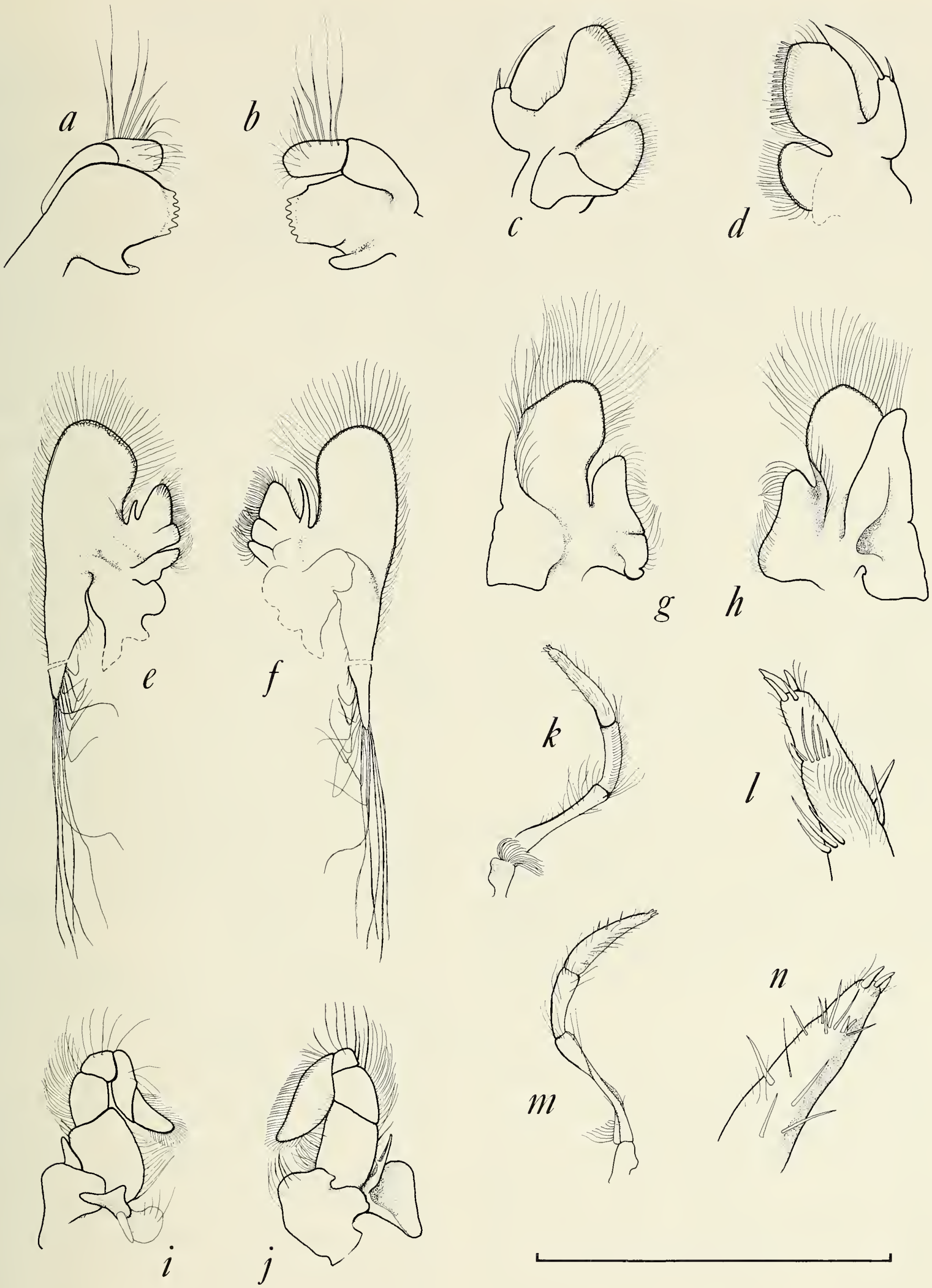

Fig. 2. *Chorocaris fortunata,* female holotype, mouthparts. a, b, right mandible in outer (a) and inner (b) view; c, d, right first maxilla in outer (c) and inner (d) view; e, f, right second maxilla in outer (e) and inner (f) view; lower part of figures e and f (area with long setae, below dotted line on basal region of exopod) taken from female paratype of similar size to holotype (CL 8.7 mm) (missing on right maxilla of holotype); g, h, right third maxilliped in outer (g) and inner (h) view; i, j, right second maxilliped in outer (i) and inner (j) view; k, l, m, and n, third maxilliped, outer view with higher magnification of tip (k, l) and inner views of same (m, n). Scale bar = 2.5 mm (a–d, l, n); 5.0 mm (e–j), and 10.4 mm (k, m).

somewhat obscuring comb row described above. Propodus rather deeply indented on outer face at 2 points (Fig. 3d). Carpus with strong dorsodistal tooth and with weak carpal brush (not illustrated). Second pereiopod (Fig. 3e, f) chelate, chela more delicate than that of first pereiopod, with propodus approximately 3.7 times longer than wide, and 1.8 times longer than dactylus; propodus and dactylus together appearing as an elongate oval. Ambulatory pereiopods similar to one another, with short dactylus bearing 4–5 heavy, corneous-tipped spines (Fig. 3g–j).

Exopods lacking on all pereiopods.

Pleurobranchs on pereiopods 1–5; arthrobranchs on pereiopods 1–4 and maxilliped 3.

Abdomen (Fig. 1a, 3k) with posterolateral angles of somites rounded, becoming broadly tapered on somite 5. Ventral border of somite 2 slightly indented. Telson (Fig. 3k) with 7–9 spines extending along lateral border and onto dorsum. Outermost uropod with single acute movable spine at outer end of suture line.

Coloration.—Preserved specimens ranged from almost pure white to a more commonly seen yellowish or rust color, caused apparently by the accumulation of bottom deposit material (oxydized sulfide according to M. Segonzac, pers. comm.) adhering to the plumose setae covering most of the appendages.

Natural history.—One specimen from the Lucky Strike vent field, given to Dr. Lipke Holthuis by Dr. W. Vervoort and not seen by us, was found "in the stomach of a hydroid polyp." Although apparently in rather poor condition, it could be readily identified as *C. fortunata* (Lipke Holthuis, pers. comm.). Thus, at least sometimes *C. fortunata* serves as food for this as yet undescribed hydroid.

Etymology.—The name is from the Latin for luck or chance, referring to the collection site (Lucky Strike hydrothermal vent field) along the Mid-Atlantic Ridge.

Discussion

The smallest ovigerous female of *C. fortunata* examined by us (TL 20.2 mm) is smaller even than the juveniles of *C. chacei* listed by Williams & Rona (1986:460, table 2). Segonzac et al. (1993:541, table 2) also gave a relatively large size for *C. chacei*; they listed a size (TL) range of 47.3 to 66.2 mm for males, and 42.3 to 57.4 mm for females. For the Pacific *C. vandoverae,* Martin & Hessler (1990:2) gave a size range of TL 16.3 to 52 mm. The largest known specimen of *C. fortunata* measures TL 33.1 mm. Thus, *C. fortunata* is a considerably smaller species than either of its two congeners.

Additionally, *C. fortunata* is rather easily distinguished from *C. chacei* (the only other described Atlantic species) by several morphological features, notably its acute antennal spine, more narrow rostrum, less produced ventrolateral carapace border, longer dactylus on pereiopod 2, and longer and narrower scaphognathite. These differences are such that even on a schematic diagram (e.g., Segonzac et al. 1993:fig. 2C) they are readily apparent; especially clear are the differences in the relative lengths of the second pereiopod dactylus/propodus and the forward extension of the anterolateral carapace border in that figure.

Size is also one of the reasons that we have attributed the 2 Broken Spur specimens (from a collection of 10 individuals that ranged from TL 18 to 27 mm) to *C. fortunata,* despite the fact that they are slightly more delicate in overall appearance and are pale in comparison to the darker coloration of the Lucky Strike samples (after fixation; we have not seen any live specimens). Apparently 3 or 4 different types of shrimp were observed at the Broken Spur site, all in close proximity to vent openings or in shimmering water from crevices with diffuse flow, although only 14 total specimens were collected (E. Southward, pers. comm.).

The new species occurs with at least one

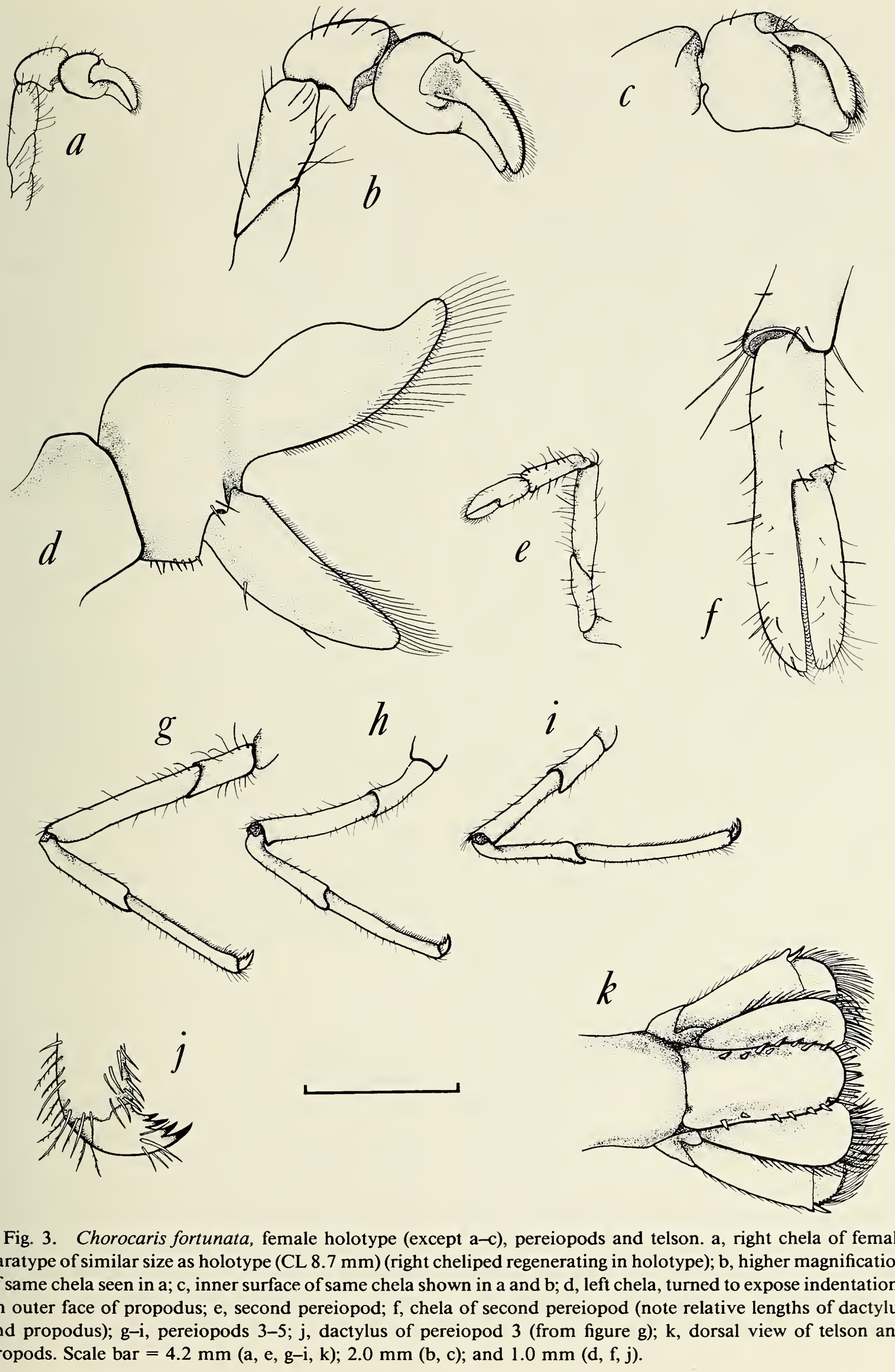

Fig. 3. *Chorocaris fortunata,* female holotype (except a–c), pereiopods and telson. a, right chela of female paratype of similar size as holotype (CL 8.7 mm) (right cheliped regenerating in holotype); b, higher magnification of same chela seen in a; c, inner surface of same chela shown in a and b; d, left chela, turned to expose indentations on outer face of propodus; e, second pereiopod; f, chela of second pereiopod (note relative lengths of dactylus and propodus); g–i, pereiopods 3–5; j, dactylus of pereiopod 3 (from figure g); k, dorsal view of telson and uropods. Scale bar = 4.2 mm (a, e, g–i, k); 2.0 mm (b, c); and 1.0 mm (d, f, j).

previously described species at the Lucky Strike vent. Among the samples sent to us that included *C. fortunata* was at least one larger specimen that was easily identified as *Chorocaris chacei*; additional specimens of *C. chacei* were collected from this site by C. L. Van Dover (pers. comm.).

The genus *Chorocaris* was originally considered a member of the family Bresiliidae, although problems with bresiliid taxonomy in general—noted by many previous workers on this family—were mentioned by Martin & Hessler (1990:9). Subsequent to that paper, Christoffersen (1991) placed the genera *Alvinocaris* and *Rimicaris* in the relatively recently erected family Alvinocarididae (Christoffersen 1986), but whether he intended for both *R. exoculata* and *R. chacei* (now *Chorocaris chacei*) to be included in this family was not made clear. Thus, *Chorocaris* was not mentioned in the original erection of the family Alvinocarididae. Christoffersen's family Alvinocarididae was recognized by Segonzac et al. (1993) in their study of trophic behavior of the three caridean genera known from vents, and a brief diagnosis of the family was given in a footnote (Segonzac et al. 1993:536). Segonzac et al. (1993) clearly stated that both *Chorocaris* and *Rimicaris,* as well as *Alvinocaris* Williams & Chace, 1982, belong to the family Alvinocarididae. Unfortunately, the two characters given in that brief diagnosis are, we feel, an insufficient basis for erecting a new caridean family. M. de Saint Laurent (author of the footnote in Segonzac et al. 1993) listed the following as characters shared by the Alvinocarididae genera: (1) lack of exopods on thoracic appendages posterior to the maxillipeds, and (2) eyestalks reduced and attached to each other and to neighboring parts. The new species exhibits these features as well. However, loss of pereiopodal exopods has occurred often among the Caridea, and reduction or modification of the eyestalks in a rather common theme among deep-sea crustaceans. Other shared features of the three "alvinocaridid" genera are given later in that paper (Segonzac et al. 1993:541), but these are somewhat vague: "similarities in the posterior region of the thorax, in the abdomen, and in the telson, and also in the structure of most cephalothoracic appendages" (from the 1994 English translation). Therefore, although the Alvinocarididae may someday prove to be a natural assemblage, we do not feel that sufficient characters have yet been established to recognize this taxon.

Holthuis (1993), in his compilation of the Recent genera of caridean and stenopodidean shrimps (which was published prior to the Segonzac et al. 1993 paper), followed Chace (1992) in recognizing only the Bresiliidae, treating Christoffersen's family Alvinocarididae as a synonym (Holthuis, 1993: 69). We have followed this more conservative approach here, i.e., treating *Chorocaris* as a member of the Bresiliidae while recognizing that the Bresiliidae is most likely an artificial assemblage.

The fact that *Chorocaris* is found in widely separated areas of the world ocean—the Mariana Back-Arc Basin and the Mid-Atlantic Ridge—raises biogeographically interesting questions. The new species is no more different from the western Pacific *C. vandoverae* than it is from the geographically closer *C. chacei.* Possible routes of dispersal that might account for distribution of species of *Chorocaris* are discussed further in Martin & Hessler (1990).

Acknowledgments

We thank Cindy Lee Van Dover for bringing these specimens to our attention and for comments on the manuscript. We also thank Eve Southward and Austin B. Williams for helpful discussions of vent shrimp taxonomy and biogeography and for keeping us informed as to developments in the literature. We are also grateful to Michel Segonzac, Lipke B. Holthuis, and Rafael Lemaitre for providing comments on the manuscript. This work was supported by an

REU supplement to NSF grant DEB 9020088 to J. W. Martin.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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A new genus and species of caridean shrimp (Crustacea: Decapoda: Bresiliidae) from hydrothermal vents on Loihi Seamount, Hawaii

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Abstract.—*Opaepele loihi,* new genus and species, is described from hydrothermal vents on Loihi Seamount, Hawaii, a mid-plate, hot-spot volcano at 18°55′N, 155°16′W, 980 m depth. This new form is related to several other bresiliid shrimps associated with hydrothermal vents, brine and hydrocarbon seeps. It has a laterally broadened triangular rostrum inconspicuously toothed on dorsal and ventral margins, carapace with pterygostomian spine present, and eyes reduced and fused mesially. This combination of characters places it in an intermediate position between a group of species in the genus *Alvinocaris* Williams & Chace with well developed compressed toothed rostrum, carapace with pterygostomian spine present, and eyes on separate movable stalks, and a group of species with rostrum absent (genus *Rimicaris* Williams) or much reduced (genus *Chorocaris* Martin & Hessler), carapace with pterygostomian spine absent, and eyestalks reduced and fused mesially. Only two of the vent/seep bresiliid species are now known from depths less than 1000 m, *A. stactophila* Williams, from hydrocarbon seeps at 534 m in the Gulf of Mexico, and the present new species at 980 m.

Most deep-sea hydrothermal systems discovered to date have been at or near tectonic plate boundaries. An exception is the system on Loihi Seamount, a mid-plate hot spot, submarine volcano located near the southern terminus of the Hawaiian Islands. The area of active hydrothermal fluid discharge is restricted to the flank of a relatively small volcanic cone on the southwest portion of the seamount approximately 10–15 m below the summit. The active field named Pele's Vents, <0.25 km^2 in area, is characterized by numerous individual vents, a few to 20 cm across, which discharge waters at temperatures as high as 37°C; ambient seawater temperature is 4°C (Karl et al. 1988, 1989). The vent fluid is exceptionally clear and nearly devoid of suspended particulate matter. Discharge velocities are 1–10 cm sec^{-1}.

Geochemical and biological evidence suggest that hydrothermal vent systems at mid-plate sites differ fundamentally from those at plate boundaries, e.g., mid-ocean ridges (Karl et al. 1988, 1989; Sedwick et al. 1992). In particular, vent waters at Pele's Vents contain extremely high amounts of total dissolved CO_2 (ca. 300 mM), more than 100 times the concentration at the Galapagos Rift vents (Edmond et al. 1987). Consequently, pH of vent waters can be as low as 4.2 (Sedwick et al. 1992). Levels of dissolved iron (ca. 1 mM) are 2×10^6 greater than ambient seawater and approximately

40 times greater than at the Galapagos Rift vents (Edmond et al. 1987). Furthermore, active vent fields on Loihi Seamount lack the luxuriant macrobenthic communities characteristic of vents at mid-ocean ridges (Grassle 1986). It is unknown whether this seemingly anomalous condition results from Loihi's geographic isolation, relatively young age, the inability of such organisms to recruit on the seamount's sediment-covered substrata, the extremely low levels of sulfide (Sedwick et al. 1992), or the potentially toxic conditions created by elevated concentrations of carbon dioxide and dissolved metals in the vent waters. Indeed, the only macrofaunal species found in Loihi's vent fields is the bresiliid shrimp described here.

Materials studied are deposited in the National Museum of Natural History, Washington, D.C. (USNM).

In the following descriptions, some anatomical structures are abbreviated as follows: mx, maxilla; mxp, maxilliped; p, pereopod; pl, pleopod. Measurements are abbreviated as: al, length of abdomen including telson; cl, carapace length, including rostrum, along dorsal midline; scl, postorbital carapace length along dorsal midline.

Description

Opaepele, new genus

Diagnosis.—Rostrum carinate; dorsal margin sweeping obliquely downward from most elevated point of carapace to tip, reaching midlength of basal article of antennular peduncle, toothless or bearing up to 6 small, subapical teeth; ventral margin toothless or bearing tiny subapical tooth; outline triangular in dorsal view, lateral margins diverging posteriorly to merge with orbital margins. Carapace with antennal and pterygostomian spines. Telson bearing 6–8 submarginal dorsal spines, convex terminal margin bearing dense row of setae and armed at either posterolateral corner with 1–3 spines. Eyestalks rather large but degenerate, broadly fused mesially, cornea unfacetted, poorly organized retinal pigment evident. Antennal scale broadly oval, blade far exceeding distolateral spine. Mandible with 2-segmented palp, distinct separation between incisor and molar processes. Mx2 with endites narrowly separated; scaphognathite rounded anteriorly, narrowed, elongate, and bearing strong setae posteriorly. Mxp1 with exopod. Mxp2 somewhat pediform but flattened, with small exopod. Mxp3 of conventional shape, distal segment trigonal in cross section, transverse tracts of fairly dense setae along lateral surface. Pereopods without exopods; p1 and p2 with merus and ischium distinct. P1 robust; chela larger than that of p2 and with long curved fingers pectinate along prehensile edges; carpus hollowed distally to receive proximal end of palm. P2 about as long as and more slender than p1. P3–5 similar, not chelate. Arthrobranchs on mxp3 and pl–4, pleurobranchs on p1–5. Pls with appendix interna simple, well developed coupling hooks only on p1 5.

Type species.—*Opaepele loihi,* new species.

Etymology.—The generic name is a construct from the Hawaiian words "opae," general term for shrimp, and "Pele," the volcano goddess. Gender feminine.

Opaepele loihi, new species
Figs. 1–3

Material studied.—Loihi Seamount, Hawaii, 18°55'N, 155°16'W, 980 m, taken in traps baited with flying fish, set and recovered by Craig Moyer in the DSRV *Pisces V*: USNM 251447, ♀ holotype; USNM 251448, ♂ allotype; USNM 251449, 6 ♂, 7 ♀, paratypes; dive #213, 28 Aug 1992. USNM 251450, 26 ♀, paratypes; dive #242, 7 Sep 1993.

Description.—Integument smooth, shining, fairly thin and pliable, inconspicuously pitted with shallow punctations and usually bearing scattered tiny setae dorsally and dorsolaterally. Carapace compressed, noticeably deeper than broad, greatest depth at about ⅔ length from tip of rostrum and greatest width approximately at midlength between tip of rostrum and posterior dorsal margin; dorsal midline arched, or slightly sinuous in some specimens.

Rostrum well developed; as in generic diagnosis. Orbit with margin evenly rounded, ending ventrolaterally in acute buttressed suborbital angle, usually bearing small spine. Pterygostomian spine small, acute, directed anteriad. Branchiostegite with ventral margin reinforced by submarginal ridge posterior to level of coxa of third pereopod, broadly rounded posterolaterally and overlapped by pleura of first abdominal segment. Posterior submarginal groove shallow but well marked.

Abdomen evenly rounded dorsally; pleura of short segment 1 broadened and asymmetrically rounded; pleura of segment 2 greatly expanded, conspicuously overlapping segments 1 and 3; pleura of segment 3 with posterolateral corner broadly rounded but bearing 0–5 spines of irregular shape, size and dispersal; pleura of segment 4 rounded anteroventrally, nearly straight ventrally, either rounded and more strongly spined around posterolateral margin than segment 3, or produced into variably spined posterolateral angle; segment 5 with posterolateral angle strongly produced into acute spine, posterior margin above angle slightly convex, bearing up to 6 or more variable small spines; segment 6 deeply notched for insertion of uropods, posterior margin sinuous and drawn to point laterally. Sternite 1 bearing pair of rudimentary, slender, poorly sclerotized submesial spines, similar spines better developed and more widely separated on sternites 2 and 3, but again closely approximated mesially on sternite 4, strong median keel on sternite 5 drawn to stout acute posterior spine bearing against sternite 6 with abdomen flexed.

Telson with length of dorsal midline 1.4 times that of segment 6; sides moderately convergent; dorsal surface with very slight suggestion of median longitudinal concavity and with submarginal row of 6–8 spines (sometimes asymmetrical) at either side along distal ⅔ of length, continued as 1–3 spines at either end of convex terminal margin bearing dense row of setae.

Eyestalks as in generic diagnosis; smooth base of obsolescent spine or tubercle evident on anterior surface of each eye near rostral margin.

Antennular and antennal peduncles well developed. Antennular peduncles stout, dorsoventrally flattened but slightly convex on dorsal side, mesial margins closely parallel; proportional length of articles from base to tip about 3.5:2.2:1; basal article with distal width nearly half its length, article 2 slightly narrower than its length, and article 3 shorter than its width. Stylocerite very strong, swollen ventrally along its middle portion but tapering to very slender point reaching to or beyond midlength of middle article. Basal article with strong distolateral spine extending as much as ¼ length of middle article, mesiodistal spine smaller, transverse fringe of setae across distodorsal margin. Second article with mesial spine stronger than corresponding spine of basal article. Flagella strong, subequal in length, inserted side by side on oblique terminal margin of distal article, lateral ramus with annuli much coarser than those on mesial ramus, and with prominent sensory setae at joints between annuli.

Antennal peduncle (Fig. 1) shorter than that of antennule, exceeded by broadly oval antennal scale almost twice as long as wide, convex lateral margin ending in short stout spine considerably exceeded by blade fringed with plumose setae, blade reinforced by oblique median ridge originating basally; flagellum similar in structure to those of antennules in their distal parts but larger in all dimensions, sweeping to tip reaching level of tail fan, scattered inconspicuous sensory setae at joints between annuli.

Gills as described for genus *Rimicaris* (Williams & Rona 1986) and cited for *Chorocaris* by Martin & Hessler (1990).

Mouthparts as figured (Fig. 3).

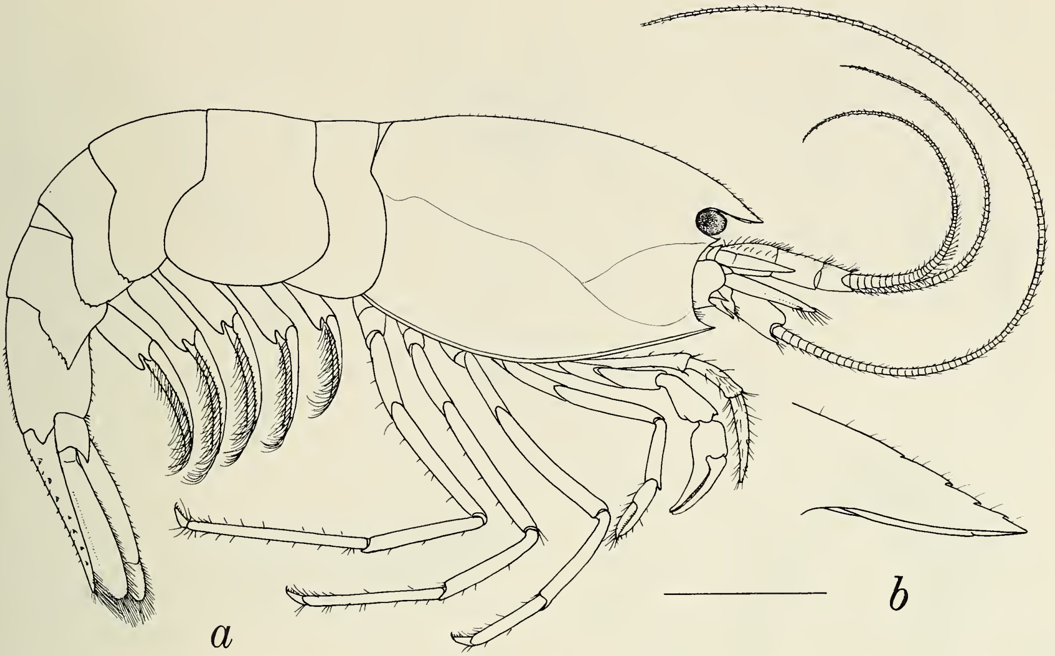

Fig 1. *Opaepele loihi,* new genus and species. Female holotype: *a,* lateral view, scale = 5 mm; *b,* rostrum enlarged.

Mx2 with proximal endite composed of 2 straplike lobes, distal endite subtriangular, elongate and flanked laterally by slightly curved straplike palp; scaphognathite greatly expanded, anterior subovate lobe with densely setose margin bearing longest setae along distomesial sector, stout posterior subtriangular lobe fringed on distomesial margin with long strong somewhat tangled and stiffened setae.

Mxp1 with prominent 2-lobed endite; palp rather stout, bearing terminal and subterminal tufts of setae; exopod symmetrically rounded and setose distally; large epipod foliaceous, bilobed.

P1 rather stout, reaching (if extended) beyond antennal peduncle by at least length of fingers but normally folded on itself at mero-carpal joint at right angle or diagonal to axis of leg, with chela and carpus oriented toward midline. Outline of chela shaped like "bird-head with bent beak" (flamingo-like); palm inflated and smooth. Fingers curved and closing without gape; flexor surfaces concave; extensor surfaces of each finger convex, opposed edges uniformly offset, each armed with row of almost uniform, minute, erect, closely set setae; acute tip of each finger slightly spooned by curved setal row, that of dactylus with elongate teeth slanting distad and curving around its distal end; line of curved sensory setae mesial to each cutting edge; dactyl broadened at base for articulation with palm but uniformly narrowed throughout most of length to about ⅓ width of fixed finger. Carpus inflated, irregularly funnel-shaped, extensor surface bent almost at right angle near tapered proximal end articulating with merus, distal margin irregularly flared, cupped to conform with shape of palm in flexed or extended position, strong tooth on flexor surface with patch of setae on its external surface. Merus club-shaped but somewhat flattened, submarginally concave along flexor surface for reception of flexed carpus.

P2 slightly more slender than other legs, extending to near distal end of antennal pe-

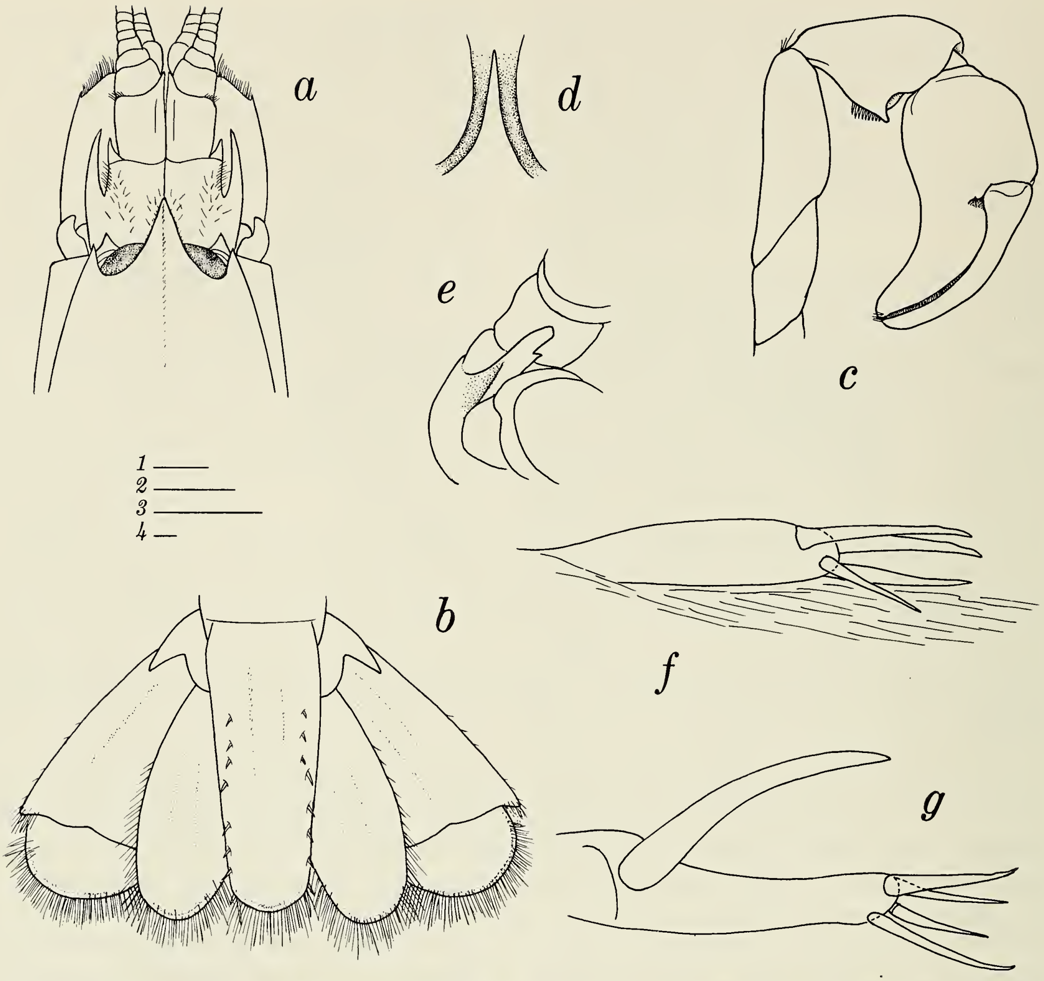

Fig. 2. *Opaepele loihi,* new genus and species. Female holotype: *a,* anterior region (dorsal view); *b,* telson and uropods (dorsal view); *c,* right first pereopod. Paratype female: spine between coxae of fifth pereopods, *d,* ventral view, *e,* oblique lateral view, left side. Paratype male: appendix masculina, *f* lateral, *g,* mesial. Scales: 1 (*a–b*); 2 (*c*); 3 (*d–e*) = 1.0 mm; 4 (*f–g*) = 0.1 mm.

duncle; chela and carpus about equal in length; fingers, slightly longer than palm, similar in size and shape, opposed edges without gape, each pectinate with single row of short spines directed obliquely distad and increasing slightly in size to end in noticeably stronger terminal spine crossing opposite member when closed.

P3–5 similar in structure but increasing in relative length from p3 to p5, p3 reaching well beyond tip of antennal peduncle by full length of propodus and dactylus; dactylus of each essentially equal in length and armed with 6 strong curved spines on flexor surface, distalmost strongest; propodi increasing in length from p3 to p5, that of p5 twice length that of p3, that of p4 intermediate in length, each armed with setae scattered along flexor surface, mainly on distal ½ and most dense on distal ⅓, prominent slender setae along extensor surface most prominent distally and in dense distal tuft; respective length of carpi, meri and ischia on p3, p4, p5 respectively similar in length, carpi dis-

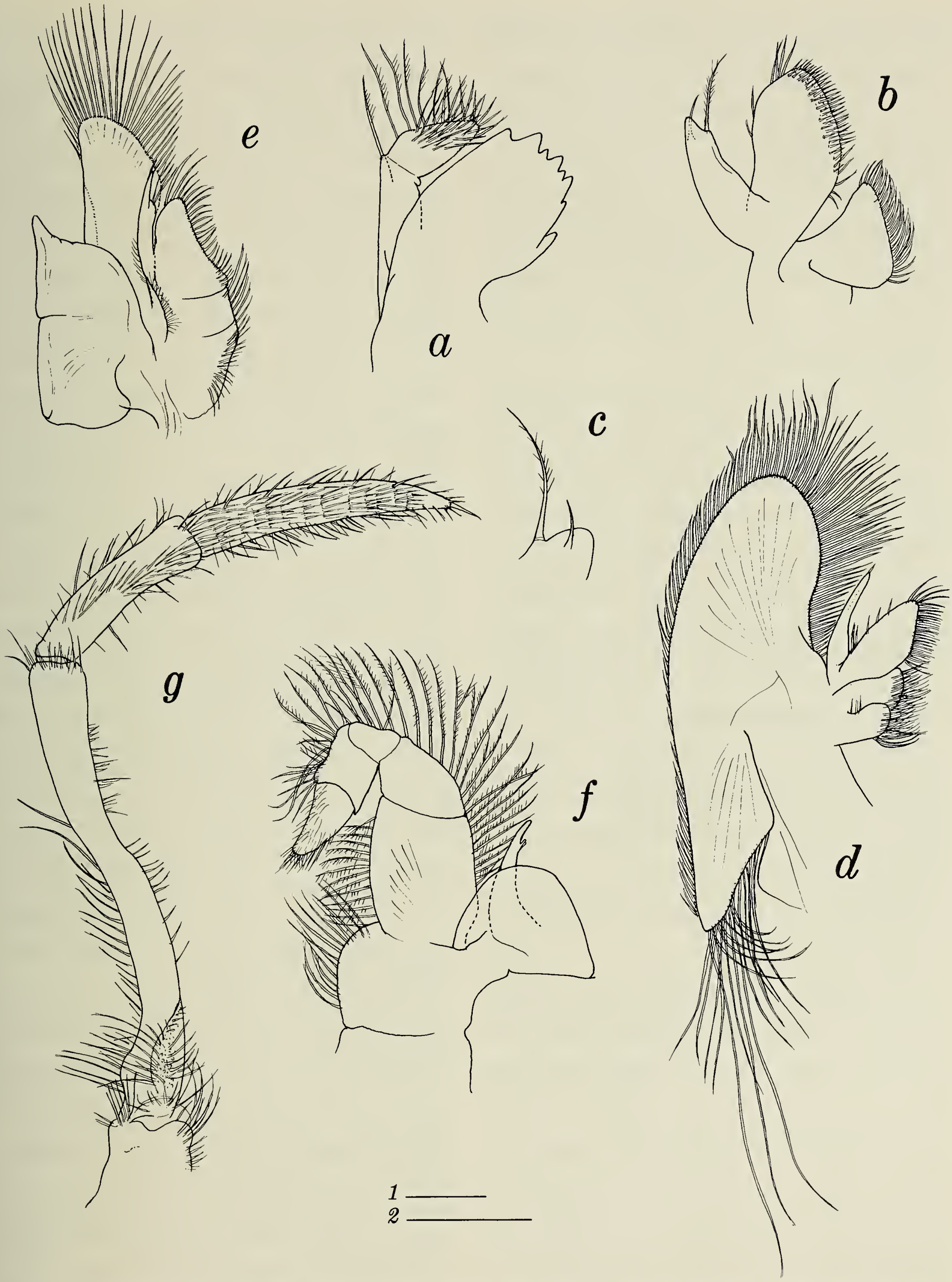

Fig. 3. *Opaepele loihi,* new genus and species, female paratype: *a,* right mandible; *b,* right first maxilla; *c,* same, tip of palp, internal view; *d,* right second maxilla; *e,* right first maxilliped (ventral view); *f,* right second maxilliped; *g,* third maxilliped, mesial oblique view. Scales: 1 (*d–g*); 2 (*a–c*) = 1 mm.

tally extended in dorsal "stop" overhanging base of propodi to prevent hyperextension.

Posterior thoracic somite (XIV) with portion of sternite posterior to base of fifth coxae smooth, slightly inclined anteriorly toward base of fifth coxae and shallowly concave mesially, that portion of sternite lying posteromesial to each fifth coxa drawn mesially from each side into flattened, weakly calcified median process, tapered, distally subtruncate, and bearing small acute spur anteriorly near base; process often obscured by appressed fifth coxae.

Pls 2–5 with appendix interna on mesial ramus slightly increasing in size from anterior to posterior in series, well developed coupling hooks only on appendix of pl 5. Small appendix masulina on mesial ramus of pl 2 in males bearing 4 terminal setae.

Uropods with both rami elongate oval, subequal in length, exceeding distal end of telson, outer ramus wider than inner ramus, with sinuous diaresis and movable spine beneath rather broad, asymmetrically acuminate distolateral tooth.

Measurements in mm.—Holotype ♀, cl 11.5, scl 10.1, al 21.8; allotype ♂, cl 13.6, scl 11.9, al 21.8; paratype ♀ 251450, cl 13.1, scl 11.3, al 23.0; paratype ♂ 251449, cl 7.9, scl 6.7, al 13.8.

Paratypes ♀, $n = 26$, scl 9.1–12.0, $\bar{X} = 10.3$. Paratypes ♂ that can be measured, n = 4 scl 6.8–9.3, $\bar{X} = 6.5$.

Color.—Color when collected, intensely orange (astaxanthin pigment). All preserved specimens examined basically white but variously mottled with deciduous orange to yellowish deposit, densest and most intense on segments of abdomen and tail fan, antennular and antennal peduncles, and proximal segments of their flagella, and as bands on pereopods, especially on carpi and adjacent portions of meri and propodi. This deposit is an accumulation of the iron oxyhydroxide particles that cover the summit of the seamount. Some of the particles are formed inorganically; others originate from the mat created by the growth and metabolism of iron-oxidizing bacteria (Karl et al. 1989, color figs.).

Etymology.—The specific name, a noun in apposition, refers to the seamount from which the species was collected.

Remarks.—Holthuis (1993) gave an ample discussion of the family makeup of the infraorder Caridea, with particular attention to recent treatments of family realignments within the group. Among the latter was recognition by Christoffersen (1989) of a dichotomy among the Bresiliidae that in his view justified elevation of one of these clusters to family status, the Alvinocarididae, which appear to be associated only with hydrothermal vents, cold brine and hydrocarbon seeps (Segonzac et al. 1993). The latter authors, in their exhaustive examination of trophic behavior, accepted this subdivision, acknowledging that many features of the group are similar to those of the genus *Bresilia* but noting absence of exopodites on thoracic appendages posterior to the maxillipeds and reduced eyestalks more or less attached to each other and adjacent regions. However, appealing, the action leaves the thus diminished Bresiliidae as a less unified group than is the family in its undivided state. Since neither of these choices is entirely satisfactory, we accept the more conservative approach of Holthuis (1993), following Chace (1992), in retaining the Bresiliidae as a unified though somewhat disparate assemblage.

Among species of bresiliids associated with hydrothermal vents and cold brine or hydrocarbon seeps are some shared morphological characters, but other features cut across these seemingly neat clusters in contrasting manners. *Opaepele loihi* is immediately recognizable as one of these bresiliids by virtue of the characteristic chelipeds shared by all members of the group. Within the group this species seems to occupy an intermediate position between those having a carinate carapace with well developed rostrum that reaches at least to mid-length of the antennal peduncle and antennal scale (including *Alvinocaris lusca* Williams & Chace, 1982, and *A. markensis, A. muricola, A. stactophila* Williams, 1988), and those in which the carapace is not carinate and the rostrum is absent (including *Rimicaris exoculata* Williams & Rona, 1986), or greatly reduced in length (including *Chorocaris chacei* (Williams & Rona, 1986) and *C. vandoverae* Martin & Hessler, 1990). Moreover, the rostral teeth of *O. loihi* are much smaller and less numerous than in species that have a long rostrum. Viewed dorsally, the lateral rostral margins of *O. loihi* are triangular in outline and merge imperceptibly with the orbital margins, but the rostrum of *C. vandoverae,* broadly oval in dorsal view, has margins that join each orbital margin at the site of an orbital prominence.

The anterior margins of the carapace in the sharply rostrate species bear antennal and pterygostomian spines, as does *O. loihi*; this set of species shares spinose margins on the posterolateral corners of the fourth and fifth abdominal segments. Those species with short rostrum or no rostrum lack these spines. It thus appears that there are two groups of species that have contrastingly spinose or non-spinose sectors on both carapace and abdomen, but this neat cleavage is compromised by other morphological features.

Alvinocaris lusca has a telson with sometimes sinuous terminal margin. This margin is convex in other species of the genus, though general breadth of the telson is much greater in *R. exoculata, C. chacei* and *C. vandoverae.*

The scaphognathite of Mx2 has a greatly expanded or anteriorly subtruncate anterior lobe in *Alvinocaris, Rimicaris* and *Chorocaris* species, whereas this element is more rounded and relatively narrower in *O. loihi.*

The relatively broad dactyls of P3–5 in *Chorocaris* species bear both marginal and plantar rows of setae on the flexor surface whereas those dactyls of the sharp spined *Alvinocaris* species have only a single row of spines on the flexor surface; between these two extremes, *R. exoculata* exhibits only marginal rows of spines on the flexor surface of its comparable rather broad dactyls.

Pl2–5 of *Rimicaris* and *Chorocaris* species bear obvious coupling hooks on the appendix internae of the inner ramus; *Alvinocaris* species apparently do not bear such hooks, and *Opaepele loihi* has them well developed only on the appendix internae of p5.

A feature possessed by all species discussed above that has not been emphasized in published descriptions is the process on thoracic sternite 5 (somite XIV) lodged between the coxae of p5. This process is much more prominent in *O. loihi* than among other genera and species in the family. There is considerable variety in development of the process, and to our knowledge only in *O. loihi* does it bear a small acute spur anteriorly near its base. The process is present on both males and females. Its function is unknown.

Bresiliid shrimps associated with hydrothermal vents, brine and hydrocarbon seeps are known from depths as great as 3660 m (Martin & Hessler 1990). Only two of these species are reported from depths less than 1000 m, *A. stactophila* from hydrocarbon seeps at 534 m in the Gulf of Mexico (Williams 1988), and the present species at 980 m.

A key to the 12 currently accepted genera of the family Bresiliidae, modified to accommodate *Opaepele* new genus, is adapted from the key given by Holthuis (1993).

1. Eyes with distinct dorsal spine on peduncle, overreaching base of cornea. Dactyl of first pereopod longer than fixed finger and with single large tooth on basal part of cutting edge . . . . *Encantada*
– Eyes without spine on peduncle. Dactyl of first pereopod, if longer than fixed finger, without single large tooth on cutting edge. 2

2\. Exopods on first two pairs of pereopods at most. Telson with three or more dorsolateral spines. First pereopod with ischium and merus distinct 3

– Exopods on all five pairs of pereopods. Telson with three or fewer dorsolateral spines. First pereopod with ischium and merus fused .. 8

3\. First two pairs of pereopods with exopods 4

– None of pereopods with exopods 5

4\. Articulation of palm and carpus of first pereopod normal, proximal end of palm articulated with distal end of carpus. Pleurobranch at base of fifth pereopod reduced. Arthrobranchs absent .... *Bresilia*

– Carpus of first pereopod articulating with chela at middle of propodus below base of dactyl, so that larger posterior part of propodus projects beyond this articulation. Pleurobranchs associated with all five pereopods. Arthrobranchs present at base of all pereopods, but that of pereopod 5 reduced .... *Agostocaris*

5\. Carapace with well developed rostrum bearing dorsal teeth and at least 1 ventral tooth (may be minute). Pterygostomian spine present. Eyes on separate movable stalks variously fused mesially .. 6

– Carapace with rostrum absent or visible as depressed angle of frontal margin, without any teeth. Pterygostomian spine absent. Eyes reduced, fused mesially 7

6\. Carapace with compressed rostrum, dorsal and ventral teeth clearly evident. Eyes on separate movable stalks narrowly fused mesially at base .... *Alvinocaris*

– Carapace with rostrum broadly triangular in dorsal view, dorsal teeth and ventral tooth minute (sometimes absent). Eyes on separate movable stalks rather broadly fused mesially .... *Opaepele*

7\. Carapace inflated, rostrum absent, frontal margin of carapace concave. Stylocerite, scaphocerite and antennular peduncle fitting tightly and forming an operculiform structure. Third maxilliped with 4 long and 2 short articles. .. *Rimicaris*

– Carapace not inflated, rostrum present, broadly rounded anteriorly. Antennules and antennae not forming an operculum. Third maxilliped with 3 long and 2 short articles .... *Chorocaris*

8\. Antennal scale narrowing distally, blade not overreaching distolateral tooth. Mandible without deep division between incisor and molar processes 9

– Antennal scale broad distally, blade overreaching distolateral tooth. Mandible with moderate to deep division between incisor and molar processes 10

9\. Mandible with palp. Last three pereopods pseudochelate, i.e., dactyl opposing distal spine of propodus, forming structure somewhat resembling a chela. Carapace without pterygostomian spine .... *Pseudocheles*

– Mandible without palp. Last three pereopods normal, not pseudochelate, no long distal spines on propodus. Carapace with pterygostomian spine present .... *Kirnasia*

10\. Rostrum reaching to end of antennular peduncle. Third abdominal somite forming gibbous cap over base of fourth somite. Third maxilliped with terminal article obliquely truncate distally. Dactyl of first pereopod not semicircular .... *Lucaya*

– Rostrum not reaching to end of antennular peduncle. Third abdominal somite not forming gibbous cap over base of fourth somite.

Terminal article of third maxilliped lanceolate. Dactyl of first pereopod semicircular 11

11. Carapace with supraorbital and branchiostegal spines present. Exopods on pereopods 1 to 3. Telson with 5 lateral and 5 distal spines .... *Tridiscias*

– Carapace without supraorbital and branchiostegal spines. Exopods on all pereopods. Telson with 2 or 3 lateral and 3 posterior spines .. *Discias*

Acknowledgments

We gratefully acknowledge the assistance of the Captain and crew of the R/V *Kila,* and DSRV *Pisces V* operations team, and the staff of the Hawaiian Undersea Research Laboratory. Craig Moyer collected the shrimps, and we appreciate his and David Karl's participation in studies at Loihi Seamount. This research was funded in part by a grant from the National Oceanic and Atmospheric Administration, project # R/OM-8, which is sponsored by the University of Hawaii Sea Grant College Program SOEST, under Institutional Grant No. NA89AA-D-SG063 from the NOAA Office of Sea Grant and by the NOAA-National Undersea Research Program, Department of Commerce. Our views expressed herein do not necessarily reflect the view of NOAA or any of its sub-agencies. We are indebted to Keiko Hiratsuka Moore for rendering the excellent illustrations, and to B. B. Collette, F. A. Chace, Jr., and R. B. Manning for critical review of the manuscript. This manuscript is Sea Grant publications UNIHI-SEAGRANT-JC-94-21 and contribution No. 3870 from the University of Hawaii School of Ocean and Earth Science and Technology.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(2):238–246. 1995.

Remarks on the taxonomy of *Sudanonautes chavanesii* (A. Milne-Edwards, 1886) (Brachyura: Potamoidea: Potamonautidae) from Central Africa

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Abstract.—The fresh-water crab *Sudanonautes chavanesii* (A. Milne-Edwards, 1886) is redescribed from new material which is compared to previous descriptions of the male type from Gabon. The gonopods and mandibles of a male from Cameroon are described and illustrated for the first time. New records of specimens from several museum collections are presented. The species is recognized by a combination of characters of the carapace, chelipeds, mandibles, and gonopod 1. The range of *S. chavanesii* has been found to be restricted to an area from south Cameroon to Gabon; the species does not occur in West Africa (from Senegal to Nigeria), as previously thought.

Sudanonautes chavanesii (A. Milne-Edwards, 1886), a fresh-water crab from Central Africa, has been recognized as a valid species by a number of authors (A. Milne-Edwards 1887, Rathbun 1905, Balss 1929, Chace 1942, Capart 1954). However, more recent authors (Bott 1955, 1959; Monod 1977) have considered this taxon to be a subspecies of *Sudanonautes* (*Sudanonautes*) *africanus* (A. Milne-Edwards, 1869). Data presented here indicate that *S. chavanesii* is indeed a valid species. Furthermore, no characters were found to support the inclusion of *S. chavanesii* in any subgenus, as has been suggested by other workers (*Parathelphusa* H. Milne-Edwards, 1854 (A. Milne-Edwards 1887, Rathbun 1905), *Potamonautes* MacLeay, 1838 (Ortmann 1897), or *Sudanonautes* Bott, 1955 (Bott 1955, 1959; Monod 1977, 1980)).

Bott's (1955) description of *S.* (*S.*) *africanus chavanesii* consisted of a one-line diagnosis apparently made without reference to type material, and gonopod 1 was not described. Published figures of gonopod 1 of the type specimen of this species (Capart 1954) indicate a short, straight terminal segment. A series of adult males from Cameroon examined in the present study indicate a different structure for gonopod 1: the terminal segment is long, slim, and curves outward. It is likely that gonopod 1 of the type specimen from Gabon is unusual. Findings are presented here based upon the structure of the entire adult male gonopods of *S. chavanesii* from Cameroon, together with other characters of the mandibles, carapace and chelipeds.

Four dimensions of the carapace were recorded using digital calipers as follows: carapace length (CL) measured along median line, carapace width (CW) at widest point, measured beneath the large tooth on the anterolateral margin, carapace height (CH) maximum height of cephalothorax, and front width (FW) width of front measured along anterior margin. Carapace proportions were calculated according to carapace length. These data were pooled and used for descriptions of growth. Statistical comparisons between species were made between sexually mature adults only. The distribution of *S. chavanesii* described here is based on data from direct examination of specimens, since literature records are not reliable. The following abbreviations are used: MNHN = Muséum national d'Histoire naturelle, Paris; USNM = National Museum of National History, Smithsonian Institution, Washington, DC, U.S.A.; NHM = Natural History Museum, London, U.K.; RCM = Royal Congo Museum, Tervuren, Belgium; IFAN = Institute Fondamental d'Afrique Noire, Dakar, Senegal; NMU = Northern Michigan University, U.S.A., ♂ = male, ♀ = female.

Sudanonautes chavanesii
(A. Milne-Edwards, 1886)
(Figs. 1–3)

Thelphusa chavanesii A. Milne-Edwards, 1886:150.

Parathelphusa chavanesii.—A. Milne-Edwards, 1887:145–146, pl. 7, fig. 3a, b.—Rathbun, 1900:285.

Potamon (*Potamonautes*) *chavanesi.*—Ortmann, 1897:305, 309.

Potamon (*Parathelphusa*) *chavanesii.*—Rathbun, 1905:232, pl. 11, fig. 1.–Balss, 1929:127.—Balss, 1936:166.

Potamon chavanesi.—Chace, 1942:209.—Capart, 1954:829–830, figs. 7, 11.

Sudanonautes (*Sudanonautes*) *africanus chavanesii.*—Bott, 1955:299, fig. 97.—Bott, 1959:1005.—Monod, 1977:1217 (not figs. 103–107).—Monod, 1980:384.

Material.—Gabon: Adult ♂, type (CW 54, CL 39 mm), MNHN B5079, vicinity of Franceville, on the river Alima, Mission de Brazza. Adult ♂ (CW 54 mm) cotype, USNM 30034, La de Franceville, Mission de Brazza. Cameroon: One ♀, MNHN B5081, Ohana, Besa, Nyong. One ♂ (CW 46 mm), MNHN B5077, Mt. M. Banbarto, river Noun. One ♂, NHM 1936.2.27.1–3, Batouri District. Two specimens, (RCM) 51.554, 1 ♀ mature (CW 70 mm), 1 ♂ (CW 48 mm), Soari, 26 Sep 1964, Thijs van den Audenaerde. RCM 53.282, 1 ♂ (CW 43 mm), Belabo, 16 May 1970, Thijs van den Audenaerde. RCM 53.290, 1 ♀ adult, Ebogo, 24 May 1970, Thijs van den Audenaerde. Three adult ♂ (CW 72.7, 69.6, 59.1 mm), RCM 53.291, Ebogo, 21 May 1970, Thijs van den Audenaerde.

Type locality.—Vicinity of Franceville, on the river Alima, Gabon.

Diagnosis.—Epibranchial tooth large, pointed outward, set back behind mid-point of postfrontal crest, positioned in line with widest point of carapace; distance between epibranchial tooth and intermediate tooth twice the distance between intermediate and exo-orbital teeth. Postfrontal crest spanning entire carapace, crest curving sharply backward before meeting epibranchial tooth; distinct notch in crest behind exo-orbital tooth; anterolateral margin smooth posterior to epibranchial tooth. Semi-circular, urogastric, cardiac, transverse branchial grooves very deep. Exo-orbital, intermediate teeth large, sharp, pointed forward; epibranchial tooth large, pointed outward. Vertical suture on flank forming y-shaped depression beneath intermediate tooth (Fig. 2b). Carapace very flat (CH/CL = 0.41). Mandibular palp 2-segmented; terminal segment single, undivided, with small hard, hair-fringed flap at junction between segments (Fig. 2a–b). Terminal segment of gonopod 1 thin and needle-like, subterminal segment gonopod 1 slim (Fig. 2d–f). Dactylus of major chelipid arched, forming oval interspace when closed; 2–3 large fused teeth in proximal regions of both fingers of the cheliped, rest of cutting edges lined with rows of rounded teeth (Fig. 1e–f).

Redescription.—Carapace (Fig. 1a, b) ovoid, widest in anterior third (CW/CL 1.37), very flat (CH/CL 0.42), semi-circular; urogastric, cardiac, transverse branchial grooves very deep, regions covered with raised circular blisters; cervical grooves present but weak. Branchial regions of carapace with fields of faint raised short lines. Front deeply bilobed, anterior margin indented, curving down, relatively narrow, less than ⅓ carapace width (FW/CW = 0.30). Postfrontal crest smooth, spanning entire carapace, straight part consisting of fused epigastric, postorbital crests, then curving

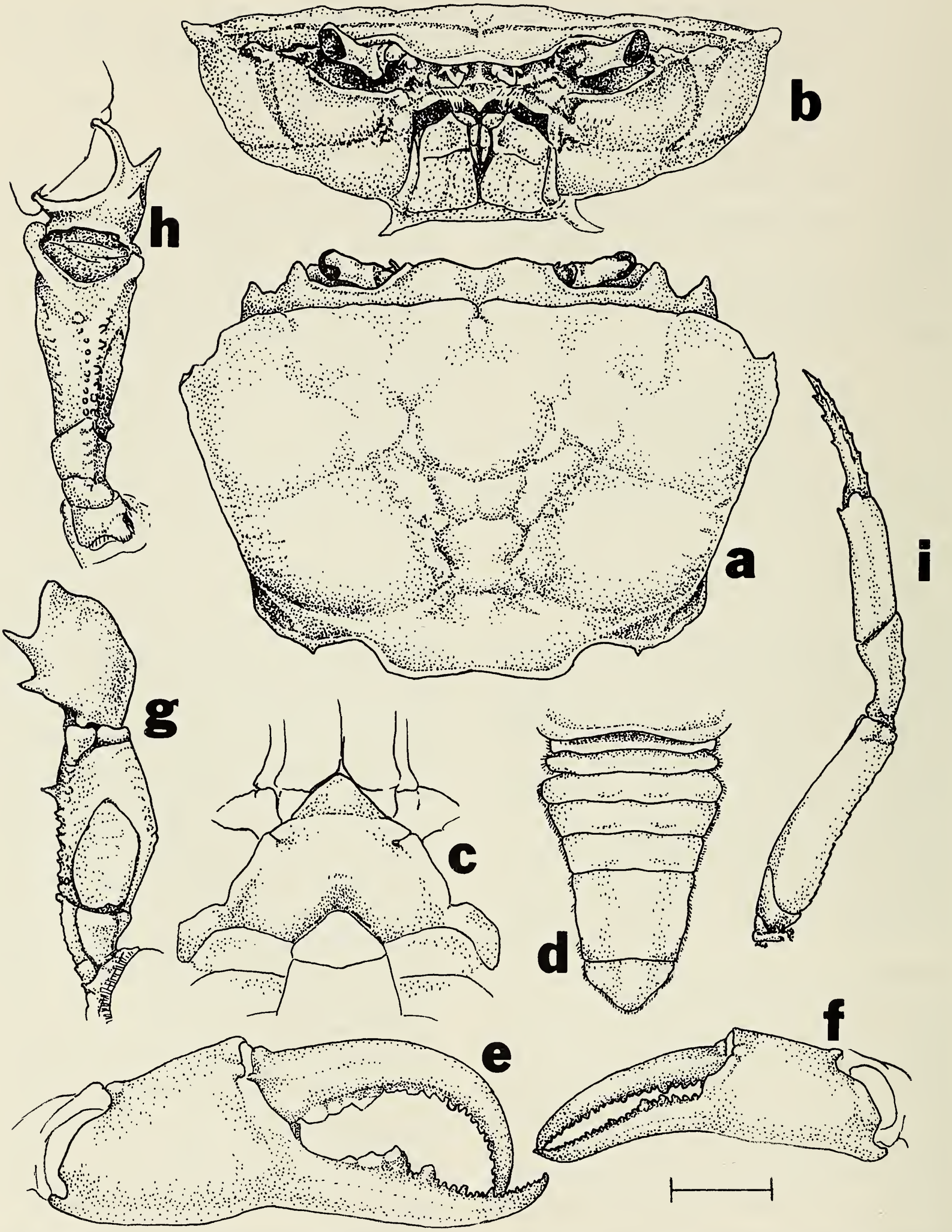

Fig. 1. *Sudanonautes chavanesii* (A. Milne-Edwards, 1886), adult male (CW 72.7 mm) from Ebogo, Cameroon (RCM 53.291). a, carapace, dorsal aspect (left epibranchial tooth broken); b, carapace, frontal aspect; c, sternum; d, abdomen; e, right cheliped, frontal view; f, left cheliped, frontal view; g, carpus, and merus of right cheliped, superior view; h, carpus, and merus of right cheliped, ventral view; i, left periopod 2. Scale bar equals 20 mm (a–d), and 16 mm (e–i).

sharply backward behind intermediate teeth to meet anterolateral margins at the epibranchial teeth. Distinct notches in crest behind exo-orbital teeth; anterolateral margin smooth posterior to epibranchial tooth. Exo-orbital, intermediate teeth large, sharp, pointed forward. Epibranchial tooth large, pointed outward, set back behind mid-point of postfrontal crest, positioned in line with widest point of carapace; distance between epibranchial tooth and intermediate tooth twice the distance between intermediate and exo-orbital teeth.

Flanks mostly smooth, with faint granules in suborbital regions. Each flank with 2 sutures, 1 longitudinal, 1 vertical, dividing flank into 3 parts (Fig. 1b). Longitudinal suture dividing suborbital, subhepatic regions from pterygostomial region, beginning medially at lower margin of orbit, curving backward across flank. Short vertical suture beneath intermediate tooth dividing suborbital region from subhepatic region, suture forming y-shaped depression beneath intermediate tooth (Fig. 1b); stem of y-shape meeting longitudinal suture. First transverse groove on sternum (between sternal segments 2 and 3) complete; second groove (between sternal segments 3 and 4) consisting of 2 small notches at sides of sternum (Fig. 1c). Third maxillipeds filling entire oral field, except for transversely oval efferent respiratory openings at superior lateral corners; long flagellum on exopod of third maxilliped (Fig. 2c); ishium of third maxilliped smooth, with clear vertical groove (Fig. 2c). Mandibular palp 2-segmented; terminal segment single, undivided, with small hard, hair-fringed flap at junction between segments (Fig. 2a–b). Segments 1–6 of abdomen four sided, last segment triangular, sides indented, rounded at distal margin (Fig. 1d); segment 3 broadest, segments 4–7 tapering inwards (Fig. 1d).

Chelipeds (Fig. 1e–h) unequal, right longer, higher than left. Dactylus of right cheliped long, arched; palm of propodus swollen; proximal region of fingers of digits of right cheliped each with 2–3 large fused teeth, forming oval interspace when closed; rest of cutting edges of fingers lined with smaller cheliped small to very small, fingers forming narrow interspace when shut. Inferior margins of merus with rows of small teeth, cluster of granules surrounding larger pointed tooth at distal end. Inner margin of carpus of cheliped with 2 large, slender, pointed teeth, second half size of first (Fig. 1g–h). Dactylus of left cheliped not arched, otherwise similar to right, but smaller in all respects (Fig. 1f). Walking legs 2–5 (pereiopods = P) slender (Fig. 1i), P4 longest, P5 shortest. Posterior margin of propodus of P2–5 smooth or slightly serrated, dactyli of P2–5 tapering to point, each bearing 4 rows of downward-pointing sharp bristles; dactylus of P5 shortest of the 4 legs (Fig. 1i).

Gonopod 1 with very slender terminal segment, long (⅓ as long as penultimate segment), curving strongly outward along entire length, tapering to pointed tip, longitudinal groove visible from caudal and superior views (Fig. 2d–e), not visible from cephalic view (Fig. 2f). Subterminal segment of gonopod 1 very slim (Fig. 2d, f), with raised flap extending halfway across segment, forming roof of chamber for gonopod 2; subterminal segment beneath flap forming lower floor of chamber for gonopod 2 (Fig. 2f). Gonopod 2 (Fig. 2g) shorter than gonopod 1 (reaching only to junction between last 2 segments of gonopod 1). Terminal segment of gonopod 2 extremely short, only $1/15$ as long as subterminal segment, sides folded inwards to form spoon-shape, tip rounded. Subterminal segment gonopod 2 widest at base, then tapering sharply inward, forming long, thin, pointed, upright process which supports short terminal segment; rounded collar at junction between terminal segment and subterminal segment.

Adult female.—Chelipeds same proportions as male of same size, right cheliped enlarged, measuring longer and higher than the left cheliped. Mature female abdomen very wide reaching coxae of pereiopods 2–

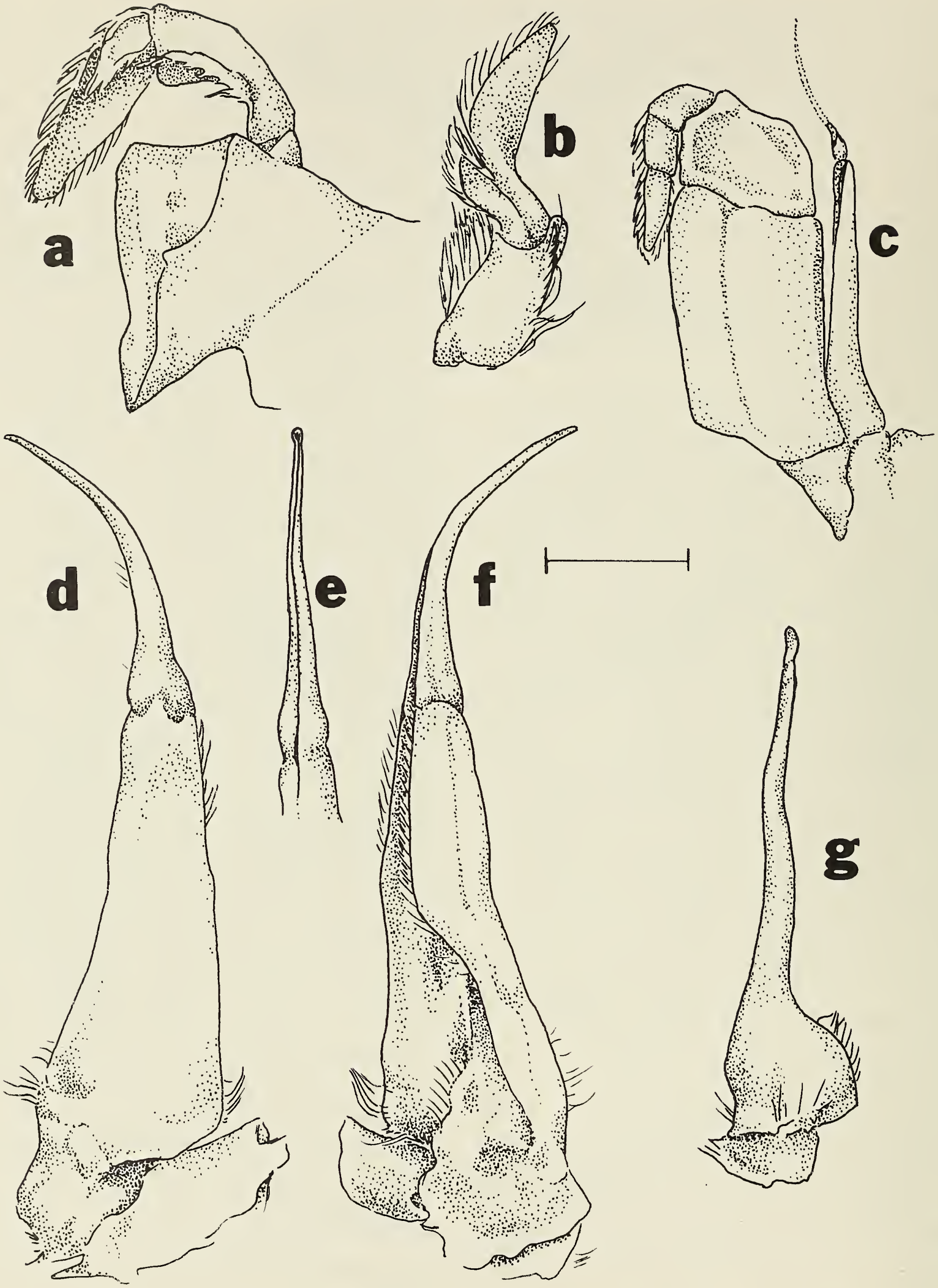

Fig. 2. *Sudanonautes chavanesii* (A. Milne-Edwards, 1886), adult male (CW 72.7 mm) from Ebogo, Cameroon (RCM 53.291). a, left mandible, anterior view; b, left mandible superior view; c, left third maxilliped (flagellum broken in this specimen); d, left gonopod 1, caudal view; e, terminal segment of left gonopod 1, superior view; f, left gonopod 1, cephalic view; g, left gonopod 2, caudal view. Scale bar equals 3 mm (a, b, d, e, f, g), and 7 mm (c).

5. Segments of female abdomen rectangular, wider than long, distal segments longest and widest; abdomen widest at groove separating segments 4, 5; segment 6, telson together forming near semicircle.

Growth (Fig. 3a, b).—Sexual maturity judged by development of female abdomen: abdomen of mature females overlapping bases of coxae of walking legs, pleopods broad, hair-fringed. Pubertal molt, from pubertal stage to sexual maturity, occurring between CW 35–45 mm. Largest known specimen (male from Cameroon) CW 81 mm. Dimensions of carapace varying with age (Fig. 3a). Relative width of carapace (CW/CL), relative height of carapace (CH/CL), and relative width of the frontal margin (FW/CL) not changing with age: proportions of adults remaining constant with age; proportions of adults not significantly different ($P > 0.05$) from those of juvenile and pubescent animals (Fig. 3b). Right and left chelipeds of juveniles (CW <35 mm) even sized, palms not inflated, cutting edges leaving no gap when closed.

Distribution.—Coastal rain forest from south Cameroon to Gabon. It is likely that *S. chavanesii* is also present in Equatorial Guinea. Bott (1955) reported *S. chavanesii* from a wider region of Central Africa (from Cameroon to Zaire). However, there are no confirmed records of this species in the Central African Republic, the Republic of the Congo, or in Zaire. Bott (1959) and Monod (1977, 1980) extended the range of *S. chavanesii* further to include West Africa, from Guinea all the way to Zaire. However, there is reason to doubt these records. Bott (1959) reported *S. chavanesii* from Guinea and Mali. Monod (1977) illustrated these same specimens, from ravin de Sokonafing, near Bamako, Mali (Monod 1977, figs. 103, 104, 106, 107), and from Fenaria, Guinea (Monod 1977, fig. 105). This same material, deposited in IFAN, from Dabola, chutes de Tinkasso, Guinea (Kindia, 5 Apr 1954, A. Villiers), and from Mali (Ravin de Sokonafing, Bamako, May 1945), were all identified here as *Liberonautes latidactylus* (De Man, 1903). There are, therefore, no confirmed records of *S. chavanesii* in any country in West Africa (i.e., from Senegal to Nigeria).

Remarks.—Bott (1955) established the genus *Sudanonautes* (type species by original designation, *Thelphusa africana* A. Milne-Edwards, 1869), and recognized two subgenera, *Sudanonautes* s.s., and *Convexonautes* Bott, 1955 (type species by original designation, *Thelphusa aubryi* H. Milne-Edwards, 1853). *Sudanonautes chavanesii* was one of three subspecies of *Sudanonautes* (*Sudanonautes*) *africanus,* viz. *S.* (*S.*) *a. africanus* (A. Milne-Edwards, 1869), *S.* (*S.*) *a. chaperi* (A. Milne-Edwards, 1887), and *S.* (*S.*) *a. chavanesii* (A. Milne-Edwards, 1886) recognized by Bott (1955, 1959) and Monod (1977, 1980). Cumberlidge (1985) subsequently referred *S.* (*S.*) *a. chaperi* to the genus *Liberonautes* Bott, 1955. Data presented here indicate that *Sudanonautes africanus chavanesii* (A. Milne-Edwards, 1886) should also be regarded as a valid species.

Identification of *S. chavanesii* depends on considering the characters of gonopod 1 of *S. chavanesii* (Fig. 2d-f) in conjunction with other characters of the carapace (Fig. 1a–b), sternum (Fig. 1c), chelipeds (Fig. 1e–h), and mandibles (Fig. 2a–b). *Sudanonautes chavanesii* is most likely to be confused with other large species occurring in the rain forests of Central Africa such as *S. africanus, S. faradjensis* (Rathbun, 1921), and *S. aubryi* (A. Milne-Edwards, 1853), all of which possess a gonopod 1 with a similar shaped terminal segment: slim, tapering, and curving outward.

Sudanonautes chavanesii can be distinguished from *S. africanus* by the position of the postfrontal crest and the shape of the epibranchial teeth. In *S. chavanesii* the lateral ends of the postfrontal crest curve sharply backward before meeting the epibranchial teeth which are set back posterior to the mid groove of the crest (Fig. 1a),

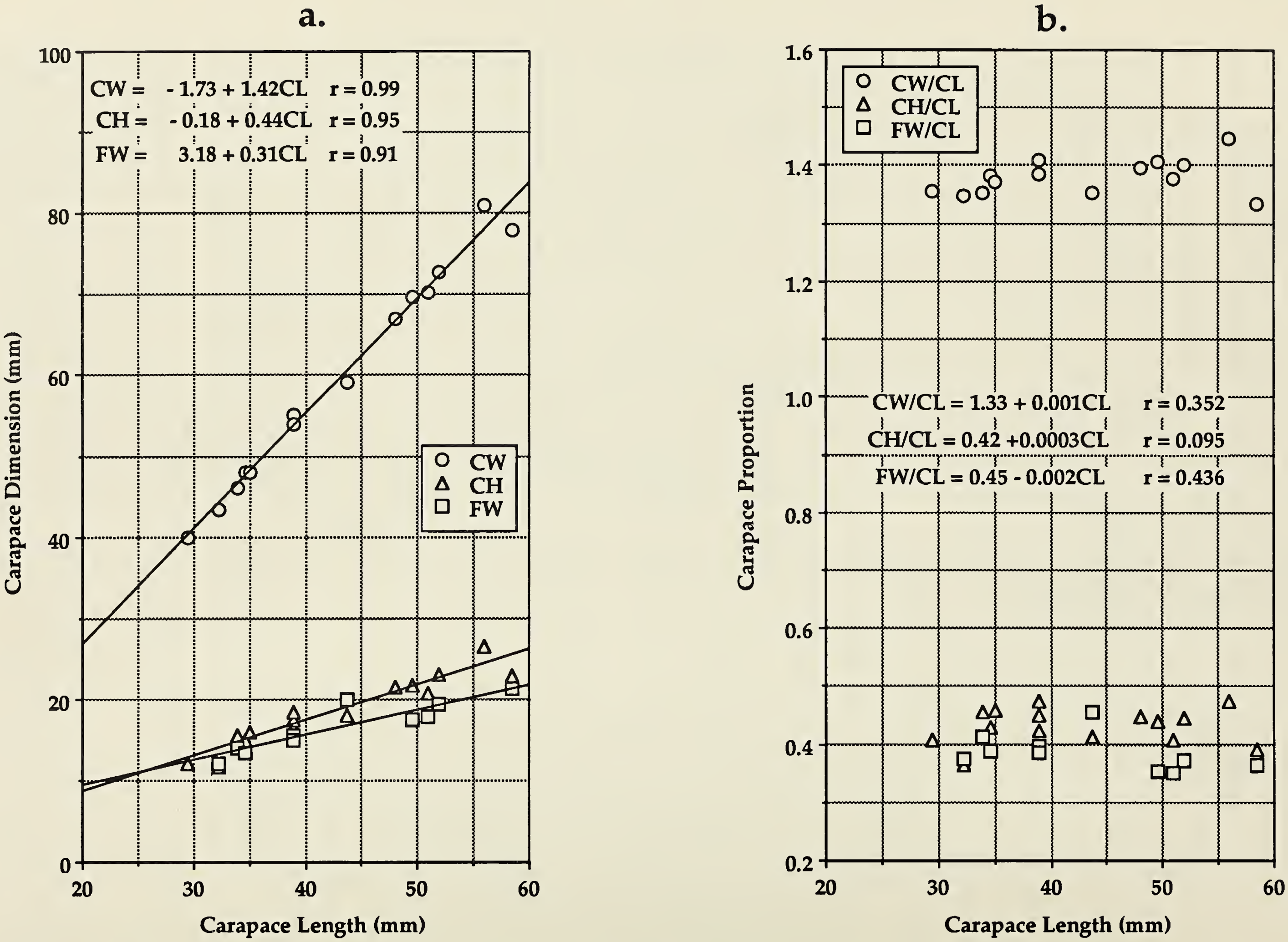

Fig. 3. Comparisons of 14 specimens of *Sudanonautes chavanesii* (A. Milne-Edwards, 1886). a, dimensions of the carapace (CW, CH, FW) compared to body size (CL); *r* values (CW, CH at $df = 13$, FW at $df = 9$) indicate a highly significant correlation ($P < 0.001$) between size classes. b, relative proportions of carapace width (CW/CL), carapace height (CH/CL), and front width (FW/CL), compared to body size (CL); *r* values (CW, CH at $df = 13$, FW at $df = 9$) indicate no significant correlation ($P > 0.05$) between size classes.

whereas in *S. africanus* the lateral ends of the crest curve forward to meet the epibranchial teeth in line with the mid groove of the crest. In *S. chavanesii* the epibranchial tooth is large, sharp, and pointed outward, and the distance between the epibranchial tooth and intermediate tooth is twice the distance between the intermediate and exo-orbital teeth (Fig. 1a, b). In *S. africanus* the epibranchial tooth is small, blunt, pointed forward, and positioned in line with the mid groove of the crest, so that the distance between the epibranchial tooth and intermediate tooth is the same as the distance between the intermediate and exo-orbital teeth. Finally, in *S. chavanesii* the vertical suture on the flank forms a y-shaped depression beneath the intermediate tooth (Fig. 1b), whereas in *S. africanus* the vertical suture on the flank is simple.

Sudanonautes chavanesii can be distinguished from *S. faradjensis* by examination of the anterolateral margin behind the epibranchial tooth: that of *S. chavanesii* is smooth, whereas in *S. faradjensis* there is a row of sharp teeth. In addition, the dactylus of the major cheliped of *S. chavanesii* is arched, forming a single oval interspace when closed, whereas that of *S. faradjensis* is straight, not arched, and forms two interspaces when closed.

Sudanonautes chavanesii can be distinguished from *S. aubryi* by examination of the carapace: that of *S. chavanesii* is significantly flatter ($P < 0.001$) than that of *S. aubryi* (CH/CL *S. chavanesii* = 0.41, *S. aubryi* = 0.52), and has patches of raised blisters, while that of *S. aubryi* is completely smooth. The postfrontal crest of *S. chavanesii* meets the anterolateral margin at the epibranchial tooth, whereas that of *S. aubryi* meets the anterolateral margin behind the epibranchial tooth. In addition, the dactylus of the major cheliped of *S. chavenesii* is arched, with large, fused teeth (Fig. 1e); these features are lacking in *S. aubryi*.

Finally, there is a small flap on the mandibular palp at the junction between the two segments (Fig. 2a–b) of *S. chavanesii* which is not present in *S. africanus, S. faradjensis* and *S. aubryi*.

Acknowledgments

The following people are thanked for hosting visits: Paul Clark (NHM); Dr. R. Roy (IFAN); Drs. D. Guinot and J. Forest (MNHN); and Dr. R. Manning (USNM). Dr. R. Joqué (RCM) is thanked for his kind hospitality and for loaning material. I am especially grateful to artist Anne C. Michelsen (NMU), for all of the illustrations used in this paper. Part of this work was supported by a Faculty Grant from NMU. Two anonymous referees and Dr. Rafael Lemaitre, Associate Editor of the Proceedings, are thanked for their helpful suggestions to improve the manuscript.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(2):247–253. 1995.

First zoea of *Dissodactylus glasselli* Rioja and new range and host records for species of *Dissodactylus* (Brachyura: Pinnotheridae), with a discussion of host-symbiont biogeography

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Abstract.—*Dissodactylus glasselli* Rioja, is a small pinnotherid crab living as an ectosymbiont on sand dollars of the American Pacific coast. The first zoea of *D. glasselli* is described in detail and compared to that of other species within the *Dissodactylus* complex. Morphometrically the larva differs from those of the sympatric species *D. nitidus* Smith, *D. lockingtoni* Glassell, and *D. xantusi* Glassell, in the relative length of carapace spines. The zoea of *D. glasselli* most closely resembles that of *D. mellitae* (Rathbun) from the Atlantic, the two being considered trans-isthmian geminate species. A geographic range extension of *Dissodactylus lockingtoni* is reported beyond the Gulf of California to Costa Rica, where it occurs on *Mellita kanakoffi* Durham, not reported previously as a host species. The range of *Dissodactylus glasselli* is extended southward from El Salvador to Costa Rica and it is reported for the first time on the hosts *M. kanakoffi* and *Encope wetmorei* Clark. *Dissodactylus mellitae* was found on the new host *Encope aberans* Martens in the Gulf of Mexico.

Members of the *Dissodactylus* complex, comprising the genera *Dissodactylus* Smith, 1870 and *Clypeasterophilus* Campos & Griffith, 1990, are known as symbionts of echinoids in tropical and subtropical regions of the Americas (Schmitt et al. 1973). *Dissodactylus* is represented by four Atlantic and five Pacific species, and *Clypeasterophilus* by three and one species, respectively. Larval development is known for five Atlantic species (Pohle & Telford 1981b, 1983; Pohle 1984, Marques & Pohle 1995a, 1995b), and for Pacific species, larvae of *D. lockingtoni* Glassell, 1935, *D. xantusi* Glassell, 1936 and *D. nitidus* Smith, 1870 have been described (Pohle 1989, 1994). *Dissodactylus glasselli* overlaps geographically with the latter three sympatric species in the southern parts of the Gulf of California. The first zoea of *D. glasselli* Rioja, 1944 is described in this paper and compared to that of other species within the *Dissodactylus* complex. New sand dollar hosts are reported for *Dissodactylus glasselli, D. lockingtoni* and *D. mellitae* (Rathbun, 1900), and the occurrence of *D. lockingtoni* has been established outside the Gulf of California.

Materials and Methods

During June to July 1992, first zoeae of *Dissodactylus glasselli* were obtained from a number of females collected along the Pacific coast of Costa Rica. Individual rearing techniques used to culture larvae, although successful for other species of *Dissodactylus* and *Clypeasterophilus* (Pohle & Telford 1981b, Pohle 1984, 1989; Marques & Pohle 1995a, 1995b), were not successful in this case. None of the larvae developed beyond

Table 1.—Dimensions (mm) of zoea 1 structures of *Dissodactylus glasselli* Rioja and other selected species.

Species	Spine length				Antennal length	Carapace length
	Rostral	Dorsal	Lateral	Rostrodorsal		
Dissodactylus glasselli	0.35 ± 0.02 (0.32–0.37)	0.20 ± 0.02 (0.17–0.22)	0.20 ± 0.01 (0.17–0.22)	0.88 ± 0.04 (0.81–0.94)	0.10 ± 0.01 (0.09–0.10)	0.37 ± 0.01 (0.36–0.39)
D. lockingtoni[1]	0.26 ± 0.01	0.16 ± 0.01	0.14 ± 0.01	0.71 ± 0.03	0.10 ± 0.01	0.35 ± 0.01
D. nitidus[2]	0.24 ± 0.02	0.12 ± 0.01	0.12 ± 0.01	0.68 ± 0.02	0.10 ± 0.01	0.36 ± 0.01
D. xantusi[1]	0.26 ± 0.01	0.12 ± 0.01	0.13 ± 0.01	0.65 ± 0.02	0.08 ± 0.01	0.37 ± 0.01
D. mellitae[3]	0.30 ± 0.02	0.21 ± 0.01	0.16 ± 0.02	0.71 ± 0.01	0.11 ± 0.01	0.32 ± 0.01
D. mellitae[2]	0.30 ± 0.02	0.24 ± 0.01	0.20 ± 0.01	0.87 ± 0.02	0.10 ± 0.01	0.36 ± 0.01

Note: Values are given as the mean ± standard deviation, with range in parentheses for *D. glasselli.*
[1] From Pohle (1994); [2] from Pohle (1989); [3] from Marques & Pohle (1995b).

the first zoea. Selection of the most lively larvae, addition of antibiotics and the use of alternate food organisms, such as oyster larvae and fertilized sand dollar eggs, did not change the outcome.

Ten specimens were measured and used for morphological description. The description of setae follows Pohle & Telford (1981a), but here includes only analysis by light microscopy, using an Olympus BH-2 microscope with Nomarski Differential Interference Contrast and camera lucida. Measurements follow Pohle & Telford (1981a). Specimens of the first zoeal stage have been deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Results

Eggs of *Dissodactylus glasselli* were incubated by crabs for 11–13 days at 32°C. Larval morphometrics are given in Table 1.

First Zoea (Fig. 1)

Carapace (Fig. 1A).—With long rostral, dorsal and lateral spines. Thickened posterior and ventral margin lacking setae. Eyes sessile. Two simple setae flanking dorsal spine. Chromatophores on each side of carapace posterior to eyes, on ventrolateral margin and base of antennules; single chromatophores located posterior to base of dorsal spine, frontally between eyes and dorsally on gut; abdominal somites 1–5 with paired melanophores; single chromatophore on labrum, mandibles and basipodites of first maxillipeds.

Abdomen (Fig. 1B).—Five somites and telson. Somite 1 naked, somites 2 and 3 with pair of dorsolateral spines; somites 2–5 with pair of simple setae dorsally.

Telson (Fig. 1C).—Bifurcated, with proximal minute furcal spine. Furcal shafts spinulous, except tips. Furcal arch with 3 plumodenticulate setae on either side of deep median depression. Denticulettes present in clusters on ventral and dorsal surface.

Antennule (Fig. 1D).—Unsegmented, smooth, conical. Terminally with 1 short and 2 long aesthetascs.

Antenna (Fig. 1E).—Elongate, uniramous. Tapered protopodite with 2 rows of spinules distally.

Maxillule (Fig. 1F).—Coxal endite bearing 4 graded plumodenticulate setae and proximal microtrichia. Basal endite with proximal microtrichia, 3 terminal plumodenticulate cuspidate setae and 2 subterminal plumodenticulate setae. Two-segmented endopodite with 4 terminal plumodenticulate setae.

Maxilla (Fig. 1G).—Coxal endite single-lobed, inflated, with semicircle of 4 plumose setae flanked by single proboscate (sensu Pohle & Telford 1981a) seta; scattered microtrichia. Basal endite with 4 plumodenticulate setae on either side of slight indentation; microtrichia present. Endopodite unsegmented, with 3 terminal plumodenticulate setae and marginal microtrichia. Scaphognathite with 4 densely plumose setae marginally, tapering to sharp terminal process bearing microtrichia.

Maxilliped 1 (Fig. 1H).—Coxopodite with a developing seta. Basipodite with 10 plumodenticulate setae arranged in four groups of 2, 2, 3, 3 proximally to distally. Five segmented endopodite with 2, 2, 1, 2, 4 + 1 setae proximally to distally; all plumodenticulate except single simple seta on segments 1, 2, and 5. Exopodite with 4 long natatory plumose setae.

Maxilliped 2 (Fig. 1I).—Coxopodite naked. Basipodite with 4 plumodenticulate setae. Endopodite 2-segmented, first segment naked, distal segment with 4–5 plumodenticulate setae. Exopodite with 4 long natatory plumose setae.

Maxilliped 3.—Not discernible.

Pereiopods.—May be present as minute buds.

Pleopods.—Absent.

Range Extension and New Hosts for Species of *Dissodactylus*

Dissodactylus lockingtoni Glassell, 1935

Dissodactylus lockingtoni Glassell, 1935: 100, pl. 27, figs. 5–8, text-fig. 68 (type locality, Punta Peñasco, Sonora, Mexico).—Griffith 1987a: 401, 413, 419, figs. 8B, 9B, 11B, 13B, 14B; 1987b:2292–2310.

D. smithi Rioja, 1944: 149, figs. 1–6, 11–15 (type locality, Playa San Benito, Chiapas, 50 km from Tapachula, Mexico).

Material examined.—Puntarenas Beach, Puntarenas, Costa Rica, 9°56′N, 84°48′W; 2 Jul 1992, free-diving 0.5–1 m, sand bottom, 1 male cw 3.6 mm on *Mellita kanakoffi* Durham, 1961.—Puntarenas Beach, Puntarenas, Costa Rica, 9°56′N, 84°48′W; 18 Jul 1992, low intertidal, sand bottom, 3 females cw 5.4, 5.1 and 4.8 mm on *M. kanakoffi.*—Puntarenas Beach, Puntarenas, Costa Rica, 9°56′N, 84°48′W; 7 Aug 1992, intertidal, low tide 0 m, sand bottom, 4 females cw 4.6, 5.0, 5.1 and 5.3 mm on *M. kanakoffi.*

Previous range records.—Punta Peñasco, Sonora, Mexico; "San Felipe, Gulf of California and Punta Peñasco . . . undoubtedly ranges throughout the Gulf of California" (Glassell 1935). Campo et pescador, North of San Felipe (31°04′N, 114°50′W) (Campos et al. 1992). La Choya Bay, Punta Peñasco, Sonora, Mexico (Pohle 1994).

Previous host record.—*Encope californica* Verrill, 1870; *E. grandis* Agassiz, 1841; *E. micropora* Agassiz, 1841; *Mellita longifissa* Michelin, 1858 (Glassell 1935).

Remarks.—The host *Encope californica* Verril listed by Glassell (1935) is presently considered a junior synonym of *E. micropora* (cf. Brusca 1980) but both are probably separate species (M. Telford, in litt.).

Dissodactylus glasselli Rioja, 1944

D. glasselli Rioja, 1944: 150, fig. 7–10, 16–21 (type locality, Playa San Benito, near Tapachula, Chiapas, Mexico).—Griffith 1987a: 413, 420, figs. 8H, 9H, 11H, 13H; 1987b: 2292–2310.

Material examined.—Manuel Antonio National Park, Manuel Antonio, Costa Rica, 9°06′N, 84°11′W; 20 June 1992, SCUBA diving 1.5–3 m, sand bottom, 3 males cw 3.6, 3.6 and 3.8 mm, 3 females cw 3.3, 4.2 and 4.2 mm on *Mellita kanakoffi* and *Encope wetmorei* Clark, 1946.—Brasilito Beach, Guanacastes, Costa Rica, 10°25′N, 85°47′W; 22 Jun 1992, SCUBA diving 1–3 m, sand bottom, 4 males cw 2.4, 3.2, 3.9 and 4.0 mm, 2 females cw 3.4 and 4.6 mm on *Encope micropora.*—Brasilito Beach, Guanacastes, Costa Rica, 10°25′N, 85°47′W; 13 Jul 1992, SCUBA diving 1–3 m, sand bottom, 3 females cw 3.0, 3.8 and 5.0 mm on *Encope micropora.*

Previous range records.—Playa San Benito, near Tapachula, Chiapas, Mexico (Glassell 1935). Puerto el Triunfo, El Salvador (Griffith 1987a).

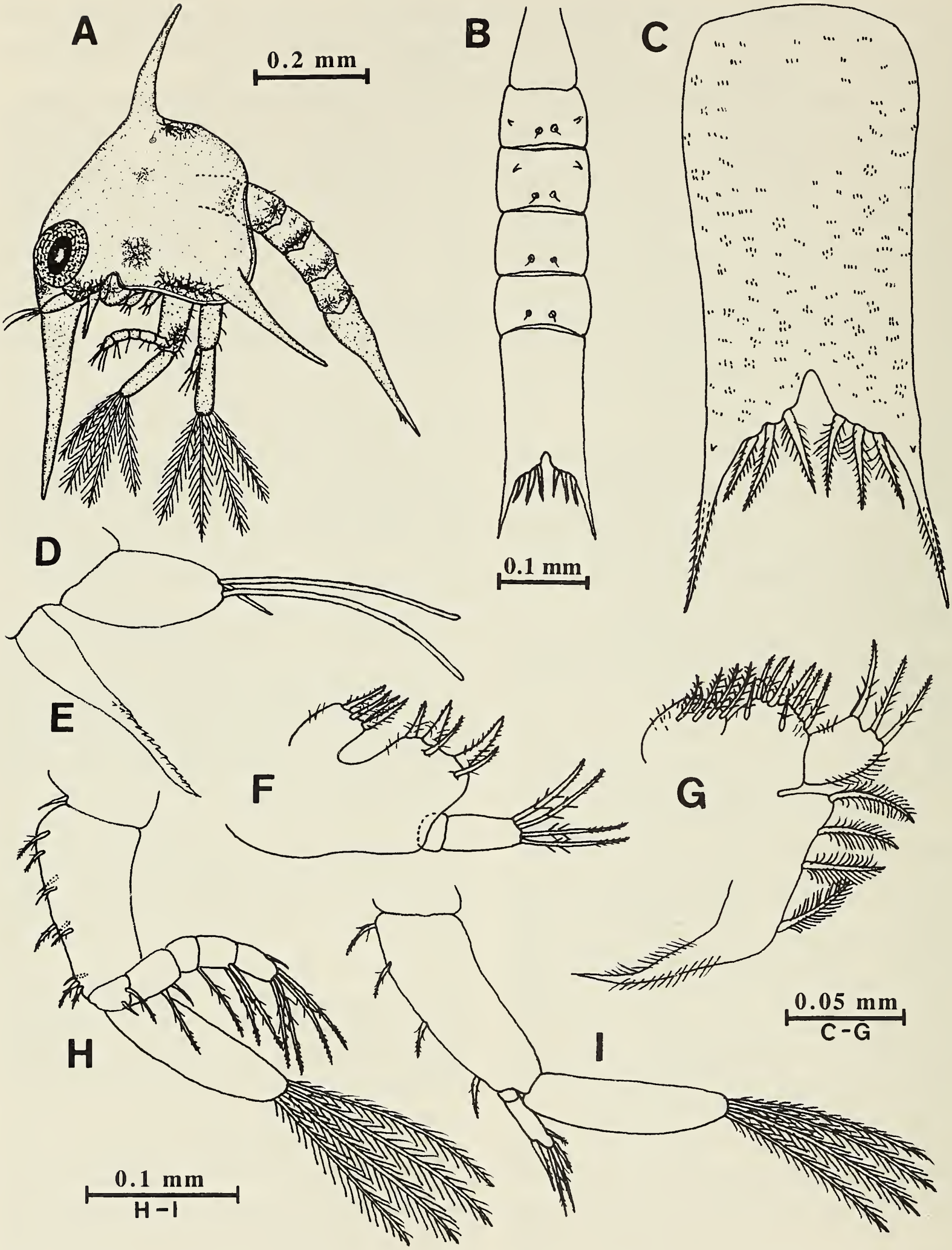

Fig. 1. First zoea of *Dissodactylus glasselli* Rioja, 1944. A, lateral view; B, dorsal view of abdomen; C, telson; D, antennule; E, antenna; F, maxillule; G, maxilla; H, maxilliped 1; I, maxilliped 2.

Previous host record.—*Mellita longifissa* Michelin (Rioja 1944).

Remarks.—The specimens collected at Brasilito Beach were sharing the same host with *Dissodactylus nitidus* Smith, 1870.

Dissodactylus mellitae (Rathbun, 1900)

Echinophilus mellitae Rathbun, 1900: 590 (type locality, Pensacola, Florida).

D. mellitae Rathbun, 1901: 22.—Griffith 1987a: 413, 420, figs. 8I, 9I, 11I, 13I, 14G; 1987b; 2292–2310.

Material examined.—East beach, Desoto Fort, St. Petersburg, Florida, Gulf of Mexico; 20 Aug 1992, free-diving 2–3.5 m, sand bottom, 2 females cw 4.0 and 4.2 mm on *Encope aberans* Martens, 1867.

Previous host records.—*Echinarachnius parma* (Lamarck, 1816), *Mellita quinquiesperforata* (Leske, 1778) (cf. Rathbun 1901, Telford 1982, Bell & Stancyk 1983, Bell 1984, 1988); *Mellita tenuis* Clark, 1940 (Marques & Pohle 1995b); *Encope michelini* Agassiz, 1841; and *Clypeaster subdepressus* (Gray, 1825) (cf. Williams et al. 1968).

Comparison of *D. glasselli* Larvae with those of Other Species of the *Dissodactylus* Complex

Meristic characteristics of the first zoea of *Dissodactylus glasselli* are identical to other species of this genus. There are, however, some morphometric differences between *D. glasselli* and the three other sympatric Pacific species, *D. nitidus* Smith, 1870, *D. lockingtoni* Glassell, 1935 and *D. xantusi* Glassell, 1936 (Pohle 1989, 1994). While the first zoea of the latter three are almost indistinguishable, *Dissodactylus glasselli* differs by significantly longer ($P < 0.01$) carapace spines (Table 1). Carapace length, however, overlaps with the other Pacific species. The closely related *Clypeasterophilus ususfructus* (Griffith, 1987a), which has recently been removed from *Dissodactylus* (Campos & Griffith 1990), is also known from near the mouth of the Gulf of California (Hendrickx 1990). Although larvae of *C. ususfructus* are unknown, it is expected that the zoeae will differ from *Dissodactylus* by the absence of dorsolateral spines on abdominal somite 3, as known for *Clypeasterophilus stebbingi* (Rathbun, 1918) and *C. rugatus* (Bouvier, 1917) (cf. Marques & Pohle 1995a, Pohle 1984).

Larvae of *D. glasselli* resemble most closely those of *D. mellitae* from the Atlantic (Marques & Pohle 1995b), *D. glasselli* differing only by the relatively longer rostral and lateral spines (Table 1). The similarity between these two species supports the conclusion by Griffith (1987b), based on an analysis of adult synapomorphies, that these are twin, or geminate, species. Trans-isthmian pairs of closely related species have been described for many taxa, including about 45% of extant decapods of Panama (Abele 1976). Under vicariant biogeographic theory (Rosen 1975), these species evolved by allopatric speciation, following the closing of the Panama seaway. The relatively recent separation accounts for the similarity of eastern Pacific and Caribbean species, such as that seen between *Dissodactylus mellitae* and *D. glasselli.*

Host-symbiont Biogeography

Dissodactylus lockingtoni has never before been reported outside the Gulf of California and thus its occurrence in Costa Rica represents about a 20° southward extension. The hosts *Mellita longifissa* and *Encope micropora* extend further south to Panama and Chile, respectively (Ghiold 1988). Thus, the geographic range of *Dissodactylus lockingtoni* may also extend beyond Costa Rica.

Dissodactylus glasselli was only known from its type locality in Mexico until Griffith (1987a) discovered a specimen amongst a lot in the Smithsonian collection identified as *D. lockingtoni* from El Salvador. The record in Costa Rica represents a 3° southward extension. The hosts *Mellita longifissa* and *M. kanakoffi* both extend further south to at least Panama (Harold & Telford 1990), indicating that *D. glasselli* may also be found there.

In terms of host specificity, *Dissodactylus mellitae* is the most generalist species within the *Dissodactylus* complex, inhabiting echinoids from three distinct clypeasteroid families. Other Atlantic species of *Dissodactylus,* except for *D. primitivus* and *D. schmitti* which live on heart urchins (Griffith 1987a), can be found on mellitid sand dollars and two species of *Clypeaster.* In contrast, the Pacific species of this genus have never been found on any of the *Clypeaster* species occurring in the area.

In contrast to *Dissodactylus,* Atlantic and Pacific species of *Clypeasterophilus* are found exclusively on *Clypeaster* (Griffith 1987a, Hendrickx 1990). The following evidence suggests that species of *Clypeasterophilus* are also more host dependent than those of *Dissodactylus*: 1) an analysis of gut contents of *Clypeasterophilus rugatus* and three species of *Dissodactylus* by Telford (1982) showed that only *C. rugatus* fed exclusively on host tissue, whereas *D. primitivus* took no more than about half of its food from the spatangoid host; 2) larvae of *Clypeasterophilus* (Pohle 1984, Marques & Pohle 1995a) could not complete larval development in absence of a host, whereas *Dissodactylus primitivus* could (Pohle & Telford 1983).

Acknowledgments

This work was supported through research grant A2313 to G. Pohle, from the Natural Sciences and Engineering Research Council, Canada. Dr. A. Dittel is thanked for arranging the use of facilities at the Centro de Investigacion de Ciencias del Mar (CIMAR), Universidad Nacional, Costa Rica, and for providing advice and equipment. We also thank technical support personnel at CIMAR. Dr. M. Telford from the Department of Zoology at the University of Toronto kindly identified the echinoid hosts. Drs. M. Telford and H. Griffith also reviewed the manuscript.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(2):254–265. 1995.

A new crab species of the genus *Pseudorhombila* H. Milne-Edwards, 1837 (Crustacea: Decapoda: Goneplacidae)

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Abstract.—A new crab species of *Pseudorhombila* was found in the southwestern Gulf of Mexico. A description of the new species, *Pseudorhombila ometlanti,* is given and is compared with other known species in the genus from the western Atlantic: *P. octodentata, P. quadridentata* and *P. guinotae.* Among western Atlantic species of the genus, *P. ometlanti* can be distinguished by carapace texture, dentition and sexual characters.

Resúmen.—Una nueva especie del género *Pseudorhombila* se recolectó en el suroeste del Golfo de México. Se presenta la descripción de *Pseudorhombila ometlanti,* especie nueva, y se compara con otras especies descritas para el Atlántico oeste: *P. octodentata, P. quadridentata* y *P. guinotae.* Entre estas especies, *P. ometlanti* se distingue por la textura y dentición del caparazón, y la morfología de los pleópodos en machos y gonoporos en las hembras.

Epibenthic macroinvertebrates from shrimp grounds along the southwestern Gulf of Mexico were studied during a three year program. Several goneplacid crab species of the genus *Pseudorhombila* H. Milne-Edwards, 1837, were found among the decapod crustaceans collected. As Guinot (1969) has stated, this is a genus in need of study. Species of this genus are typical catometopian crabs with a large part of the eighth sternite visible at the level of the second abdominal segment and its juncture with the seventh sternite. The sternal position of the male genital openings is another diagnostic characteristic.

Pseudorhombila crabs are a common component of the macroinvertebrate fauna of the southwestern Gulf of Mexico (Vázquez Bader & Gracia G. 1994). While studying our collections, we found that some of the specimens did not represent any of the species of this genus in the western Atlantic, all of which occur in the Gulf of Mexico (*P. octodentata* Rathbun, 1906; *P. quadridentata* (Latreille, 1828) and *P. guinotae* Hernández-Aguilera, 1982), and actually represent an undescribed species.

A complete description of this new species of the genus *Pseudorhombila* is given and its affinities with other known species of the genus are discussed.

Materials and Methods

The specimens used in this study were collected during the study "Monitoreo de las Fases de Pre-reclutamiento de las Especies Estuarino-dependientes de Importancia Comercial frente a Laguna de Términos" (MOPEED) conducted in Banco de Campeche, Campeche, Mexico; and during the cruises by the R/V *Oregon II* in the southern Caribbean (Panamá, Colombia). In the Gulf of Mexico samples were taken quarterly on board the R/V *Justo Sierra* of Universidad Nacional Autónoma de México, using a semicommercial otter trawl.

The material examined is listed as follows: location (MOPEED 1 and 3 or R/V *Oregon II* station number), latitude, longi-

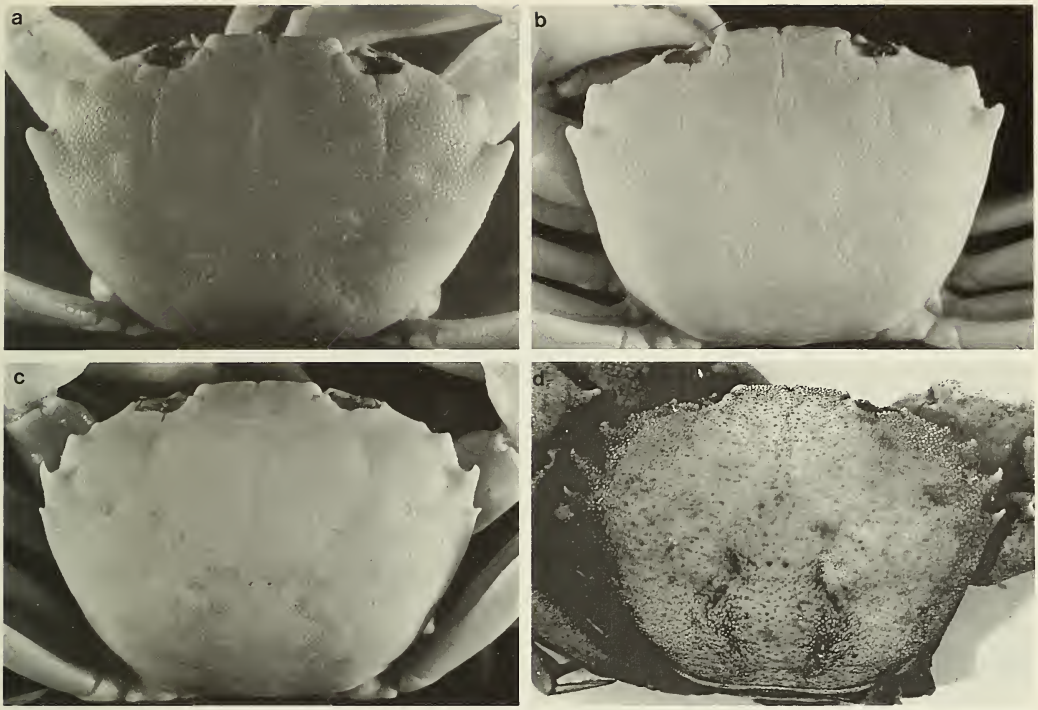

Fig. 1. Carapace, dorsal surface. a, *Pseudorhombila ometlanti,* new species, male holotype. Carapace length 26.5 mm (SMIOM 4065); b, *Pseudorhombila quadridentata* (Latreille), male, carapace length 25.2 mm (USNM 171616); c, *Pseudorhombila guinotae* Hernández-Aguilera, male holotype, carapace length 29.0 mm (SMIOM 000304); d, *Pseudorhombila octodentata* Rathbun, male, carapace length 24.1 mm (photograph by D. Guinot).

tude, depth, date, number, sex, and museum number. All specimens have been deposited in the Colección de la Secretaría de Marina, México, D. F., México (SMIOM) and in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). Other abbreviations used are, p, pereiopod, and pl, pleopod.

Pseudorhombila ometlanti, new species
Figs. 1a, 2, 3a, 4a–b, 5a, 6a, 7a,
Table 1

Material examined.—Southwestern Gulf of Mexico: MOPEED3 sta C-2 (Banco de Campeche, Campeche, Mexico) 19°30.96′N, 91°50.09′W; 45 m, 14 Sep 1992, 1 ♂ holotype, SMIOM 4065; MOPEED 1 sta R-1 (vicinity of Laguna de Cármen y Machona, Tabasco, Mexico), 18°38.43′N, 93°46.68′W; 79 m, 18 Feb 1992, 1 ♂, 1 ♀ SMIOM 4066. Southern Caribbean: R/V *Oregon II* sta 10259 off Barranquilla, Colombia, 10°59′N, 75°17′W; 72 m, 12 Feb 1968, 2 ♂ USNM 268442; sta 11234, Gulf of Urabá, Colombia 8°49′N, 76°53′W, 50 m, 11 Feb 1970, 1 ♂ USNM 268443.

Description.—Carapace much broader than long, coarse granulation visible at naked eye, more evident on and adjacent to margins. Regions partially marked. Carapace broadest at second anterolateral tooth. Frontorbital width more than ½ carapace width. Front convex divided by distinct median notch into 2 rectangular lobes.

Supraorbital margin bissected by 2 sutures with granulation continued to outer orbital tooth (first anterolateral); suborbital margin mesially with triangular tooth visible in dorsal view. Anterolateral margin

Fig. 2. *Pseudorhombila ometlanti*, new species, male holotype (SMIOM 4065). a, ventral surface of anterior region; b, sternum, postero-ventral view.

convex, projecting 2 teeth; first tooth granulated, rounded; second tooth triangular, granulate, directed anteriorly, acute and distinctly separated from first. Posterolateral margin converging posteriorly.

Epistome broadest at mid-length, with thick lip medially, finely granulate. Sternum granulate, first segments and abdominal depression with long soft setae, episternal sutures 4, 5, and 6 marked, 7 poorly defined; abdominal depression broad and shallow. In male, posterior sternal segments separated from preceding segments by genital groove. In female, gonopores large, circular, with margin slightly elevated posteriorly.

Abdomen in both sexes broad, punctate. In male, segment 1 widest and longest of all, segment 2 narrow; large portion of eighth sternite visible between second and third abdominal segment, segment 3 with lateral angles not acute and not reaching coxa of fifth pereiopod; segments 3–5 partially fused, sutures remaining conspicuous. Abdomen of female widest at segment 1; segment 6 longer than any of preceding ones, last segment spear-like.

Eyestalks very broad, anterior surface with coarse granulation, with long soft setae dorsally and anteriorly; cornea dilated.

Anntenules prominent, folding transversely, basal article thickest, with longitudinal crest granulate; second article elongate, subcylindrical; third article nearly equal in length to second, with long marginal setae distally.

Basal anntenal article broad, closing orbital hiatus between frontal lobe and suborbital tooth, basally with operculum of excretory pore occupying part of closed suture at anterolateral corner of epistome; following articles free, elongate, subcylindrical, and decreasing in length.

Third maxilliped very granulated, pilose, ischium with medial longitudinal furrow, merus densely granulated with depression at either side of raised median area, distomesial margin terminating in angular lobe, distolateral corner rounded, granulated.

Chelipeds (p1) slightly shorter than first walking leg (p2), slightly unequal in female. Movable finger or major cheliped with lobiform proximal tooth. Fixed finger with 2 longitudinal ridges on outer surface. Palm with inner surface smooth; outer surface smooth to punctate; inferior surface with granulated crest. Carpus with strong, triangular tooth on inner angle, tip directed anteriorly, concentration of coarse granules below tooth and on superior and inferior margin. Merus with external surface very granulated and with stiff bristles, inner surface smooth, superior margin ending in sharp distally-directed tooth. Dactyls of walkings legs 1–4, each with corneous tip and with longitudinal rows of setae. Propodi of legs 1–3 granulate, elongate and with long setae, propodi of p4 with shorter setae; superior surface of meri of pereiopods with depression delimited by small granules; inferior surface with strong granulation (less evident on p4). Carpi with superior margin densely granulated, (more so in p1–3), inferior margin with coarse granules.

Male gonopod (pl1) elongate, apex terminating in hump continued in large lobe with approximately 19 spines. Anteromesial margin with approximately 34 small, spaced spinules, distal end with 19 large, recurved spines; proximal boss on posteromesial surface with row of about 8 bristles. Male pl2 elongate, narrow, sigmoid, terminal process curved, with small spinules and distally strap-like.

Size.—Carapace length and width of male holotype 26.5 and 35.2 mm, respectively; males 27.8 and 38.0 mm (SMIOM 4066), 24.0 and 31.8 mm (USNM 263442), 21.7 and 27.9 mm (USNM 268442), 25.0 by 33.8 mm (USNM 368443); female 27.4 and 37.0 mm (SMIOM 4066).

Color.—Not known in fresh specimens. In alcohol, the specimens are salmon-pink.

Known range and habitat.—Western Atlantic from the southwestern Gulf of Mexico (Banco de Campeche, Campeche, Mexico) to southern Caribbean (Golfo de Urabá,

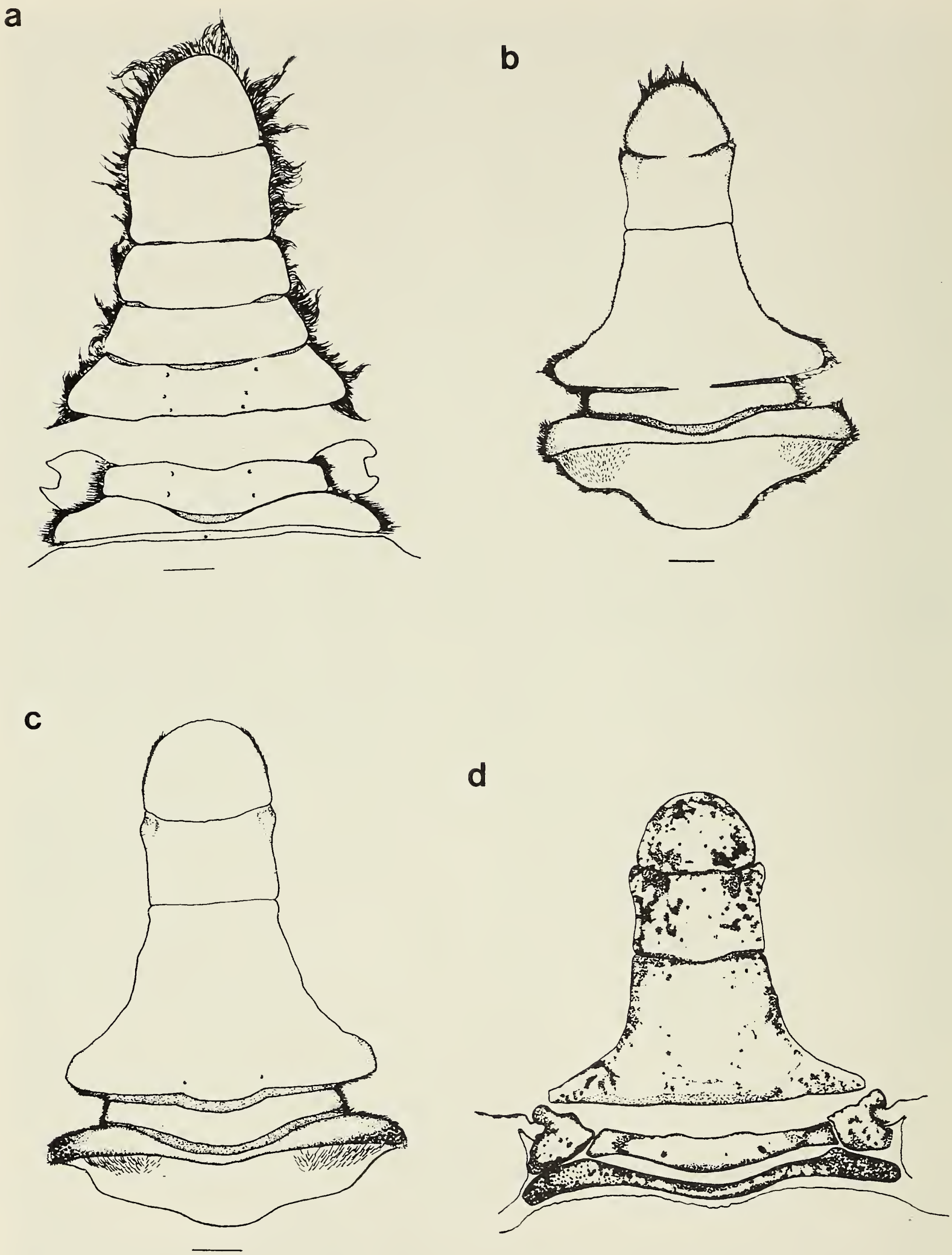

Fig. 3. Male abdomen and telson. a, *Pseudorhombila ometlanti,* new species, male holotype (SMIOM 4065), abdomen and telson; b, *Pseudorhombila quadridentata* (Latreille) (USNM 171616); c. *Pseudorhombila guinotae* Hernández-Aguilera, holotype (SMIOM 000304); d, *Pseudorhombila octodentata* Rathbun, holotype (USNM 32690). Scales = 1 mm.

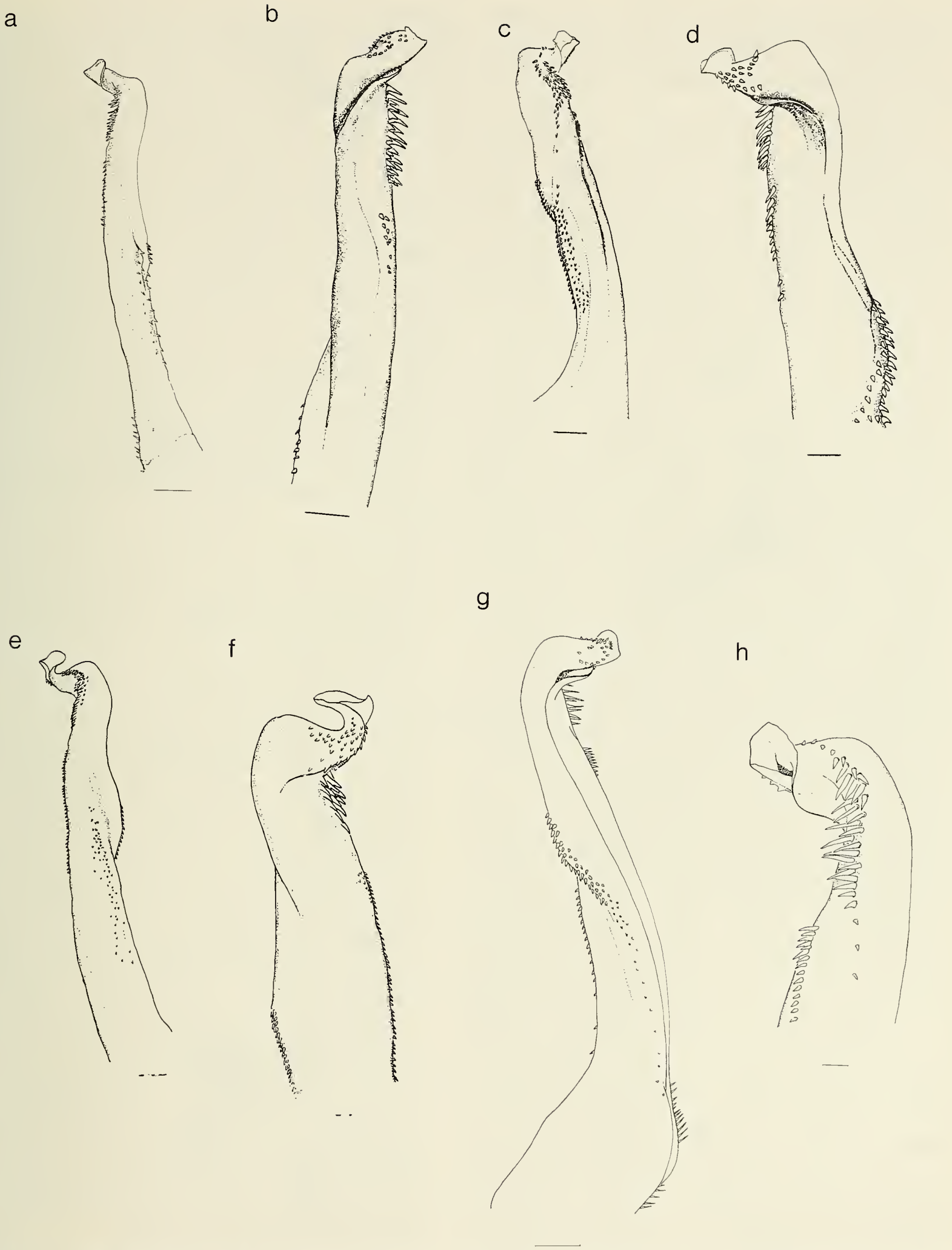

Fig. 4. Male first gonopod. a–b. *Pseudorhombila ometlanti,* new species, holotype (SMIOM 4065): a. left mesial surface; b, enlarged tip of same posterior surface. c–d, *Pseudorhombila quadridentata* (Latreille) (USNM 171616); c, right mesial surface; d, enlarged tip of same posterior surface. e–f, *Pseudorhombila guinotae* Hernández-Aguilera holotype (SMIOM 000304); e, left mesial surface; f, enlarged tip of same posterior surface. g–h, *Pseudorhombila octodentata* Rathbun, holotype (USNM 32690); g, left posterior surface; h, enlarged tip of same mesial surface [g–h, after Guinot (1969)]. Scales = 1 mm.

and off Barranquilla); from 23 to 72 m depth. During the MOPEED study, *P. ometlanti* was collected on substrates composed mostly of mud.

Etymology.—The specific name is from the nahuatl language, *ome* meaning two, and *tlanti* meaning tooth, and is a noun in apposition. The name is given in reference to the two anterolateral teeth of the carapace.

Remarks.—*Pseudorhombila ometlanti* is the fourth species of the genus *Pseudorhombila* known to occur in the western Atlantic. The new species can be distinguished from the other species on the basis of carapace texture and dentition, and shape of male and female abdomen. Also, the forms of the first and second pleopods in the male, and the female gonopores, are distinctive (Table 1). The carapace granulation of *P. ometlanti* is stronger than in *P. quadridentata* (Fig. 1b) and *P. guinotae* (Fig. 1c), but it is less strong than in *P. octodentata* (Fig. 1d). With respect to carapace shape and dentition, *P. ometlanti* is similar to *P. quadridentata.* Both have two anterolateral teeth, whereas the other two species have three and four teeth. However, Hernández-Aguilera (1982), reported that *P. guinotae* can present two anterolateral teeth. Abdomen shape is another character that distinguishes the new species. The abdomen in the other three species is narrower than in *P. ometlanti,* with segments 3–5 fused and undistinguishable sutures (Fig. 3b, c, d). The holotype male of *P. ometlanti* has a broader abdomen than the other three species, and is fitted in a shallower and broader abdominal depression. Although in male paratypes the abdomen is not so broad as in the holotype, it can be easily distinguished from the abdomen of the other three species. In all the specimens examined of *P. ometlanti,* the sutures of the abdominal segments are present; only the suture of segment 4 is interrupted in a small portion of the median line.

With respect to pl1, the four species of *Pseudorhombila* show distinct differences in the shape of lobe apex and number of spines (Figs. 4c–d, e–f, g–h; Table 1). The Pl2 of the three previously known species is slightly shorter than in *P. ometlanti,* not recurved, and the terminal processes are distally tapered; whereas in the new species the terminal process is strap-like (Fig. 5b, c, d). Although the female abdomen of all four species have all segments free, the last segment differs in shape (Fig. 6b, c). The gonopores in the four species also differ. *Pseudorhombila guinotae* and *P. octodentata* exhibit oval-shaped gonopores, whereas in *P. quadridentata* and *P. ometlanti* the gonopores are nearly circular (Fig. 7b, c, d).

The following key separates the species of *Pseudorhombila* known in the western Atlantic.

Key to the Species of *Pseudorhombila*

1. Anterolateral margin of carapace with 2 teeth 2
– Anterolateral margin of carapace with 3 to 4 teeth 3
2. Dorsal surface of carapace with fine granulation. Male abdomen narrow, sutures not evident. Anteromesial margin of male gonopod (Pl1) with approximately 55–60 small spines, distally with more than 60 spines, apex terminating in well defined hump. Female gonopores nearly circular . . *Pseudorhombila quadridentata*
– Dorsal surface of carapace with coarse granulation. Male abdomen broad, segments 3–5 almost free, sutures well marked. Anteromesial margin of male gonopod (Pl1) with approximately 34 small spines, distally with 19 recurved spines, apex terminating in poorly defined hump. Female gonopores circular. .... *Pseudorhombila ometlanti*
3. Dorsal surface of carapace with very coarse granules. Anteromesial margin of male gonopod (Pl1) with approximately 25 spinules. Apex ter-

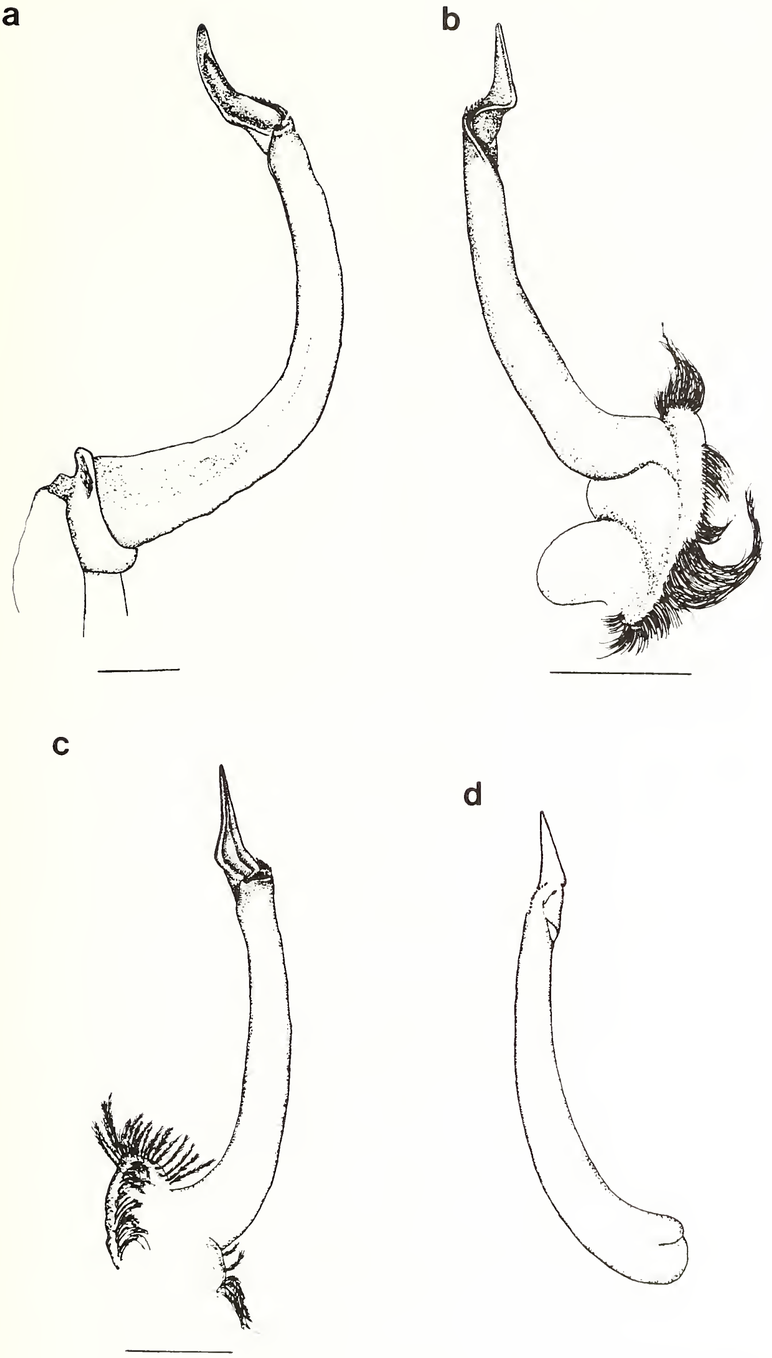

Fig. 5. Male second gonopod, a, *Pseudorhombila ometlanti,* new species, holotype (SMIOM 4065), right mesial surface. b, *Pseudorhombila quadridentata* (Latreille) (USNM 171616), left mesial surface. c, *Pseudorhombila guinotae* Hernández-Aguilera (SMIOM 4067), right mesial surface. d, *Pseudorhombila octodentata* Rathbun, holotype (USNM 32690), left mesial surface [d, after Guinot (1969)]. Scales = 1 mm.

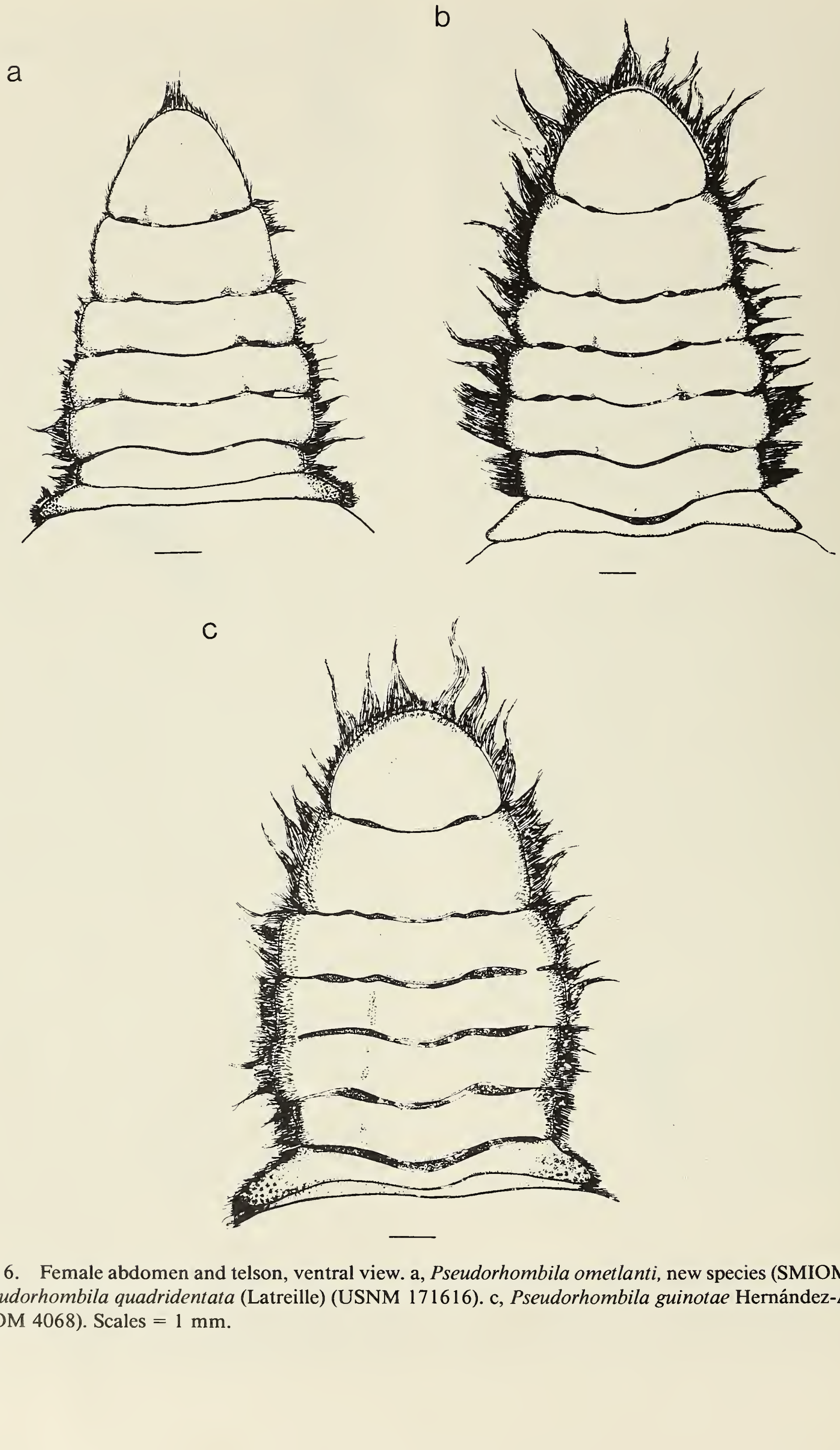

Fig. 6. Female abdomen and telson, ventral view. a, *Pseudorhombila ometlanti,* new species (SMIOM 4066). b, *Pseudorhombila quadridentata* (Latreille) (USNM 171616). c, *Pseudorhombila guinotae* Hernández-Aguilera (SMIOM 4068). Scales = 1 mm.

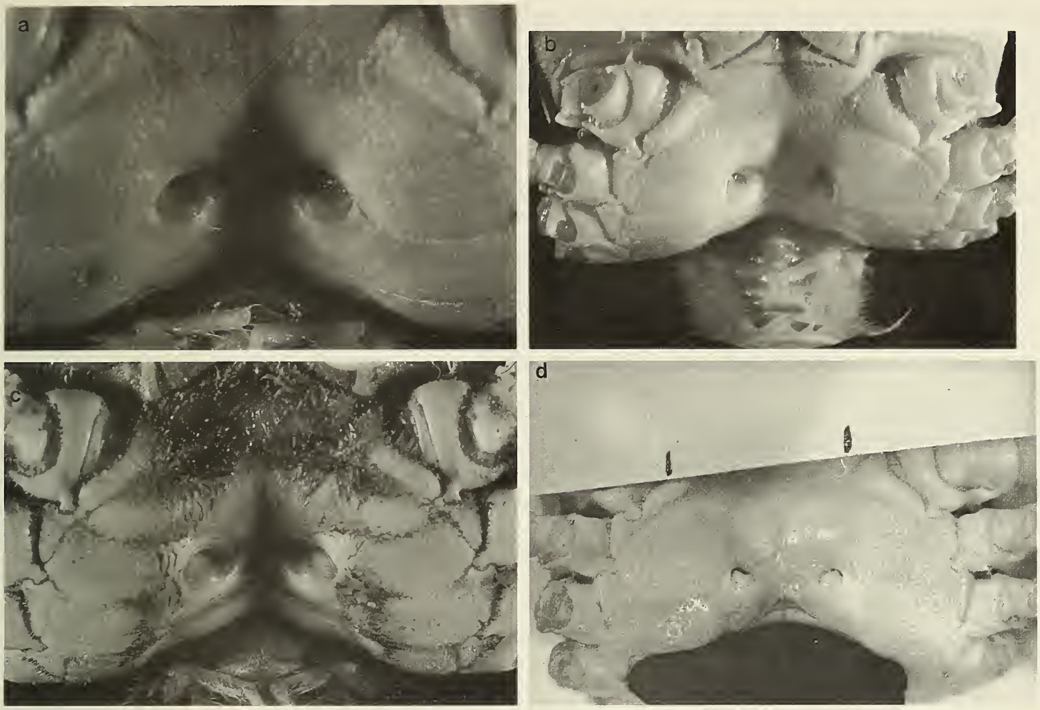

Fig. 7. Female sternum and gonopores. a, *Pseudorhombila ometlanti,* new species, carapace length 27.4 mm (SMIOM 4066). b, *Pseudorhombila quadridentata* (Latreille), carapace length 24.1 mm (USNM 171616). c, *Pseudorhombila guinotae* Hernández-Aguilera, carapace length 30.5 mm (SMIOM 4068). d, *Pseudorhombila octodentata* Rathbun (Muséum national d'Histoire naturelle, París; photograph by D. Guinot).

minating in poorly defined hump. Female gonopores oval and narrow .... *Pseudorhombila octodentata*

– Dorsal surface of carapace with very fine granulation. Anteromesial margin of male gonopod (Pl1) with approximately 41 small separated spines, distally with approximately 49 large recurved spines, apex terminating in hump not prominent. Female gonopores oval and broad .... *Pseudorhombila guinotae*

Three species of *Pseudorhombila* have been reported in the Gulf of Mexico, *P. ometlanti, P. quadridentata* and *P. guinotae.* According to J. L. Hernández-Aguilera (pers. comm.), *Cyrtoplax bidentata* Gómez & Ortiz, 1975, found in Cuba, is a junior synonym of *P. quadridentata,* so its geographic range includes the Caribbean. The new species is also distributed outside of the Gulf of Mexico, off the Colombian coast. *Pseudorhombila octodentata* is only known from the Lesser Antilles (Dominica and Martinique) at 180 m depth (Rathbun 1906, 1918). Hernández-Aguilera (1982) mentions that the latter species occurs in the northwestern Gulf of Mexico; however, Vázquez Bader & Gracia G. (1994) did not find this species in the southwestern Gulf of Mexico. The depth range is similar among the four species. *Pseudorhombila guinotae* has a relatively wide depth range, from 57 to 112 m, while *P. ometlanti* and *P. quadridentata* have a narrower depth range, from 45 to 79 m for the former, and 20 to 63 m for the latter.

Pseudorhombila ometlanti is more similar to *P. quadridentata* with respect to car-

Table 1.—Diagnostic characters of species of *Pseudorhombila* H. Milne Edwards, 1837.

	P. octodentata	*P. guinotae*	*P. quadridentata*	*P. ometlanti*
Carapace	Dorsal surface with very coarse granules	Dorsal surface with very fine granulation	Dorsal surface with fine granulation	Dorsal surface with coarse granulation
Carapace dentition	4 anterolateral teeth	3–4 anterolateral teeth	2 anterolateral teeth	2 anterolateral teeth
Abdomen	Male: narrow, segments 3–5 fused; sutures not evident Female: segments 1–7 free	Male: narrow, segments 3–5 fused; sutures not evident Female: segments 1–7 free, last segment rounded	Male: narrow, segments 3–5 fused; sutures not evident Female: segments 1–7 free, last segment triangular	Male: broad, segments 3–5 almost free; sutures well marked Female: segments 1–7 free, last segment spear-like
Male gonopod (pl1)	Anteromesial margin with approx. 25 spinules. Apex terminating in poorly defined hump, continuing in short lobe, with approx. 25 spinules	Anteromesial margin with approx. 41 small separated spines, distally with approx. 49 large recurved spines. Apex terminating in hump not prominent, continuing in a large lobe, with 34 spines	Anteromesial margin with approx. 55–60 small spines; distally with more than 60 large recurved spines. Apex terminating in well defined hump, continuing in a broad lobe, with 33 spines	Elongate, anteromesial margin with approx. 34 small spines; distally with 19 recurved, large spines. Apex terminating in poorly defined hump, continuing in a large lobe, with 19 spines
Male gonopod (pl2)	Short, not recurved, terminal process distally tapered	Short, not recurved, terminal process distally tapered	Short, not recurved, terminal process distally tapered	Elongate; recurved, terminal process with small spinules and distally strap-like
Female gonopores	Oval, narrow; margin slightly sinuous	Oval, broad; margin sinuous	Nearly circular margin sinuous	Circular, large; margin prominent

apace shape and dentition, than to any of the other three species in the genus. The shape of the abdomen, pleopods, and gonopores clearly distinguishes *P. ometlanti* from its other congeners.

Acknowledgments

Types deposited in SMIOM were collected under projects IN202092 and IN203893 from the Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México (UNAM). We are grateful to R. Lemaitre for loans of additional specimens, help during our visit to Smithsonian Institution, and for his thorough revision of the manuscript. We wish to thank D. Guinot for her useful comments on the revision of the manuscript. We also thank J. L. Hernández-Aguilera, (Secretaría de Marina) for the loan of specimens of *P. guinotae*; R. Mendoza for drawings; and A. I. Bieler (Laboratorio de Microcine, Facultad de Ciencias, UNAM) for taking the photographs. Photographs of carapace and gonopores of *P. octodentata* were taken by D. Guinot, Muséum national d'Histoire naturelle, Paris. Thanks are given to C. Flores and staff of the Laboratorio de Zooplancton for their support in the field and in the laboratory. This study was conducted with the support from grants IN202092-PAPIID, IN203893-PAPIIT and 030334-PADEP of the Dirección General de Asuntos del Personal Académico, UNAM.

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Description of the ghost shrimp *Sergio mericeae,* a new species from south Florida, with reexamination of *S. guassutinga* (Crustacea: Decapoda: Callianassidae)

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Abstract.—*Sergio mericeae* is here described from intertidal sandflats of the Atlantic coast of Florida, where it shares habitats with *Neocallichirus rathbunae* and *N. grandimana.* This new species, formerly identified with the Brazilian species, *Sergio guassutinga* (until recently assigned to *Neocallichirus*), bears a strong resemblance to its Brazilian counterpart in body size, the unique dactylar dentition of the major chela, and most other morphological features. However, these apparent sibling species can be distinguished on the basis of body coloration and subtle but consistent differences in the third maxilliped and major cheliped. Immature specimens from Louisiana, Texas and Tamaulipas, Mexico, strongly resemble topotypic juveniles from Fort Pierce, Florida, and suggest that *S. mericeae* ranges into the western Gulf of Mexico.

Uniqueness of the species described below was recognized in the course of our ongoing effort to document diversity of infaunal decapods inhabiting intertidal substrates of the Indian River Lagoon on the Atlantic coast of Florida. Our collecting efforts in this region of marked tropical to warm-temperate faunal transitions have employed yabby pumps (Hailstone & Stephenson 1961, Manning 1975) for extraction of a speciose assemblage of thalassinid ghost shrimp and associated fossorial forms. Materials from this region have led to comparative studies of thalassinids from throughout the western Atlantic, as well as systematic revisions and new distribution records, especially for members of the Callianassidae (Felder & Manning 1994; Manning 1987, 1993; Manning & Felder 1986, 1991, 1992; Manning & Heard 1986; Manning & Lemaitre 1994; Rodrigues & Manning 1992). Collection of new materials from Florida was essential in order for us to reexamine the populations previously reported on by Biffar (1971), as many specimens upon which his earlier records were based were lost in a laboratory fire just prior to publication of his work.

Recent studies of the American Callianassidae have revealed a number of cases where species formerly thought to be of wide distribution were actually complexes comprised of regionally endemized species (Felder et al. 1991, Felder & Manning 1994, Felder & Rodrigues 1993, Manning 1993). In the context of those patterns, the previous report of the Brazilian *Callianassa guassutinga* Rodrigues from south Florida (Biffar 1971) suggested such an extensive range that we were led to question the conspecific assignment of its northern and southern populations. As materials that Biffar assigned to this species from Florida were for the most part destroyed in the aforementioned fire (see Biffar 1971), detailed comparisons with the Brazilian form were delayed until we could accumulate an adequate series of adult specimens from the

Florida population. In the course of making those collections, we photographically documented coloration in northern populations which differed markedly from reported coloration of the Brazilian species (Rodrigues 1966, 1971), and this further encouraged us to undertake detailed morphological studies and the present description of a new species.

Material examined is listed by location followed by date, collector (coll), number of specimens per sex and condition (mutl = mutilated, ov = ovigerous, immat = immature), and museum number. Size is expressed as postorbital carapace length (cl) or total length (tl) measured in millimeters (mm). The holotype and some paratypes of *Sergio mericeae* have been deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC. Paratypes have been deposited in the University of Southwestern Louisiana Zoological Collections (USLZ), Lafayette, Louisiana, the Harbor Branch Oceanographic Museum (HBOM; formerly the Indian River Coastal Zone Museum, (IRCZM), Fort Pierce, Florida, and the Florida Marine Research Institute Invertebrate Collection (FSBC-I), St. Petersburg, Florida. Comparisons with the Brazilian species *Sergio guassutinga* were based upon the published figures and descriptions by Rodrigues (1966, 1971) and examination of a mature female from Aracaju, Brazil (USNM 268644), herein illustrated, as well as comparisons with a female topotype (USNM 221802), a male paratype (USNM 256886), a male from Praia de Pirangi-Sul, Rio Grande do Norte, Brazil (USNM 221810), and a female specimen from Natal, Rio Grande do Norte, Brazil (USNM 221804).

Sergio Manning & Lemaitre, 1994

Sergio mericeae, new species

Figs. 1a–f, 2a–f, 3a–f, 4a–f, 5a–g

Callianassa guassutinga.—Biffar, 1971: 651, 653, 674, figs. 9, 10 [Virgina Key, Miami, Florida. Not *Callianassa guassutinga* Rodrigues, 1966, 1971].—Abele & Kim, 1986: vii, 26, 294, 296, 298, figs. a–c on 299.—Williams et al., 1989: 28, 61.

"near *Callianassa guassutinga*".—Manning & Felder, 1989: 16.

Callianassa (nr. *C. guassutinga*).—Rabalais et al., 1989: 35.

Sergio sp.—Staton & Felder, 1995: 505.

Sergio guassutinga.—Manning & Lemaitre, 1994: 40 [Florida record only. Not listed and figured Brazilian materials].

Type material.—*Holotype*: North side of Fort Pierce Inlet, Florida, island immediately west of Coon Island, St. Lucie County, Indian River Lagoon, intertidal sandflat just shoreward of sparse seagrass, 27°28.2′N, 80°18.8′W, 20 May 1994, coll D. L. Felder and W. D. Lee, 1 ♂ (cl 29.8 mm), USNM 268645.

Paratypes: Same site as holotype, 6 Mar 1985, coll W. D. Lee and S. Petry, 1 ♂ (cl 28.3 mm; tl 106 mm), USNM 268682; 5 Mar 1985, coll W. D. Lee and S. Petry, 1 mutl ♂ (cl ca 30 mm), USNM 268683; no date, coll W. D. Lee and S. Petry, 1 ♀ (cl 31.1 mm; tl 115 mm), USNM 268684; north side of Fort Pierce Inlet, Florida, Dynamite Point site near Fort Pierce Inlet State Park, St. Lucie County, Indian River Lagoon, 27°28.3′N, 80°17.8′W, 12 Aug 1989 (RBM station FP 89-5), coll D. L. Felder and R. Brown, 1 ♂ (cl 20.4 mm), USNM 268685; 3 Jun 1993, coll D. L. Felder, 1 ♀ (cl 10.7 mm; tl 35.8 mm), USLZ 3542; north side of Fort Pierce Inlet, Florida, Coon Island, St. Lucie County, Indian River Lagoon, 27°28.2′N, 80°18.2′W, 3 Apr 1985, coll W. D. Lee and S. Petry, 1 ♂ (cl 31.1 mm; tl 115.2 mm), USNM 268686; 16 Jul 1994, coll W. D. Lee, 1 ♀ (cl 27.1 mm; tl 105.6 mm), USLZ 3543; north side of Fort Pierce Inlet, Florida, northeast of Coast Guard Station, near exposed sand bar, 0.3 m depth, 25 Apr 1972, coll H. B. Russell, 1 ♂ (cl 29.7 mm; tl 118 mm), HBOM 89:103; south side of Fort Pierce Inlet, Florida, intertidal sand bar just north of and separated by shallow channel from U.S. Highway A1A causeway between Fort Pierce and South Hutchinson Island, St. Lucie County, Indian River Lagoon, 27°27.7'N, 80°18.7'W, 23 Jul 1985 (RBM station FP 85-4), coll R. B. Manning and D. L. Felder, 1 mutl ♀ (cl ca. 29 mm), USNM 268687; 12 Aug 1986 (RBM station FP 86-4), coll R. B. Manning, D. L. Felder, and W. D. Lee, 1 mutl ♂, USNM 268688; 15 Aug 1986 (RBM station FP 86-7), coll R. B. Manning, D. L. Felder, and W. D. Lee, 1 mutl ♂ (cl 13.7 mm), 2 ov ♀♀ (1 mutl, other cl 30.5 mm; tl 114.9 mm), USNM 268689; 2 Mar 1987 (RBM station FP 87-2), coll R. B. Manning and W. D. Lee, 2 ♂♂ male (cl 9.1, 9.4 mm), USNM 268690; 3 Mar 1987 (RBM station FP 87-4), coll R. B. Manning and W. D. Lee, 1 mutl ♀, USNM 268691; 5 Mar 1987 (RBM station FP 87-6), coll R. B. Manning and W. D. Lee, 2 ♂♂ (cl 10.4, 17.5 mm), USNM 268692; 17 Apr 1988 (RBM station FP 88-1), coll R. B. Manning and M. Schotte, 1 mutl ♂ (cl ca. 15 mm), USNM 268693; 1 Jun 1993, coll D. L. Felder, 1 ♀ (cl 26.5 mm, dissected for hindgut study), USLZ 3544; 2 Jun 1993, coll D. L. Felder, 1 ♂ (cl 12.3 mm, dissected for hindgut study), USLZ 3545; 6 Aug 1993, coll D. L. Felder and J. M. Felder, 1 ♀ (cl 14.0 mm), USLZ 3546; St. Lucie, Florida, intertidal unvegetated sand flat just inside St. Lucie Inlet, Martin County, Indian River Lagoon, 27°10.5'N, 80°10.4'W, 11 Feb 1983 (RBM station FP 83-2), coll R. B. Manning, W. D. Lee, and H. Schiff, 3 ♂♂ (cl 8.3, 9.2, 10.2 mm), USNM 268694; Lake Worth Inlet, Florida, intertidal, sparsely vegetated, sandy to shelly-sand flats on north side of Peanut Island, Palm Beach County, 26°46.7'N, 80°2.9'W, 4 Mar 1987 (RBM station FP 87-5), coll R. B. Manning and W. D. Lee, 3 ♀♀ (cl 10.6, 18.7, 30.0 mm), USNM 268695; 10 Aug 1987 (RBM station 87-8), coll D. L. Felder, W. D. Lee, P. Mikkelsen, and R. Bieler, 1 ♂ (cl 12.5 mm), USNM 268696; 11 Aug 1987 (RBM station 87-9), coll D. L. Felder and W. D. Lee, 2 ♂♂ (1 mutl, other cl 27.2 mm), USNM 268697; 12 Aug 1987 (RBM station 87-10), coll D. L. Felder, W. D. Lee, and P. Mikkelsen, 1 ♂ (cl 17.0 mm), USNM 268698; 1 ♂ (cl 14.5 mm, photographic voucher), USLZ 3547, 2 ♂♂ (cl 13.4, 13.8 mm), 2 mutl ov ♀♀, FSBC-I 47980; 8 Sep 1985, coll W. Lee and P. Mikkelsen, 1 ♂ (cl 16.0 mm), USNM 268699; 23 July 1994, coll D. L. Felder, J. M. Felder, R. D. Felder, and W. D. Lee, 2 ♀♀ (cl 11.9, 18.5 mm), USLZ 3548; Seaquarium Flats, Virginia Key, Dade County, Florida, 29 Feb 1964, coll S. Dobkin, 1 ♀ (cl 10.3 mm; tl 37.4 mm), USNM 122732.

Other material examined.—Louisiana: Just off Cat Island Pass, mouth of Terrebonne Bay, 28°56.8'N, 90°33.7'W, trawl, depth of 12–13 m, 12 Jul 1984, coll N. N. Rabalais and students, 5 mutl immat (cl 6.5–7.9 mm), USLZ 3549. Texas: Port Isabel, Texas, lower Laguna Madre near Brazos Santiago inlet, muddy sand flat just north of mainland end of old abandoned causeway to South Padre Island, Cameron County, Jul 1991, coll D. L. Felder, J. M. Felder and R. D. Felder, 1 mutl ♀ (cl 10.4 mm), USLZ 3550. Mexico: Barra del Tordo, Tamaulipas, Mexico, depth ca. 0.3 m, margins of sandy *Halodule* flat just inside inlet at mouth of Rio Carrizal estuary, 24 May 1982, coll D. L. Felder and R. K. Tinnin, 5 ♂♂ (cl 9.5, 9.7, 9.9, 10.6, 12.0 mm), 3 ♀♀ (cl 9.5, 10.6, 10.8), USLZ 3551 (two are photographic vouchers).

Diagnosis.—Front of carapace with three small spinous anterior projections, usually subequal or with medial slightly longer than laterals. Eyestalks broad, tapered over length, usually terminated in spine, tubercle or acute angle, often not reaching to distal end of first antennular segment. Third maxilliped with dactyl arched and propodus broad, height of propodus greater than length of dactyl; diagonal length of merus-ischium less than or equal to 2 times width at joint between these articles. Major cheliped of adults with inferior margin of merus armed proximally by elongate process of 2–3 fused spines, beyond which is short gap in marginal dentition, lateral surface with low, rounded longitudinal carina; carpus about half as long as palm; dactylus shorter than palm, cutting edge with rectangular tooth proximally, acute recurved tooth at midlength, and series of smaller acute teeth distally. Minor cheliped with dactylus usually longer than palm. Uropodal exopod with dorsal plate much shorter than ventral plate. Telson with posterior margin weakly emarginate.

Description.—Adults of relatively large size, with postorbital carapace lengths sometimes >30 mm and total lengths occasionally >110 mm.

Frontal margin of carapace (Figs. 1a, 5a, b) with three anterior prominences, each acute or terminated by short spine, median of which is slightly more produced on triangular base to form rostrum, lateral of which overlie inner margins of antennal peduncles; low, obtuse tooth on anterolateral margin just lateral to outer margin of antennal peduncle. Rostrum extending less than ⅓ visible length of eyestalks in dorsal view. Carapace lacking rostral carina, with distinct linea thalassinica, and with a defined dorsal oval marked posteriorly by deep transverse cardiac furrow, furrow extending 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 and usually sculpted by weak crenelations on upper surface. Subantennular region of epistome with dense tuft of long setae bracketing those of antennular peduncle.

Eyestalks flattened, weakly concave dorsally, length equal to or slightly less than 2 times basal width, in dorsal view tips reaching to or nearly to distal end of basal antennal article; mesial surfaces of eyestalks closely opposed over proximal portion of midline, divergent terminally; weakly sinuous anterolateral margin arching from broad base of eyestalk to anterior taper, joining mesial margin anteriorly in variable terminus, ending as spinule, tubercle or acute corner; rarely with subterminal spinule or tubercle in addition to terminal one. Cornea dark, area of pigmentation sexually dimorphic; in both sexes, rounded corneal surface is small, subterminal, anterolateral in position, larger relative to eyestalk and more bulbous in immature than in adult animals; in adult males, pigmented area large, often diffuse, almost broad as stalk, often occupying much of distal third to ⅔ of eyestalk; in adult females and juveniles, pigmented area smaller, more restricted to area of rounded corneal surface.

Antennular peduncle shorter and heavier than antennal peduncle, terminal article slightly longer than penultimate and reaching to or beyond midlength of terminal article on antennal peduncle; penultimate and terminal articles of peduncle with ventromesial and ventrolateral rows of long setae, those of ventrolateral row longer, denser, and continued onto ventral ramus of flagellum; rami of flagellum subequal in length, 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 with penultimate article subequal to or slightly longer than terminal article; basal article with dorsolateral carina above laterally produced excretory pore; 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; 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; fourth article narrower than

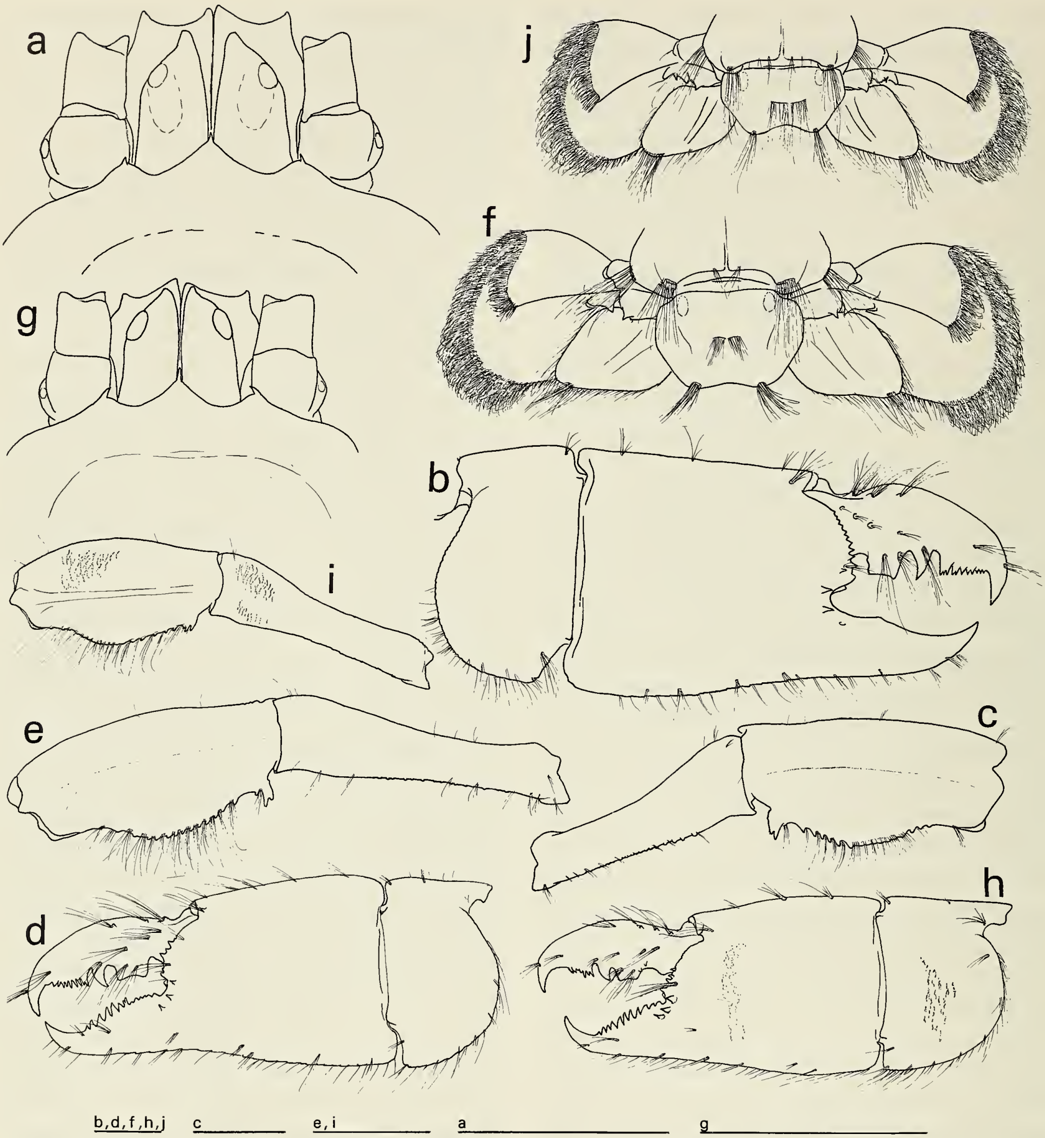

Fig. 1. *Sergio mericeae,* new species, type materials from Fort Pierce Inlet, Florida; a–c, f, male holotype (cl 29.8 mm), USNM 268645; d, e, female paratype (cl 26.5 mm), USLZ 3544. a, Carapace front, eyestalks, basal antennal segments, dorsal view, setae not shown; b, Major cheliped of mature male, carpus and chela, external surface; c, Major cheliped of mature male, ischium and merus, external surface; d, Major cheliped of mature female, carpus and chela, external surface; e, Major cheliped of mature female, ischium and merus, external surface; f, Telson, uropods and part of sixth abdominal segment, dorsal view. *Sergio guassutinga* (Rodrigues) from Aracaju, Brazil, female (cl 23.5 mm), USNM 268644; g, Carapace front, eyestalks, basal antennal segments, dorsal view, setae not shown; h, Major cheliped of mature female, carpus and chela, external surface; i, Major cheliped of mature female, ischium and merus, external surface; j, Telson, uropods and part of sixth abdominal segment, dorsal view. Scale lines indicate 5 mm.

third; flagellum 2–2.5 times length of antennular flagellum.

Mandibles (Fig. 2a) with large, 3-segmented palp, elongated third article of palp slightly tapered and terminally rounded, long setae on external and distal surfaces of second article and on proximal extensor surface of third, field of short setae on most of extensor surface and terminal end of third article; incisor process with well-defined, terminally corneous teeth on cutting margin, teeth largest, less coalesced on proximal two thirds of cutting margin, internal surface with lip giving rise to molar process proximal to incisor teeth, molar process with 4–6 small marginal teeth; paragnath (not figured) rounded, scaliform, poorly sclerotized, set against and below molar process. First maxilla (Fig. 2b) with endopodal palp long, narrow, terminal article deflected proximally at articulation; proximal endite densely setose on sinuous margin, terminal lobe additionally with field of large, terminally bifurcate setae; distal endite elongate, proximally narrow, broadening terminally where armed with short stiff bristles and field of short setae, some with bifurcate tips; exopodite low, truncate and setose. Second maxilla (Fig. 2c) with endopod narrowed distally, first and second endites each longitudinally subdivided, internal surface of first endite fused to broad, rounded, marginally setose plate; exopod forming large, broad, scaphognathite. First maxilliped (Fig. 2d) with proximal endite narrowly produced, dentiform, marginally setose; distal endite robust, subquadrate, mesial half of external surface and margins heavily setose, longest setae terminal, internal surface concave; exopod ovoid, divided by transverse suture marking notch on mesial margin, longest setae in field on external surface and mesial margin proximal to notch; epipod large, broad, anterior end tapered to narrow terminus. Second maxilliped (Fig. 2e) with long, narrow endopod; endopodal merus length exceeding 4 times width, flexor margin with dense fringe of long, close-set setae; carpus short; propodus slightly arcuate, heaviest distally, length almost 3 times width; dactylus short, about ⅓ length of propodus, with terminal brush of stiff bristles; exopod phylloform, nearly as long as endopodal merus, marginally fringed by long setae; epipod small, sutures subdividing into 2 proximal lobes and minute trianguliform terminal lobe. Third maxilliped (Figs. 2f, 3a) without exopod; endopod with long, dense setation on mesial margin, terminal 3 articles also with long setation on extensor margins; length of endopodal merus-ischium about 2 times width; ischium subquadrate, slightly longer than broad, diagonal length in adults about 1.6 times width at suture with merus, proximomesial margin forming subacute corner, internal surface with poorly defined, longitudinally oriented elevation bearing curved row of small denticles; merus subtriangular, distinctly broader than long; carpus heavy and subtriangular, with setose lobe on flexor margin, internal surface with dense field of fine setae in distal third; propodus large, subquadrate in adults, height often exceeding length, internal surface with narrow median field of fine, dense setae, opposable margin slightly emarginate; dactylus narrow, arcuate, in adults distinctly shorter than height of propodus, terminally with small brush of stiff bristles.

Branchial formula includes exopods and epipods as described for first and second maxillipeds above; branchiae limited to single rudimentary arthrobranch on second maxilliped, pair of arthrobranchs on third maxilliped, and pair of arthrobranchs on each of the first through fourth pereopods.

First pereopods of two sides forming dissimilar chelipeds, major cheliped heavy, massive in adults of both sexes (Fig. 1b–e), much less altered from minor cheliped in juveniles than in adults (Fig. 5c–f). Major cheliped of adults strongly calcified; ischium slender, superior margin weakly sinuous, inferior (flexor) margin with row of minute denticles; merus about twice as long

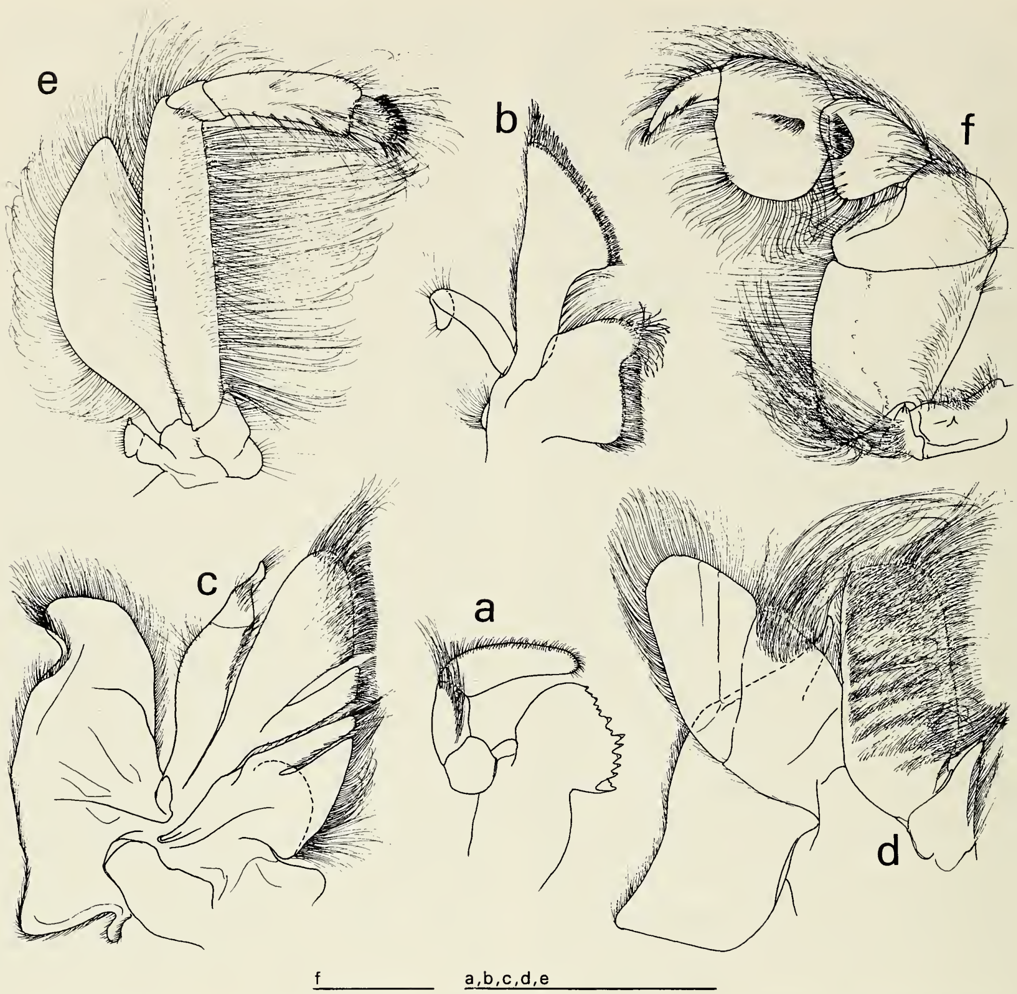

Fig. 2. *Sergio mericeae,* new species, type materials from Fort Pierce Inlet, Florida; a–e, female paratype (cl 26.5 mm), USLZ 3544; f, male holotype (cl 29.8 mm), USNM 268645, right mouthparts. a, Right mandible, external surface; b, First maxilla, external surface; c, Second maxilla, external surface; d, First maxilliped, external surface; e, Second maxilliped, external surface, rudimentary arthrobranch not shown; f, Third maxilliped, internal surface. Scale lines indicate 5 mm.

as high, superior margin weakly sinuous, sometimes with few minute tubercles proximally, inferior margin more strongly arcuate, proximally with strong projecting often bifurcate process of 2–3 fused spines, margin distal to process with short unarmed region beyond which margin is lined by small inferodistally directed teeth; carpus broad, relatively shorter and higher in adults than in immature specimens, in large adults length about $^6/_{10}$ of height, superior margin nearly straight, forming thin unserrated keel slightly overhanging internal surface, proximoinferior margin regularly rounded in outline, serrations of keel most evident on internal surface; propodus heavy, length (including fixed finger) in large adults about 1.7 times height, height greatest basally, superior margin of palm forming unserrated keel, especially in proximal half, inferior

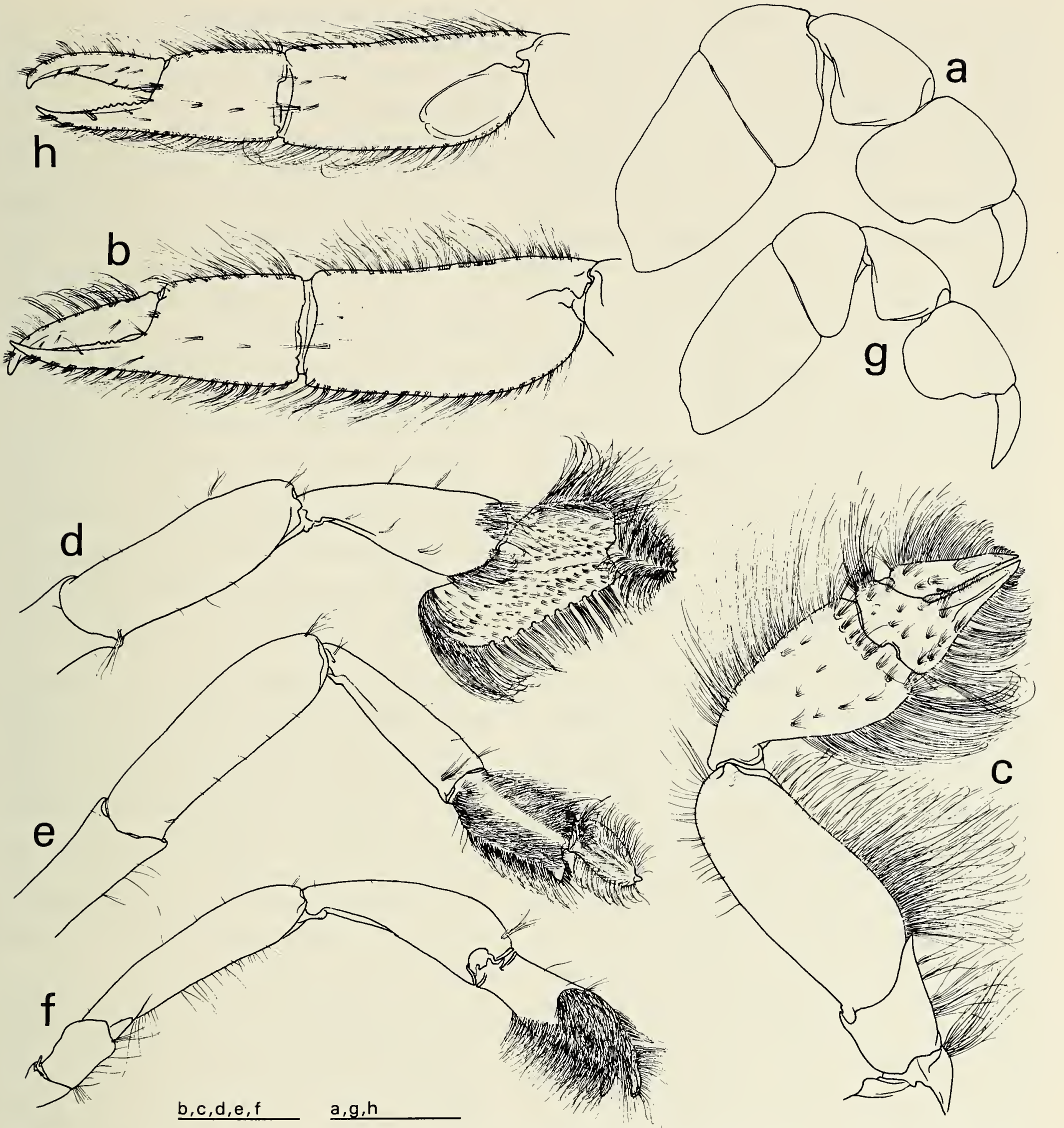

Fig. 3. *Sergio mericeae,* new species, type materials from Fort Pierce Inlet, Florida; a, b, female paratype (cl 26.5 mm), USLZ 3544; c–f, male holotype (cl 29.8 mm) USNM 268645. a, Right third maxilliped, external surface, setae not shown; b, Minor cheliped, internal surface; c, Right second pereopod, external surface; d, Right third pereopod, external surface; e, Right fourth pereopod, external surface; f, Right fifth pereopod, external surface. *Sergio guassutinga* (Rodrigues) from Aracaju, Brazil, female (cl 23.5 mm), USNM 268644: g, Right third maxilliped, external surface, setae not shown; h, Minor cheliped, internal surface. Scale lines indicate 5 mm.

surface with serrated keel most developed proximally, usually with 2–3 sharp short spines or teeth on external surface just proximal to gape; fixed finger in adults with prehensile margin ranging from strongly serrate to unarmed; dactylus (movable finger) subequal in length to palm, prehensile margin at midlength with large, hooked acute tooth bearing a single setose punctum at its base, separated proximally by deep emargination from a single heavy, quadrate basal tooth, and distally by another deep emargination from serrate margin on distal third of finger, finger terminated in acute, hooked tip.

Minor cheliped (Fig. 3b) slender, elongate in adults; ischium narrow, unarmed; merus elongately ovoid, length subequal to or slightly less than 2 times height, subequal to length of ischium; carpus rectangular, slightly longer than merus, length twice height, smooth; chela about as long as carpus; palm subrectangular, length slightly exceeding height; fixed finger subequal in length to palm, prehensile margin weakly serrate; dactylus (movable finger) in adults consistently exceeding length of palm, prehensile margin very weakly serrate.

Second pereopod (Fig. 3c) chelate, patches of long setae on inferior margin of ischium, most of flexor margin on merus and both margins of carpus lined with evenly spaced long setae, inferior margin of propodus with similar long setae proximally, progressively more reduced in length and stiffened distally, subterminally becoming dense patch of short, stiff bristles; prehensile margins of both fingers corneous, finely and uniformly microserrate along straight edge over most of length in both, microserration terminated distally in thickened corneous tips of fingers; superior margin of dactylus slightly sinuous, with long marginal setation becoming increasingly shorter length distally, replaced by dense patch of short stiff bristles subterminally; external surface of carpus, propodus and dactylus with scattered patches of short setae.

Third pereopod (Fig. 3d) merus length about 3 times width; carpus broadest distally, terminally with large patches of long setae overreaching propodus; propodus with strong proximally directed lobe on inferior margin, lobe terminally with long distally directed setae giving way to subdivided tufts of slightly shorter setae along inferodistal margin, superior margin with field of long setae, patterned tufts of lighter setae on outer face of article; dactylus tear-shaped, terminated in slightly cornified tip hooked toward external side, external surface densely setose, setae arranged in transverse bands on superior half.

Fourth pereopod (Fig. 3e) subchelate, inferodistal corner of propodus produced to form short fixed finger; soft dense setation on outer surface of propodus and dactylus, that of propodus divided into upper and lower fields, setae slightly longer in lower field which continues onto lower half of internal surface; dactyl terminated in narrow tip hooked toward external side.

Fifth pereopod (Fig. 3f) minutely chelate, opposable surfaces of propodus and minute dactylus excavate, spooned, terminally rounded, forming beak-like chela obscured by dense fields of setation on distal ½ of propodus and superior surface of dactylus; corneous prehensile lip of propodus pectinate.

Anterior abdominal somites smooth dorsally, surface sculpture of third through fifth tergites progressively more pitted, eroded, or undulated in appearance; second tergite with tuft of long setae on posterolateral lobe; third through fifth tergites each with a small broadly transverse field of very soft dense setae on the lateral lobe; sixth with distinct transverse, terminal, posteriorly facing groove above telson.

First pleopod of male and female uniramous, composed of 2 articles; in male (Fig. 4a), distal article subequal in length to or slightly shorter than proximal, subdivided into 2 lobes by weak longitudinal furrow, in mature male anterior lobe terminally rounded, posterior lobe terminally acute with tip directed anteroventrally; in female (Fig. 4b) proximal article subequal in length to terminal article, terminal article with weakly produced shoulder just beyond midlength. Second pleopod of male and female biramous; in male (Fig. 4c), dense setation largely restricted to tufts on lateral margin of exopod, distal extreme of exopod, lateral margin of endopod and appendix masculina, appendix masculina weakly separated from and not overreaching end of distal lobe of endopod, no evidence of appendix interna; in female (Fig. 4d, e), both rami with long setae, appendix interna small and acutely tapered distally. Third to fifth pleopod pairs (Fig. 4f) forming large, posteriorly cupped fans when coupled at mesial margins of endopods; endopod of each subtriangular, appendix interna embedded into mesial margin of endopod.

Telson (Figs. 1f, 5g) broader than long, subhexagonal, broadest at lateral lobes at midlength or in anterior half, posterior emargination producing pair of weak lobes or obtuse posterolateral corners, each terminated by a tuft of long setae; dorsal surface with low, lightly setose boss near each anterolateral corner, medially with subdivided short transverse carina bordered posteriorly by line of setae. Uropod with acute, posterolaterally directed spine on protopod, spine overreaching anterolateral margin of endopod; endopod broad, trapezoidal, slightly longer than broad, dorsal surface with tuft of long setae near posterolateral corner, setae of posterior margin longest posterolaterally; exopod with anterodorsal plate falling well short of distal exopod margin, distal edge of plate lined with short, thick spiniform setae grading to thinner longer setae of exopod margin and long stiff, spiniform setae at posterodistal corner of plate, distal margin of exopod with dense fringe of setation, fringe diminished and replaced by row of short spiniform setae on posterior margin.

Size.—Among the materials examined, the largest male (cl 31.1 mm; tl 115 mm) and largest female (cl 30.7 mm; tl 115 mm; ovigerous) were both taken from the immediate vicinity of Fort Pierce Inlet, Florida. Eggs on ovigerous specimens are small with sizes (max. diameter) after preservation ranging from 0.58–0.62 mm for immature eggs without developed eyespots to 0.62–0.68 mm for more mature eggs with well developed eyespots.

Color (from notes and color photographs of live specimens).—Variable and fading quickly to opaque white in alcohol. In life most adult specimens with violet pink to rose pink ground color, occasionally very pale; usually with darker pink to scarlet or orange-red on the chelae, cardiac region of carapace, dorsal tergites of abdominal segments 1–2, mid-dorsal and posterior extremes of abdominal tergites 3–5, telson and uropods. Sixth abdominal tergite usually with 2 faint, reddish longitudinal bands to either side of midline in anterior ⅔. Juveniles often with striking scarlet red to rosy red coloration almost overall, but also with pigment deepest in same body areas as indicated for adults above.

Known range and habitat.—Known from intertidal to shallow subtidal in the Indian River Lagoon and along the lower Atlantic coast of Florida, USA, and (on the basis of juveniles only) from coastal Gulf of Mexico localities in Louisiana, south Texas, and Tamaulipas, Mexico. The single immature specimen of *Sergio* collected from Mayaguez, Puerto Rico, in 1934 (coll: V. Biaggi, Jr., tl 73 mm, USNM 77462) which was previously reported as *S. guassutinga* by Biffar (1971) may or may not be correctly assigned to that species, but we must defer this determination until additional, fully mature and better preserved materials of that southerly population become available.

While most specimens have been taken with yabby pumps from intertidal to shallow subtidal substrates, specimens from off Louisiana were taken in a trawl deployed at a depth of approximately 12–13 m. In virtually all cases, the animals appear to be distributed within or near inlets to the open ocean. In inlets of the Indian River Lagoon, where they burrow alongside *Neocallichirus rathbunae,* they typically occupy less vegetated areas of sandbars, often just shoreward of where larger mounds of ejecta mark the burrows of *N. rathbunae.* At least in shallow waters, adults of *Sergio mericeae* appear to have mud-lined burrows with surface openings 6–10 mm in diameter, and may or may

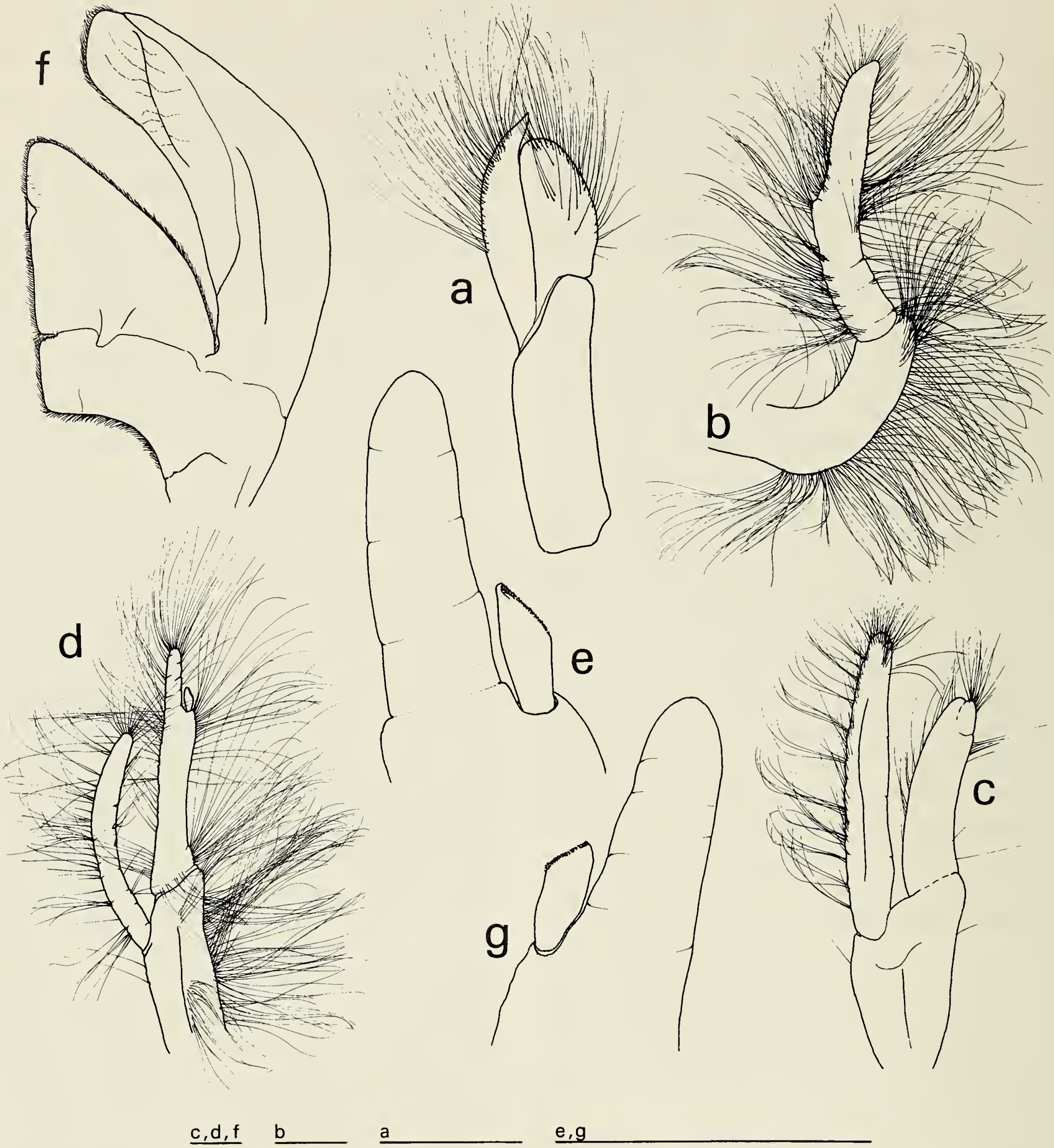

Fig. 4. *Sergio mericeae,* new species, type materials from Fort Pierce Inlet, Florida; a, c, f, male holotype (cl 29.8 mm), USNM 268645; b, d, e, female paratype (cl 26.5 mm), USLZ 3544. a, Right first pleopod of male, internal surface; b, Right first pleopod of female, lateral surface; c, Right second pleopod of male, posterior surface; d, Right second pleopod of female, posterior surface; e, Right second pleopod of female, distal endopod and appendix interna, posterior surface; f, Right third pleopod, anterior surface. *Sergio guassutinga* (Rodrigues) from Aracaju, Brazil, female (cl 23.5 mm), USNM 268644: g, Left second pleopod of female, distal endopod and appendix interna, posterior surface. Scale lines indicate 2 mm.

not have the burrow opening surrounded by a sand mound. Where mounds do occur, they are small, rarely exceed an elevation of 3–5 cm, and often are of muddier composition than the surface sand. Substrate cores extracted with yabby pumps in the more densely burrowed areas reveal relatively clean surface sands underlain by much muddier strata.

Etymology.—This species is named for

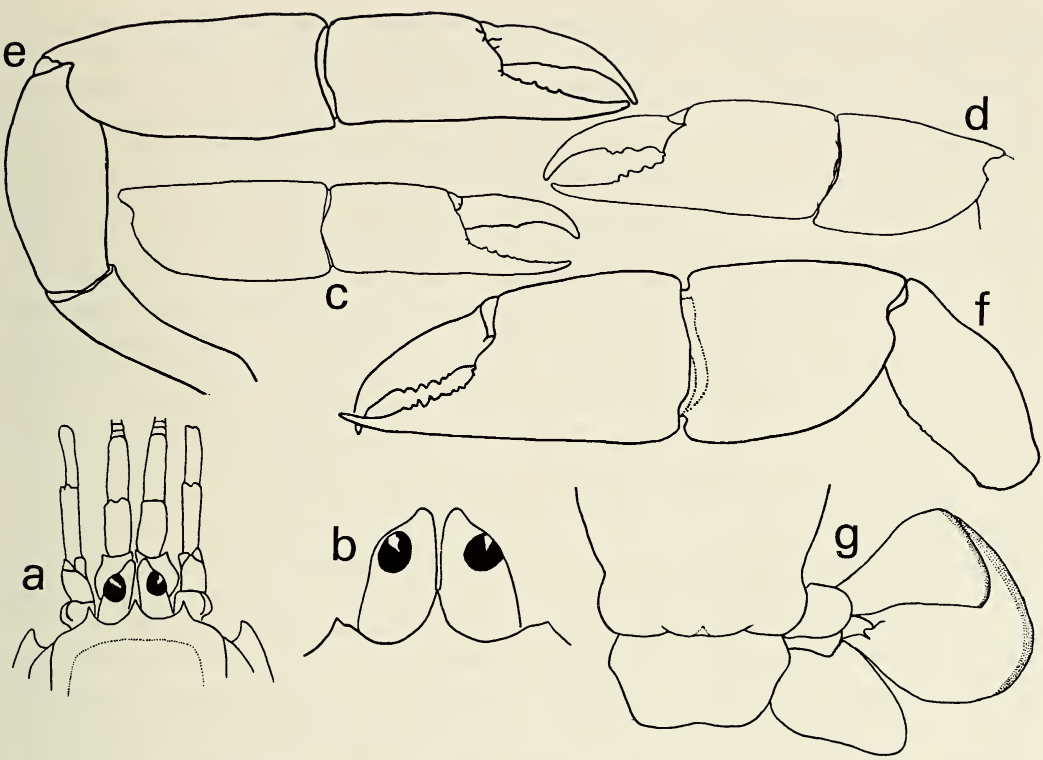

Fig. 5. *Sergio mericeae,* new species, juvenile paratypes from Fort Pierce Inlet, Florida, setae not shown; a, c, d, g, male (cl 8.3 mm), USNM 268694; b, male (cl 10.4 mm), USNM 268692; e, f, female (cl 10.6 mm), USNM 268645. a, Anterior carapace, eyestalks, antennal peduncles of immature male, dorsal view; b, front and eyestalks of immature male; c, Minor chela, internal surface, immature male; d, Major chela, internal surface, immature male; e, Minor chela, external surface, immature female; f, Major chela, external surface, immature female; g, Telson, right uropods, sixth abdominal segment, dorsal view, immature male. Not scaled.

our friend and colleague, Dr. Mary E. Rice, Director of the Smithsonian Marine Station– Link Port, Fort Pierce, Florida, in recognition of both her own substantial contributions in the field of marine invertebrate zoology and the generous assistance that she has provided to a large number of students, postdoctoral trainees, and fellow research scientists.

Remarks.—Like other species of the genus *Sergio, S. mericeae* can be distinguished from members of the closely related genus *Neocallichirus* on the basis of its relatively shorter and more angular, posteriorly emarginate telson and its narrower, more elongate uropodal endopods. In Florida, *S. mericeae* often occurs alongside *N. rathbunae, N. grandimanus,* and a third (yet to be described) *Neocallichirus* sp., all of which are also often reddish or pink in coloration. While mature and intact specimens of these species are readily distinguished from *S. mericeae* on the basis the major chela, all three of these *Neocallichirus* species also have broad, subquadrate uropodal endopods and a relatively long telson, the posterior margin of which is not notably emarginate but usually nearly straight or slightly convex in shape.

Distinction of *S. mericeae* from its southern equivalent, *S. guassutinga,* can in mature specimens be based upon several characters of the major cheliped. In *S. mericeae,* the merus of this appendage has a more rounded, less sharply defined longitudinal carina on the external surface and has a more produced proximal prominence on the inferior margin. In *S. mericeae* this prominence is also offset by a short gap from the remaining dentition of the inferior margin, while in *S. guassutinga* the dentition is more or less equally spaced in the region just beyond the prominence, the potential gap being interrupted by one or more sizable teeth. Overall, the dentition of this inferior border in *S. mericeae* is also more ventrally directed than in *S. guassutinga,* where the marginal teeth in mature specimens are usually either lower or slightly more hooked and are thus directed more distally. The proximal end of superior margin of this article in mature specimens also often bears a more defined row of low tubercles in *S. mericeae* than in *S. guassutinga.*

In the larger mature specimens of *S. mericeae,* the carpus of the major chela is relatively shorter and of slightly different shape than in the largest *S. guassutinga* specimens we have seen; while in the Brazilian specimens of *S. guassutinga* carpal length was greater than ½ the palm length and was never less than $^7/_{10}$ of carpal height, in *S. mericeae* the carpal length was about half of the palm length and nearer $^6/_{10}$ of carpal height. Given this difference in dimensions, the arcuate inferior margin of this article in *S. mericeae* is shorter than in *S. guassutinga* and semicircular in shape.

The somewhat broader third maxilliped in *S. mericeae* may also serve to distinguish it from *S. guassutinga.* However, differences in specimen preservation can cause variable shrinkage in the soft internal tissues of this appendage, and caution must be used determining article dimensions. As folding and crenelation of the integument were conspicuous in most specimens of *S. guassutinga* available to us, we briefly soaked the third maxillipeds in water to reinflate them prior to determining dimensions. The length of the merus-ischium (measured as a single unit) is consistently subequal to 2 times its maximum width in *S. mericeae,* while it is at least 2.2 times its width in *S. guassutinga.* Similarly, the diagonal length of the ischium alone is 1.6 to 1.7 times its width in *S. mericeae,* while it consistently exceeds 1.8 times its width in *S. guassutinga.* On the internal surface of the ischium, an elevated row of spines (the *crista dentata*) on the internal surface of the ischium, which is moderately developed in *S. guassutinga,* is much less developed and difficult to discern over part of its length in *S. mericeae.* The propodus of the third maxilliped also differs in the two species, with the greatest height of this article occurring in its proximal third in *S. mericeae.* By contrast, greater development of the inferodistal lobe of the propodus in *S. guassutinga* usually produces a greatest height near its midlength.

Other characters may further serve to differentiate these species, although they cannot be clearly established with presently limited comparative materials. Shrinkage and distortion in preserved specimens of *S. guassutinga* preclude our making of very detailed and quantitative comparisons of eyestalks, nephridiopore sculpture, anterior pleopods and telson, despite some evidence of divergence in morphology of these features. While sculpture of the male gonopod is often of considerable value in separating of closely related species, and the terminal shape in *S. mericeae* appears to differ strikingly from that illustrated for *S. guassutinga* by Rodrigues (1971, fig. 56), our close examination of available males for the latter species reveals a very similar gonopodal structure to that we have illustrated for *S. mericeae* (Fig. 4a, c). In both species the posterior lobe may have a terminally acute tip varying in degree of development with maturity. While the terminal posterior and anterior lobes appear to be slightly more divergent in males of *S. guassutinga* than in mature males of *S. mericeae* that we examined, only one of two available males of the former species is a large fully mature specimen, and we cannot therefore account for the range of possible variation in that species.

The color in life of *S. mericeae,* with its bright red chelipeds and overall bright red color is different from that described by Rodrigues (1971: 207, 209) for *S. guassutinga,* with the females whitish and the males with a pink abdomen and pink-yellowish larger cheliped in the male.

In the Indian River Lagoon, Florida, *S. mericeae* is almost always taken along with scarlet red commensal polyclad worms, 4–7 mm in length. In some cases 8–12 or more of these commensals are taken with materials extracted from a single host burrow. These are either found moving over surfaces of the captured ghost shrimp or are seen when water and mud extracted from the burrow with the yabby pump are washed over a sieve. The occurrence of these commensals in such washings appears to be definitive evidence that the burrow contains *S. mericeae,* as thorough extraction from such burrows never yields other species of callianassids. While we remain uncertain of the generic assignment for this commensal, Rodrigues (1971) has also observed, in addition to clausidiid copepod and reddish nemertean commensals, occurrence of an undescribed reddish species of the polyclad genus *Stylochoplana* with *S. guassutinga.* In both Lake Worth, Florida, and the Rio Carrizal Estuary, Tamaulipas, Mexico, burrows of callianassids herewith assigned to *S. mericeae* may also host the pinnotherid crab, *Pinnixa cristata* Rathbun (see Manning & Felder 1989, Rabalais et al. 1989).

Acknowledgments

We sincerely thank Sergio de Almeida Rodrigues, Instituto de Biociências, Universidade de São Paulo, Brazil, and Paula M. Mikkelsen, then Curator, Harbor Branch Oceanographic Museum, who provided access to comparative specimen materials, as well as Mary E. Rice, Director of the Smithsonian Marine Station at Link Port, who facilitated access to collecting sites and laboratory facilities at Fort Pierce, Florida. Among many individuals who assisted with our field collections and laboratory observations, we especially thank J. M. Felder, R. D. Felder, W. D. Lee, L. K. Manning, P. M. Mikkelsen, S. Petry and N. N. Rabalais, S. C. Rabalais, and R. K. Tinnin. We also thank Lilly King Manning for preparation of numerous comparative study sketches and Figure 5 for the present paper. This study was supported through an ongoing program of Smithsonian Marine Station project grants to R. B. Manning and D. L. Felder. Partial support was also provided to D. L. Felder through U.S. Minerals Management Service Cooperative Agreement 14-35-0001-30470, U.S. Fish and Wildlife Service Cooperative Agreement 14-16-0009-89-963, Task Order No. 6, and a small grant from the Coypu Foundation. This is contribution No. 249 for the Smithsonian Marine Station and contribution No. 48 for the USL Laboratory for Crustacean Research.

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Contribution to the knowledge of *Reynoldsia* Malloch (Diptera: Muscidae)

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Abstract.—Redescriptions are made of *Reynoldsia* Malloch and five species: *R. pectinata, R. brevitarsis, R. pteropleuralis, R. rufoapicata,* and *R. scutellata.* The morphology of the genital segments is described.

Malloch (1934) described and distinguished *Reynoldsia* from other Neotropical Coenosiinae by the subquadrate head, pointed upper apex of the flagellomere, long proboscis, slender, long and slightly clavate palpus, and presence of 2 presutural dorsocentral bristles, among other characters. Malloch (1934) figured the "forceps and penis" (Fig. 41c) of *R. rufoapicata,* but no complementary description of the genital segments was included. Seven species were originally described in *Reynoldsia,* and Malloch (1934) transfered *Limnophora aurifera* Bigot to this genus. Pont (1972) doubtfully included one more species, *Coenosia robusta* Stein, in the genus.

This analysis is based on specimens in the Museu Nacional (Rio de Janeiro) collection and material recently collected by Dr. Stephen Marshall (University of Guelph, Ontario, Canada). Study of these specimens made it possible to add new knowledge of some species, particularly about the morphology of the male and female genitalia. Some notes made by the late Dr. Dalcy de Oliveira Albuquerque (+ 1982) during his study of types in the National Museum of Natural History (Washington, D.C.) were also used.

In this study, a full redescription of *Reynoldsia pectinata,* the type species, and comparative redescriptions of four other species are presented.

Reynoldsia Malloch

Reynoldsia Malloch, 1934:210 [key], 230 [description]; Hennig, 1965:67 [citation]; Pont, 1972:36 [catalog]; Couri & Lopes, 1985:24 [key], Carvalho et al., 1993:132.

Type species.—*Reynoldsia pectinata* Malloch, 1934 (orig. desig.).

Diagnosis.—Eyes with or without small and sparse cilia; male dichoptic; head subquadrate in profile; epistome produced (Fig. 1); antenna with apex of flagellomere 1 acutely pointed; arista with very small cilia; palpus long, slender with slightly clavate apex. Prealar absent; scutellum bare below and laterally; prosternum bare; proepisternals 2; propleurals 2, directed upwards, posterior one about 2.5 times the length of other; katepisternals 1:1:1, forming equilateral triangle, lower calypter about 1.5–2.0 times as long as upper; dorsocentrals 2:3; wings with bare veins; veins R4 + 5 and M1 + 2 parallel at apex. Legs with claws and pulvilli well developed. Hind tibia with at least 2 anterodorsal and 2 posterodorsal bristles. Sternite I bare. Male: sternite V "U"-shaped (Fig. 6); cercal plate and surstyli strongly developed, elongate inferiorly (Figs. 7–8); hypopygium produced, phallic complex modified with elongate hypandrium (Fig. 9). Female: proboscis with haustellum partially sclerotized; prestomal teeth developed (Fig. 23); ovipositor long with microtrichia in all segments; cerci long, surpassing hypoproct (Figs. 16–17). Egg: *Phaonia* type (Figs. 30–31).

Comments.—*Reynoldsia* is endemic to southern South America. Adults range in size from 7.0–9.0 mm. The arrangement of the katepisternal bristles in an equilateral triangle and the presence of microtrichiae at sternites VI and VII place this genus among the Coenosiinae, Coenosiini (sensu Carvalho 1989). This is probably a primitive Coenosiinae, as evidenced by an included species with a setulose anepimeron (*R. pteropleuralis*).

Reynoldsia pectinata Malloch
Figs. 1–10

Reynoldsia pectinata Malloch, 1934:230 [key], 235-236 [description ♂♀], 238 [Fig. 41a, mid femur ♂]; Pont, 1972:36 [catalog], Carvalho et al., 1993:132.

Holotype.—♂. Tierra del Fuego, Rio Grande (BMNH, London).

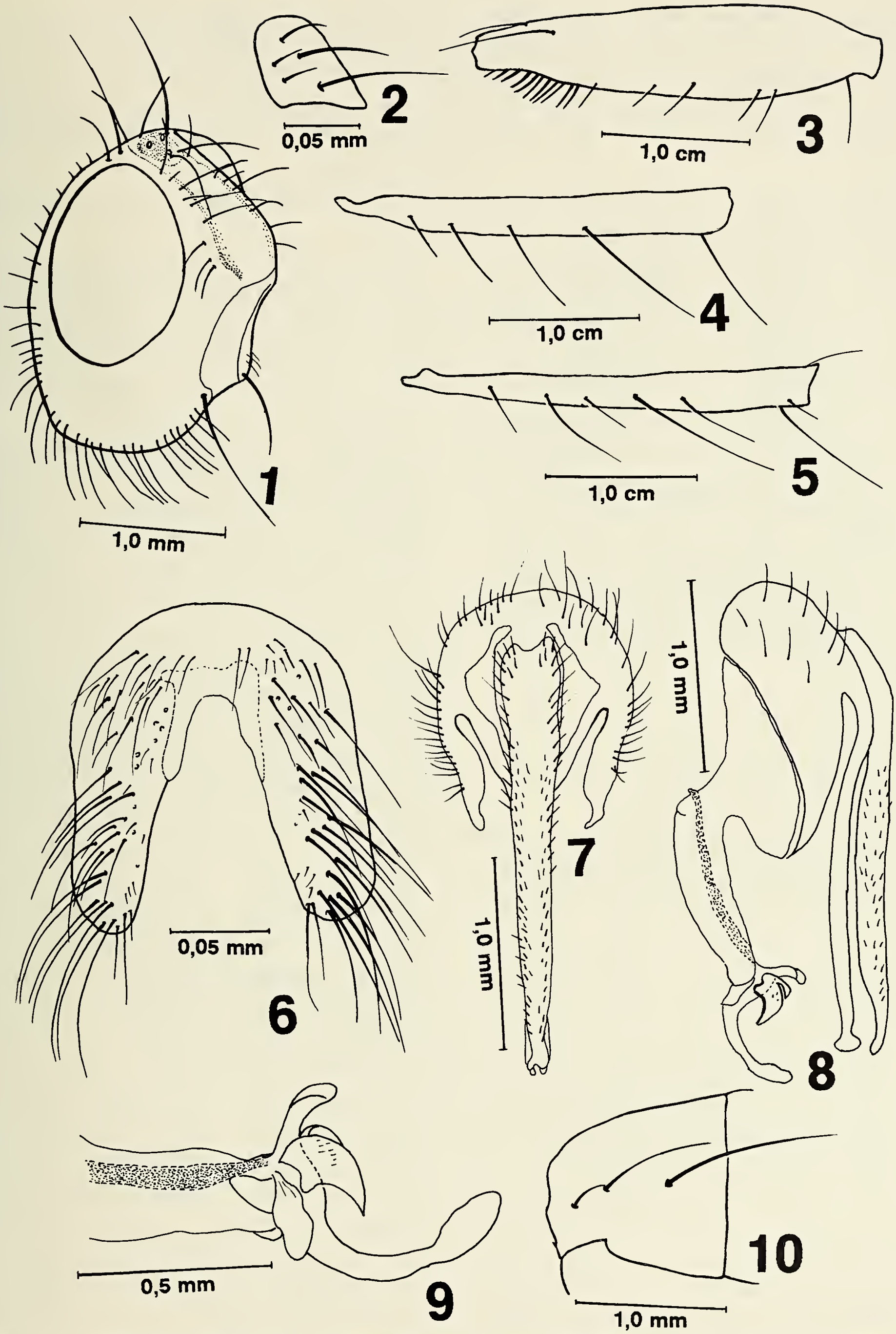
Diagnosis.—Frons brown, strongly silvery pollinose; antenna with flagellomere 1 about 1.8 as long as pedicel (Albuquerque's notes); acrostichal presutural bristles differentiated; brown vittae at acrostichal and intralar surfaces, the 2 intralar vittae reaching apex of scutellum; halter yellow with knob brown; hind femur at posteroventral surface with comb-like row of bristles at apical-3rd, more developed in male; hind tibia at anteroventral surface with 3 bristles at middle 3rd, the basal one weaker; abdomen grayish with lateral dark brown subtriangular spots in all tergites, so that they are largely shining black in center. Cercal plate fine (Fig. 7).

Coloration.—Parafacial, parafrontal, face, lunule and genae brown, strongly silvery pollinose. Gena reddish-brown. Ocellar triangle dark brown. Antenna, arista and palpus dark brown. Mesonotum brown, gray pollinose, and with 3 large brown vittae at acrostichal and intralar surfaces. Pleurae of same color of mesonotum. Calypter whitish. Halter yellow with knob brown. Legs dark brown with apical 3rd or less of femora and entire tibiae yellow. Abdomen grayish pollinose as thorax, with lateral dark-brown sub-triangular spots in all tergites, so that they are largely shining black.

Male.—Body length 8.0 mm; wing length 7.0 mm.

Head.—(Fig. 1). Eyes with very small and sparse cilia. Eyes separated, at anterior ocelli level, by a space about 0.41 of head width. Frons with 6 pairs of long bristles. Inner vertical long, parallel and directed posteriorly, outer vertical shorter and divergent. Antenna broken in the examined specimen (flagellomere 1 about 1.8 length of pedicel—Albuquerque's notes).

Thorax.—Acrostichal presutural differentiated, irregular and long, in number of 4 in the observed specimen and a prescutelar pair; humerus with 5 bristles disposed as in Fig. 2; presuturals 1; supralar 1; post-supralar 2. Notopleuron with 2 similar bristles. Scutellum with a lateral and an apical pair of strong bristle. Fore femur at dorsal, posterodorsal, posteroventral and ventral surfaces with a row of bristles. Fore tibia at posterior surface with a median seta. Mid femur at anterior and anterodorsal surfaces with a row of bristles at basal ⅔, anteroventral surface with a complete row of bristles, posterior surface with 2 preapical bristles, posteroventral surface with a comb-like row of bristles at apical 3rd (Fig. 3). Mid tibia at anterodorsal and posterior surfaces with 3 long bristles at middle 3rd, apical bristles at all surfaces, the anteroventral and posteroventral ones longer. Hind femur at anterodorsal, anterior, anteroventral, ventral and posteroventral surfaces with a row of bristles, the anterior one irregular. Hind tibia (Figs. 4–5) at anteroventral surface with 3 bristles at middle 3rd, the basal on weaker, anterodorsal surface with 4 bristles, posterodorsal surface with 5 bristles, the 2nd and the 4th longer, dorsal and posterodorsal surfaces with a preapical bristle, anterior surface with 3 apical bristles and ventral surface with one.



Figs. 1–10. *Reynoldsia pectinata*, ♂: 1. Head, profile; 2. Humerus, lateral view; 3. Femur II, posterior view; 4. Tibia III, anterior view; 5. Tibia III, posterior view; 6. Sternite V, dorsal view; 7. Cercal plate and surstyli, dorsal view; 8. Cercal plate, surstyli and phallic complex, lateral view; 9. Phallic complex, lateral view; 10. Prescutum, ¾ view.

Abdomen.—Tergites I–IV with developed lateral bristles at disc and apex, tergite V with a complete row of bristles at disc and apex. Sternite V with bristles on disc, more numerous and longer at "U" arms (Fig. 6).

Genitalia.—Cercal plate fine (Fig. 7); aedeagal apodeme surpassing margin of hypandrium, distiphallus straight (Figs. 8–9).

Material examined.—Chile: 1 ♂, Punta Arenas, 31 Dec 1950, R. Bassiento (MNRJ).

Comments.—Albuquerque examined one male and two females from Punta de Arenas (31/XII/1950, R. Bassiento col.) and noted that each has three dorsocentral presutural bristles. This could complicate the generic diagnosis. In the specimen examined (probably the same male as studied by Albuquerque), the extra bristle is actually present but is much shorter than the others and not aligned with them (Fig. 10). I examined no females.

Reynoldsia brevitarsis Malloch
Figs. 11–15

Reynoldsia brevitarsis Malloch, 1934:231 [key]; 233-234 [description ♂♀]; Pont, 1972:36 [catalog], Carvalho et al., 1993: 132.

Holotype.—♂. Argentina, Lake Guitiérrez (BMNH, London).

Diagnosis.—Frons brown, silvery pollinose; antenna with flagellomere 1 about 2.7 length of pedicel; acrostichal presutural bristles not differentiated; mesonotum with brown vittae at acrostichal and intralar surfaces, the 2 lateral ones reaching apex of scutellum; halter yellow with knob yellowish brown; mid and hind femora at ventral surface with numerous long and fine bristles; hind femur at posteroventral surface without a comb-like row of bristles at apical 3rd; hind tibia at anteroventral surface with 2 bristles; abdomen grayish pollinose; tergites III–V with lateral quadrangular brown spots. Cercal plate large (Fig. 14)

Differs from *R. pectinata* as follows:

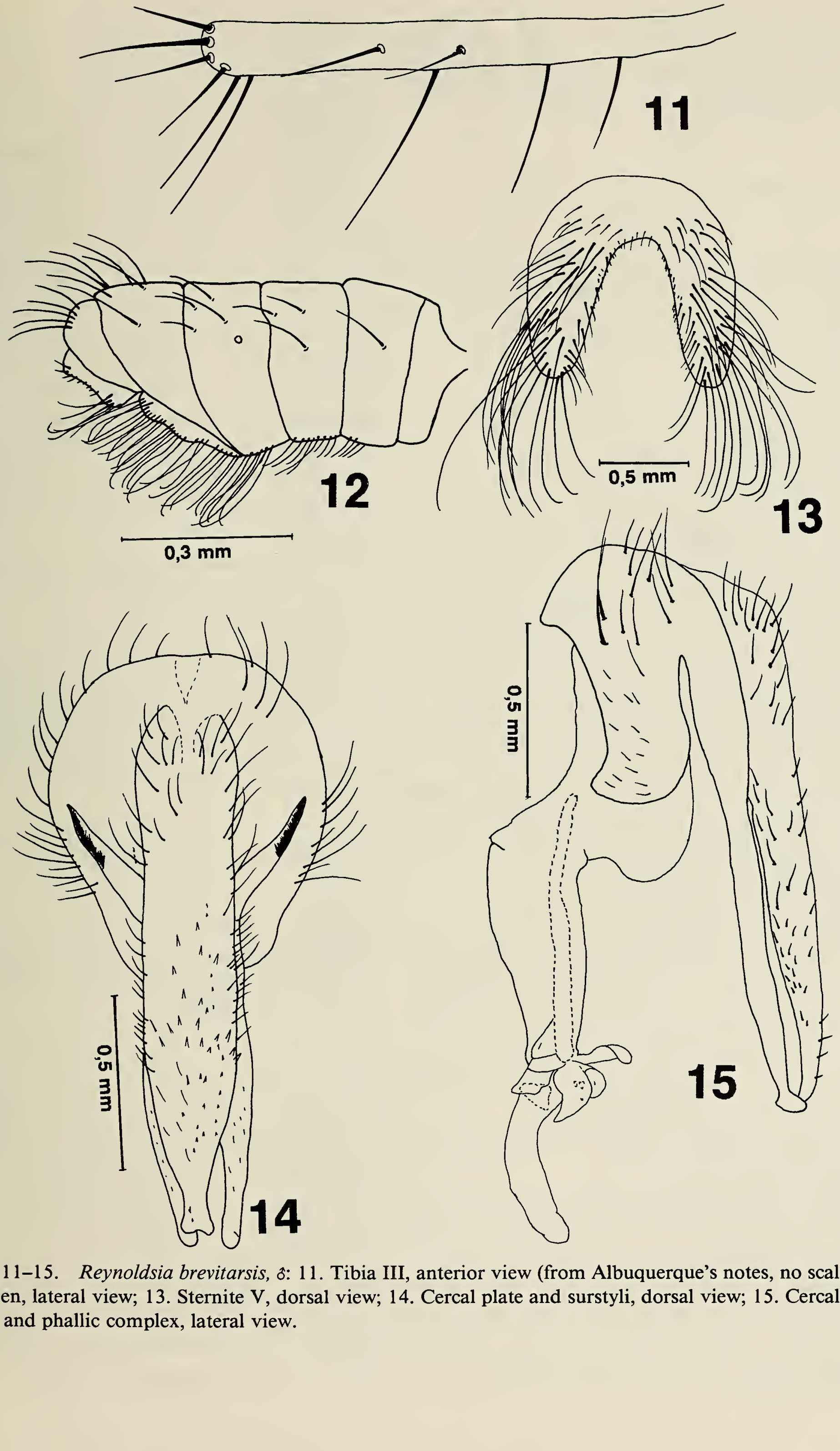
Coloration.—Mesonotum with faint brown vittae; halter yellow with knob yellowish brown; abdomen grayish pollinose; tergites III–V with lateral quadrangular brown spots.

Male.—Body length 7.0 mm; wing length 6.5 mm.

Head.—Eyes separated, at anterior ocelli level, by a space about 0.45 of head width. Frons with 5 pairs of long and strong bristles and with 4 intercaleted fine, short ones. Antenna with flagellomere 1 about 2.7 times the length of pedicel.

Thorax.—Acrostichal presutural not differentiated; humerus with 3 long bristles disposed as an equilateral triangle. Mid and hind legs broken in the examined specimen. Adding Malloch's description, Albuquerque had written in his notes (legs of ♂ and ♀): mid femur at anterior surface with a row of bristles, a little beyond basal half and with a preapical one; anteroventral surface in females with a series of strong bristles at apical half, in males, anteroventral, ventral and posteroventral surfaces with a row of long and fine bristles, specially at base; posterior surface with 2 preapical bristles. Mid tibia at anterior surface with 3 bristles; posterodorsal surface with 2–3 bristles at basal half. Hind femur at anterior surface with a row of bristles, more developed in females; anteroventral surface, in females, with a row of bristles; in males, anteroventral, ventral and posteroventral surfaces with long and fine bristles, specially at base; dorsal and posterior surfaces with an apical bristle. Hind tibia at anterodorsal and posterodorsal surfaces with 3 bristles each, inserted almost at same level, reaching a little more than basal half, anteroventral surface with 2 bristles. Dorsal, anterodorsal, anterior, and anteroventral surfaces with one apical bristle and ventral surface with 2 apical ones (Fig. 11, from Albuquerque's notes).

Abdomen.—Ventral surface, at apical half, specially sternite V with long and curled hairs (Figs. 12–13).



Figs. 11–15. *Reynoldsia brevitarsis,* ♂: 11. Tibia III, anterior view (from Albuquerque's notes, no scale); 12. Abdomen, lateral view; 13. Sternite V, dorsal view; 14. Cercal plate and surstyli, dorsal view; 15. Cercal plate, surstyli and phallic complex, lateral view.

Genitalia.—Cercal plate large (Fig. 14); distiphallus large (Fig. 15).

Material examined.—Argentina: 1 ♂, Bariloche, paratype no. 49875, Rio Negro, Nov 1926, R. & E. Shannon.

Reynoldsia pteropleuralis Malloch
Figs. 16–18

Reynoldsia pteropleuralis Malloch, 1934:232 [key], 237–238 [description ♂♀], 238 [Fig. 41b: hind tibia, 41c: forceps and penis]; Pont, 1972:36 [catalog], Carvalho et al., 1993:132.

Holotype.—♀. Argentina. Lake Nahul Huapi (BMNH, London).

Diagnosis.—Frons brown, silvery pollinose; antenna with flagellomere 1 about 2.5 length of pedicel; acrostichal presutural bristles not differentiated; brown vittae at acrostichal and intralar surfaces, the 2 lateral ones reaching apex of scutellum; halter yellow with knob black; anepimeron with short cilia at disc; hind femur at posteroventral surface with a comb-like row of bristles at apical 3rd; hind tibia at anteroventral surface with 2 bristles at middle 3rd; abdomen grayish pollinose with lateral quadrate dark spots in all tergites. Sternite VII with a row of small spines (Figs. 16–17). Spermatheca as in Fig. 18.

Differs from *R. pectinata* as follows:

Coloration.—Parafacial, parafrontal, face, lunule, and genae brown, silvery pollinose. Halter brownish yellow with knob dark brown. Legs dark brown with apical half of femora and entire tibiae yellow. Abdomen grayish pollinose as thorax, with lateral quadrate dark spots in all tergites.

Female.—Body length 9.0 mm; wing length 7.5 mm.

Head.—Eyes separated, at anterior ocelli level, by a space about 0.38 of head width. Antenna with flagellomere 1 about 2.5 times length of pedicel.

Thorax.—Acrostichal presutural not differentiated, humerus with 3 bristles. Anepimeron with a few fine hairs at middle. Mid femur at anterior surface with a row of bristles at basal half and one bristle inserted at apical 3rd, ventral surface with sparse long bristles at basal half, posterior surface with a complete row of bristles and with 2 preapical bristles. Mid tibia at anterodorsal surface with 3 long bristles at middle 3rd, posterior surface with 2 bristles at middle 3rd. Hind femur at anterodorsal and anteroventral surfaces with a row of long and sparse bristles. Hind tibia at anteroventral surface with 2 bristles at middle 3rd, anterodorsal and posterodorsal surfaces with 3 bristles at basal half, the anterior ones weaker.

Abdomen.—Tergites I–IV with developed lateral bristles at disc and apex.

Genitalia.—Epiproct with a reentrance on basal margin; sternite VII with a row of small spines (Figs. 16–17).

Material examined.—Argentina: 1 ♀, San Martin de los Andes, 1900 m, 28 Dec 1989. S. A. Marshall.

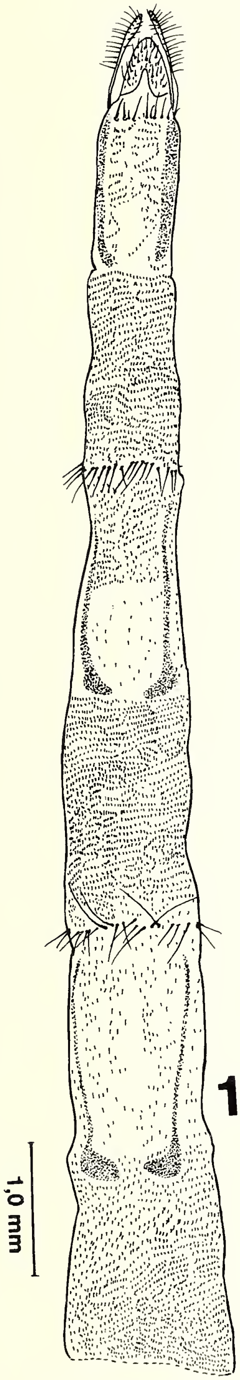
Comments.—Malloch (1934: 238, Fig. 41c) noted the peculiar male hypopygium, a character that should distinguish this species from its congeners. The modification of male phallic complex, however, is found in all studied species.

Reynoldsia rufoapicata Malloch, 1934
Figs. 19–26

Reynoldsia rufoapicata Malloch, 1934:231 [key], 239 [description ♂♀], 238 [Fig. 41d: hind tibia]; Pont, 1972:36 [catalog], Carvalho et al., 1993:133.

Holotype.—♂. Argentina. Bariloche (USNM, Washington).

Diagnosis.—Frons dark, with whitish-gray or brownish-gray dust; antenna with flagellomere 1 about 2.0 length of pedicel; acrostichals presutural bristles differentiated; brown vittae at acrostichals and intralar surfaces, the 2 lateral ones reaching apex of scutellum; halter yellow with knob black; hind femur at posteroventral surface without a comb-like row of bristles at apical 3rd; hind tibia at anteroventral surface with 2



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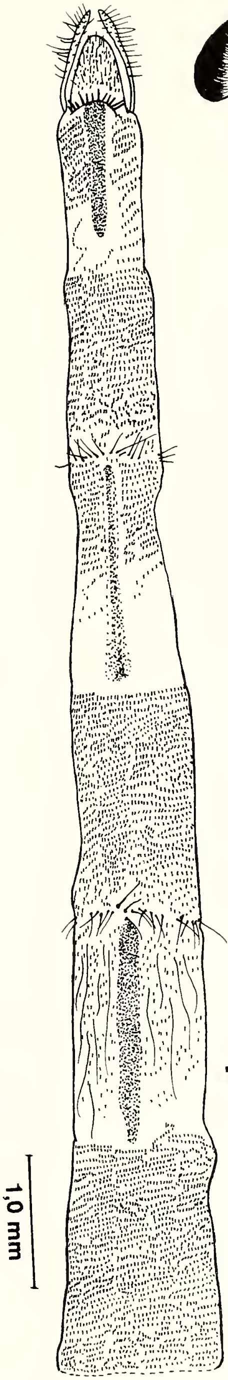

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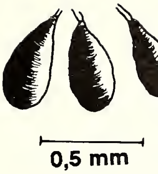

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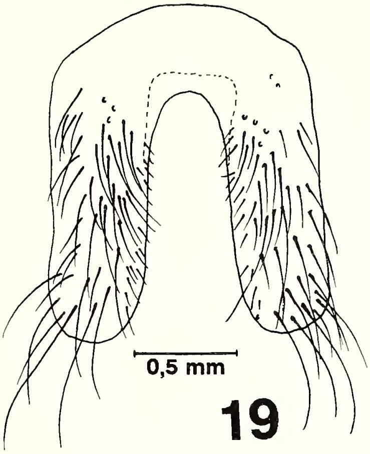

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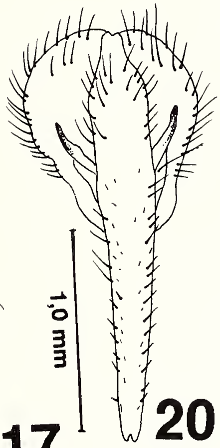

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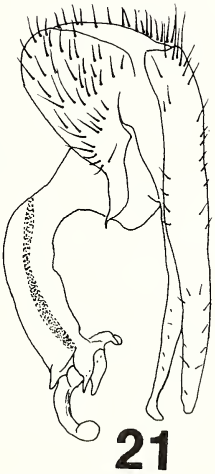

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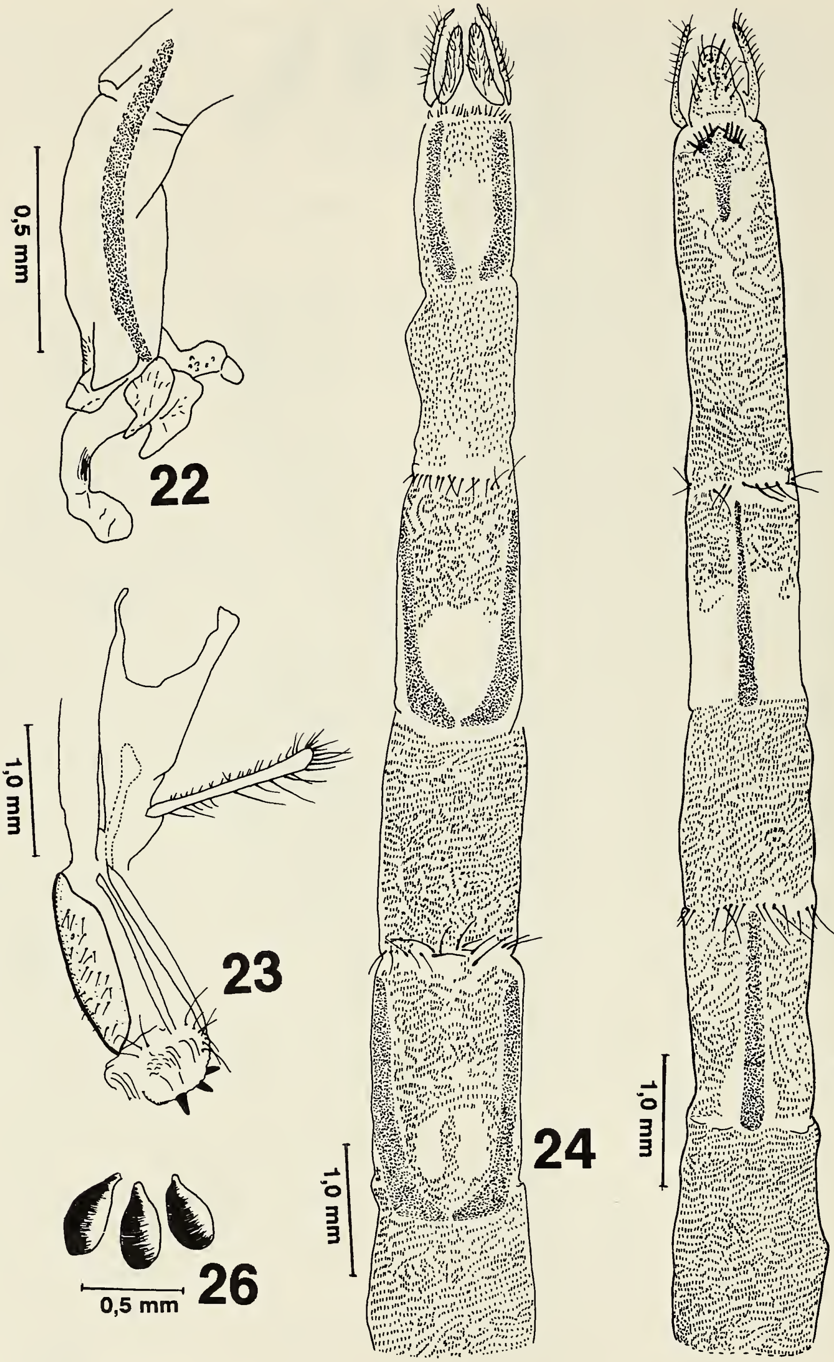
Figs. 16–21. *Reynoldsia pteropleuralis*, ♀: 16. Ovipositor, dorsal view; 17. Ovipositor, ventral view; 18. Spermatheca. *Reynoldsia rufoapicata*, ♂ and ♀: 19. Sternite V, dorsal view; 20. Cercal plate and surstyli, dorsal view; 21. Cercal plate, surstyli and phallic complex, lateral view.



Figs. 22–26. *Reynoldsia rufoapicata,* ♂ and ♀: 22. Phallic complex, lateral view; 23. Proboscis, ♀; 24. Ovipositor, dorsal view 25. Ovipositor, ventral view; 26. Spermatheca.

bristles at middle 3rd; abdomen black, lateral spots more visible in female.

Differs from *R. pectinata* as follows:

Coloration.—Parafacial, parafrons, face, lunule and genae brown, gray pollinose. Legs dark brown with apical 3rd of femora and entire tibiae yellow. Abdomen black, lateral spots more visible in female.

Male.—Body length 8.0 mm; wing length 7.5 mm.

Head.—Eyes separated, at anterior ocelli level, by a space about 0.40 of head width. Frontal row with 8 long pairs of bristles. Antenna with flagellomere 1 about 2.0–2.1 times length of pedicel.

Thorax.—Mid femur at anterior surface with a row of bristles at basal ⅔ and one at apical 3rd, anteroventral surface with a row of bristles at basal half, posterior surface with 2 preapical bristles. Mid tibia at anterodorsal surface with 3 long bristles at middle 3rd, posterior surface with 2 bristles at middle 3rd. Hind femur at anterior surface with 3 bristles at middle 3rd, anterodorsal surface with a complete row of bristles, anteroventral surface with a row of bristles at basal ⅔ and one bristle at apical 3rd. Hind tibia at anterodorsal and posterodorsal surfaces with 3 bristles at middle 3rd, anteroventral surface with 2 bristles at middle 3rd.

Abdomen.—Sternite V with anterior concavity deep (Fig. 19).

Genitalia.—Cercal plate straight; surstyli longer than cercal plate (Figs. 20, 21, and 22).

Female.—Body length 7.0 mm; wing length 8.0 mm. Similar to male.

Genitalia.—Epiproct completely divided; sternite VII with row of short spines in each side (Figs. 24–25). Spermatheca as in Fig. 26.

Material examined.—Argentina: 6 ♂, 3 ♀, San Martin de los Andes, slope of Cerro Chapelco, 1.500 m, 28 Nov 1989. S. A. Marshall (MNRJ).

Comments.—Malloch (1934) stated that this species is very similar to *R. pectoralis,* differing mainly in the lack of pteropleural hairs, coloration on apex of femora and the apical bristling of hind tibia.

Reynoldsia scutellata Malloch

Reynoldsia scutellata Malloch, 1934:232 [key], 234–235 [description ♀]; Pont, 1972: 36 [catalog], Carvalho et al., 1993:133.

Holotype.—♂. Argentina, Puerto Blest (BMNH, London).

Diagnosis.—Frons brown, brown dusted; antenna with flagellomere 1 about 3.0 times length of pedicel; acrostichals presutural bristles differentiated; brown vittae at acrostichals and intralar surfaces, none of them reaching scutellum, which is uniformly brownish-gray; halter brownish-yellow; trochanters yellow; hind femur at posteroventral surface without a comb-like row of bristles at apical 3rd; hind tibia at anteroventral surface with 1 bristle at middle 3rd; abdomen grayish with lateral dark-brown subtriangular spots in all tergites.

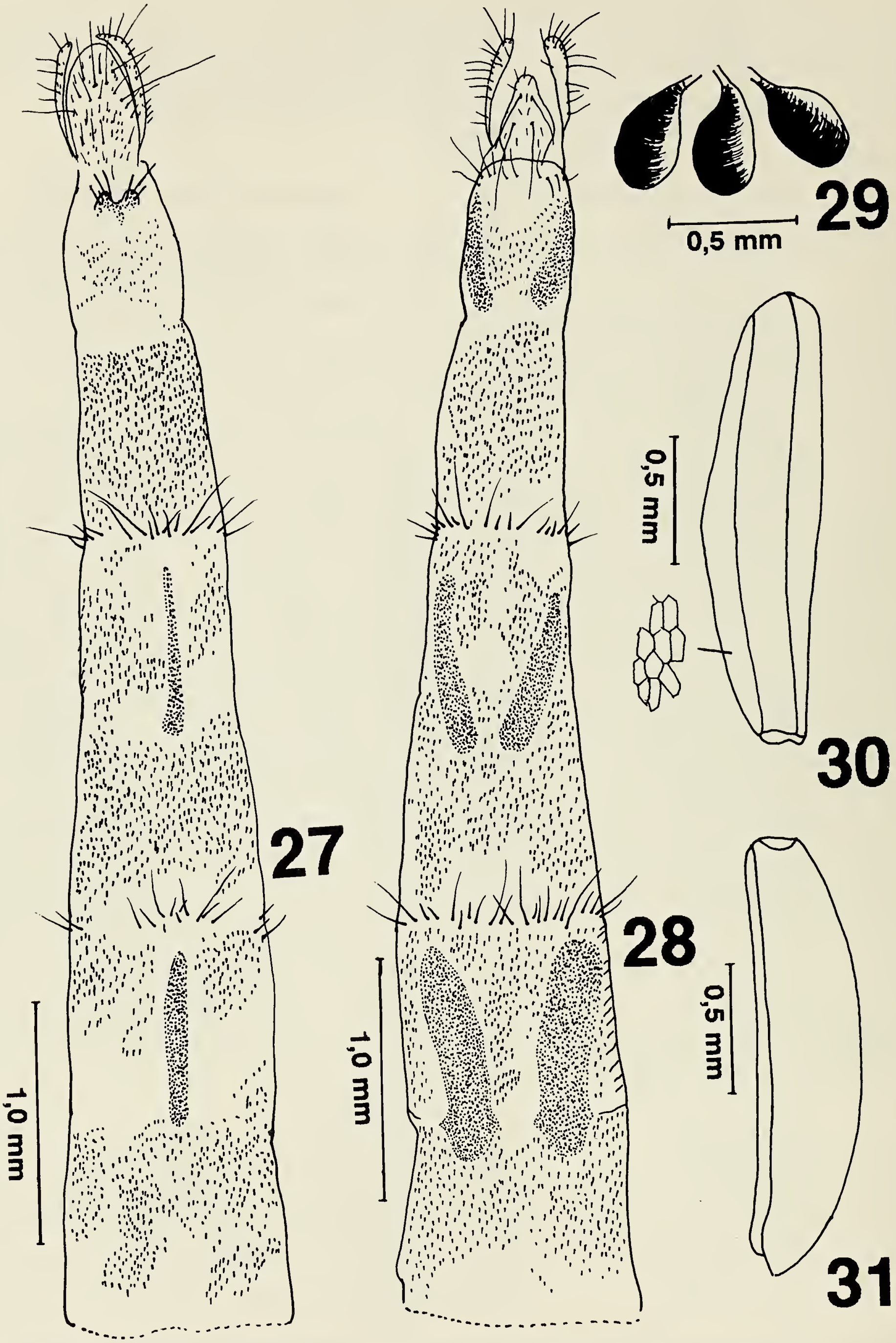
Differs from *R. pectinata* as follows:

Coloration.—Parafrontal, frons and lunule brownish yellow. Parafacial and gena silvery pollinose. Gena brown at vibrissal level. Mesonotum with the lateral brown vittae not continuing to scutellum, which is entirely brownish gray. Halter brownish-yellow. Trochanters yellow. Abdomen gray, tergites III and IV with very faint lateral brown spots.

Female.—Body length 7.0 mm; wing length 6.5 mm.

Head.—Eyes separated by a space about 0.55 of head width, at anterior ocelli level.

Thorax.—Humerus with 2 bristles, the outer one longer. Fore femur at posterodorsal and posteroventral surfaces with a row of bristles. Fore tibia at posterior surface with a median bristle. Mid femur at anterior surface with 4 sparsed bristles at basal half, ventral surface with 3 bristles at



Figs. 27–31. *Reynoldsia trochanterata,* ♀: 27. Ovipositor, dorsal view; 28. Ovipositor, ventral view; 29. Spermatheca; 30. Egg; 31. Egg, lateral view.

basal 3rd, the last one longer, one median bristle and a row of short bristles at apical 3rd. Mid tibia at anterodorsal surface with 2 bristles at middle 3rd, apical bristles at anteroventral and posteroventral surfaces long. Hind femur at anterodorsal, anterior, anteroventral, ventral and posteroventral surfaces with a row of bristles, the anterior one irregular. Hind tibia at anteroventral surface with 3 bristles at middle 3rd, the basal one weaker, anterodorsal surface with 4 bristles, posterodorsal surface with 5 bristles, the 2nd and the 4th longer, dorsal and posterodorsal surfaces with a preapical bristle, anterior surface with 3 apical bristles and ventral surface with one.

Genitalia.—Ovipositor not so long as in the other species; tergites larger (Figs. 27–28). Spermatheca as in Fig. 29. Egg as in Figs. 30 and 31.

Material examined.—Chile: 1 ♀, Cerros de Nahuelbuta, Angol 650 m, 12 Oct 1931, D. S. Bullock (MNRJ).

Comments.—Malloch's (1934) descriptions of *R. scutellata* and *R. trochanterata* are very similar. Both species have yellow trochanters and a uniformly colored scutellum, which are diagnostic characters to Malloch (1934). A more detailed analysis of the types could clarify if they are really synonyms.

Acknowledgments

I am grateful to Dr. Stephen Marshall (University of Guelph, Ontario) for the donation of specimens to the Museu Nacional, Rio de Janeiro, and to Dr. Raymond Gagné (Systematic Entomology Laboratory, Department of Agriculture, Washington, D.C.) for suggestions and comments.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(2):292–297. 1995.

Rediagnosis of the brittlestar genus *Ophiosyzygus* and notes on its type species *O. disacanthus* (Echinodermata: Ophiuroidea: Ophiomyxidae) based on the type specimens from Japanese waters and new material from the Gulf of Mexico

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Abstract.—Two specimens of the ophiomyxid brittlestar *Ophiosyzygus disacanthus* H. L. Clark, 1911 represent the first new record of the species since the original description. The new specimens are from the Gulf of Mexico and are conspecific with the type material from Japan. The generic diagnosis is emended to include radial shields and dorsal arm plates. Evidence is given that these types of ossicle have been overlooked frequently in ophiomyxids.

In 1911, H. L. Clark described a new monotypic genus of ophiomyxid brittlestar, *Ophiosyzygus,* based on two specimens from U.S. Fisheries Commission Steamer *Albatross* stations off the southwestern coast of Japan. Among other characters, the genus was diagnosed as lacking radial shields and dorsal arm plates. Two specimens of the type species, *O. disacanthus* H. L. Clark, 1911, were recently collected from the Gulf of Mexico off the southwestern coast of Florida, U.S.A., and they differ little from the type material. Our discovery of radial shields and dorsal arm plates in the Gulf of Mexico specimens and, subsequently, in Clark's North Pacific specimens prompts us here to emend the generic diagnosis. Examination of some museum material and a review of literature on the Ophiomyxidae indicate to us that small radial shields and thin dorsal arm plates have been overlooked often in this family.

Family Ophiomyxidae Ljungman, 1867
Subfamily Ophiomyxinae Ljungman, 1867
Genus *Ophiosyzygus* H. L. Clark, 1911

Ophiosyzygus.—Clark, 1911:275–276 (diagnosed), 279 (compared to *Ophioleptoplax*).—Clark, 1915:172 (listed).—Fell, 1960:14 (key).—Spencer & Wright, 1966: 89 (listed in systematic review).

Diagnosis (emended).—Disc covered with skin in which are embedded, at least near margin, numerous minute delicate scales, on which are borne larger, presumably calcareous granules. Radial shields small. Tentacle scales lacking. Arm spines few, with upper ones successively united to each other by a broad, thin, horizontal membrane. Dorsal arm plates thin, simple, multiperforate. Teeth a cluster of a few, minute, rough spinelets at apex of jaw. Oral papillae small, few, and unlike teeth.

Type species.—*Ophiosyzygus disacanthus* H. L. Clark, 1911, by original designation. The genus is monotypic.

Etymology.—Given by Clark (1911), in reference to the webbing of the upper arm spines by horizontal and vertical webs of skin in dried and alcoholic specimens. Hendler & Miller (1991) found that the webbing of arm spines on dried *Ophiogeron supinus* is an artifact from desiccation of the gelatinous tissues of the arm. They were unable to induce swimming in live *O. supinus* by methods that worked successfully on four other species. These authors joined Mortensen (1932) in refuting Clark's (1911) initial implication and his (Clark 1941) later prediction that the webbed spines of ophiomyxids are used for swimming. Based on the findings of Hendler & Miller (1991), arms of *Ophiosyzygus disacanthus* in life probably are fleshy, not webbed.

Remarks.—Clark's (1911) diagnosis of the genus included the absence of radial shields and dorsal arm plates. We found both kinds of plate in the material listed below for *O. disacanthus.* Clark (1911, fig. 139a) illustrated small triangular radial shields (Fig. 1B) on *O. disacanthus,* but he described them as the "expanded ends of genital plates." Dissection of the new material from the Gulf of Mexico and re-examination of the types revealed that they indeed are radial shields, each articulating with a paired slender genital plate and genital scale (Fig. 1A). In fact, Clark's (1911) figure includes the ends of the genital plates below the misidentified radial shields (Fig. 1B). The dorsal arm plates of type and new specimens are simple multiperforate plates (Fig. 2) that are difficult to see in situ and similar to those of *Ophiodera serpentaria* (Mortensen 1933a, figs. 1, 2) and of *Ophioscolex inermis* (Mortensen 1933b, fig. 36b). Clark (1911) overlooked them, although he reported similar dorsal arm plates in *Ophioleptoplax megapora.*

Paterson (1985:18) described the Ophiomyxidae generally as having "rudimentary and inconspicuous radial shields." Equally or more rudimentary and inconspicuous in some ophiomyxids are the dorsal arm plates. Byrne & Hendler (1988) concluded that the Ophiomyxidae have a reduced skeleton in which the function of some parts has been largely assumed by mutable collagenous tissue. The loss of basic elements of the ophiuroid skeleton in some ophiomyxids might, therefore, not be surprising. Numerous genera have been diagnosed as lacking radial shields and dorsal arm plates. Subsequent examination by us and other authors has, however, confirmed the presence of radial shields or dorsal arm plates in some of these genera.

Clark (1911) mistook radial shields for the distal ends of genital plates in his new genera *Ophioleptoplax* and *Ophiocynodus* as he did in *Ophiosyzygus.* Our examination of type material (*Ophioleptoplax megapora,* USNM 25619; *Ophiocynodus corynetes,* USNM 25607) revealed his error. Koehler (1914) described *Ophioleptoplax atlantica* from a specimen that only had "traces [of its disc] left on the upper face of the arms." Koehler did not indicate the presence of radial shields; but we have found them attached to the genital plates and scales in the holotype (USNM 32304) as they appear unlabelled in Koehler's (1914) photograph (pl. 15, fig. 6) of the specimen. *Ophioscolex* was included by Fell (1960) among the ophiomyxid genera lacking radial shields, but Lyman (1882) and Paterson (1985) described them to be present, although inconspicuous, in the type species, *O. glacialis.* Verrill (1899) described as "rudimentary" the radial shields that were overlooked by Lyman (1875) in his original description of *Ophioscolex stimpsonii.*

Mortensen (1933b:314) alluded to the potential for oversight of dorsal arm plates when he wrote about *Ophioscolex inermis*: "At first glance one would rather say that dorsal plates are lacking; but . . . they are so delicate as to let the vertebrae shine through . . . ." Dorsal arm plates in many ophiomyxid species are described as small, thin,

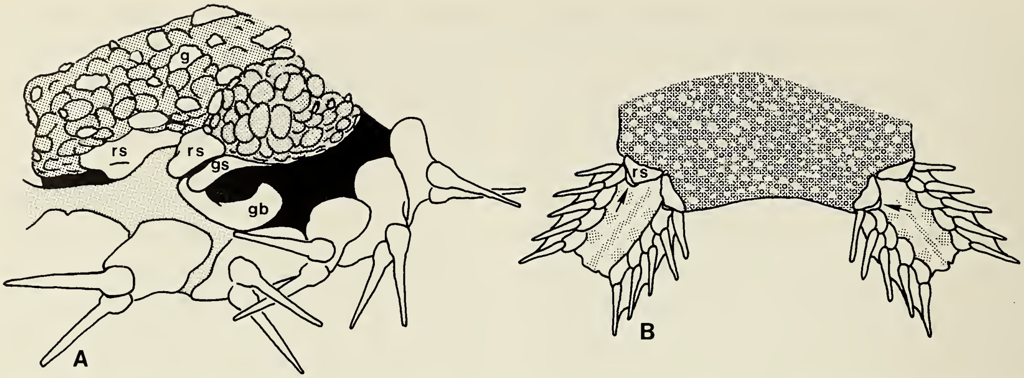

Fig. 1. *Ophiosyzygus disacanthus.* A. Paratype, oblique view of arm base, with part of ventral interradial integument removed to reveal basal five lateral arm plates with spines and the articulation of the radial shield (rs) with the genital scale (gs) and genital plate (gb). Calcareous granules (g) are shown among the dorsal scales of the disc. B. Aboral view of part of the disc and two arms (after Clark 1911, fig. 139a; probably based on the Paratype). Arrows indicate the exposed ends of the genital plates below the radial shields (rs).

multiperforate, and hyaline (Lyman 1878, 1880, 1882, 1883; Clark 1911; Koehler 1914; Matsumoto 1915; Mortensen 1933a; Fell 1960). In many cases, the plates were overlooked in earlier or later studies; and we found similar delicate plates in *Ophiocynodus corynetes,* which Clark (1911) diagnosed as lacking dorsal arm plates. Lyman's (1883) statements about the absence of dorsal arm plates in *Ophiobyrsa hystricis, Ophiobyrsa rudis,* and *Ophiobrachion uncinatus* were qualified by his reference to paired nodules or spiny tubercles over each arm joint. The purported absence of dorsal arm plates should be re-evaluated in several other ophiomyxid genera, particularly in light of the recent discovery by Hotchkiss (1993) of dorsal arm plates in the Paleozoic Oegophiurida.

It may be assumed that the small radial shields and delicate dorsal arm plates, as well as the apparent absence of either type of plate, in ophiomyxids are apomorphic reductions or losses of typically robust plates found in many other ophiuroids. Byrne & Hendler (1988; see above) gave a plausible explanation for skeletal reduction in ophiomyxids. In view of the high potential for homoplasy in reductive character states, speculation about the phylogenetic informativeness of these characters is, however, best deferred until a more complete revision of the Ophiomyxidae can be accomplished.

Ophiosyzygus disacanthus H. L. Clark, 1911
Figs. 1–2

Ophiosyzygus disacanthus Clark, 1911:18 (station list), 276–277 (described, part), fig. 139.—Clark, 1915:172 (material).—Fell, 1960:14 (listed).—Spencer & Wright, 1966:89 (listed).—Downey, 1969:183 (listing of type material, part).

Non *Ophiosyzygus disacanthus.*—Clark, 1911:277 (material, part).—Downey, 1969:183 (listing of type material, part).

Material examined.—Holotype: USNM 25671, 12 mm disc diam, *Albatross,* Sta 4934, 16 Aug 1906, 30°58′20″N, 130°32′00″E, 103–152 fm, rocky, off Sata Misaki Light, Eastern Sea, Japan.—Paratype: MCZ 3277, 8 mm disc diam, *Albatross,* Sta 4936, 16 Aug 1906, 30°54′40″N, 130°37′30″E, 103 fm, stones, off Kagoshima Gulf, Japan.

Non-type material: USNM E44353, 1 dry specimen, 5 mm disc diam, U.S. Bureau of Land Management, Southwest Florida Shelf

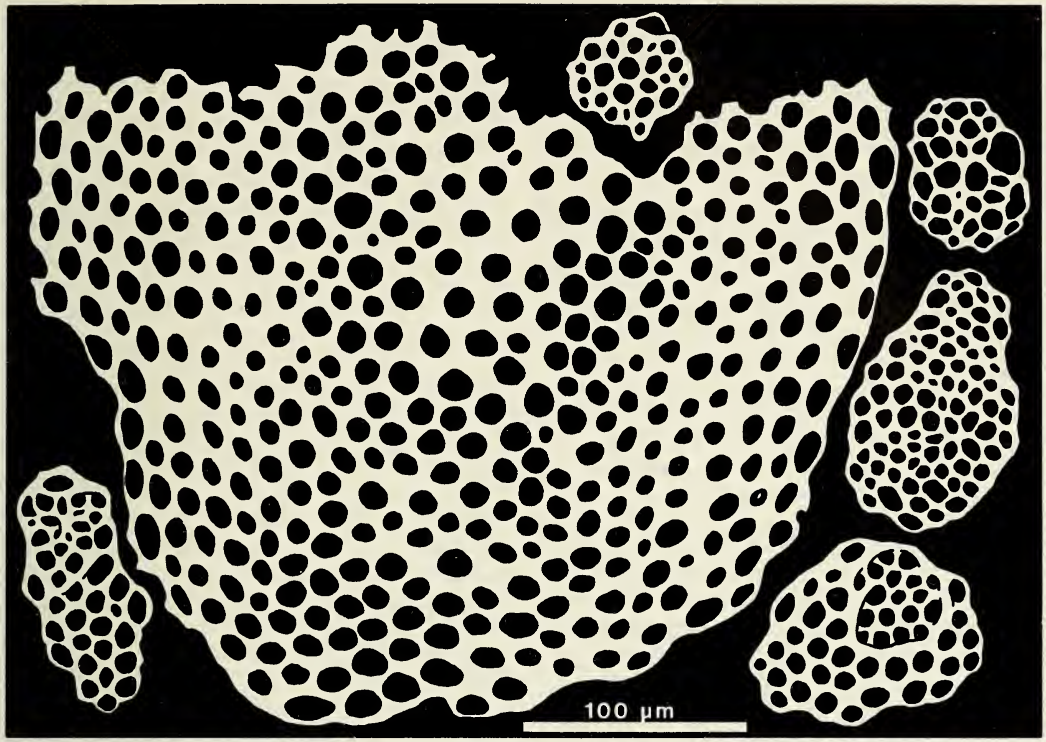

Fig. 2. *Ophiosyzygus disacanthus.* LACM 81-218.1. A large dorsal arm plate and five small plates of the ventral interradius of the disc.

Ecosystems Study, Year 2, Cruise II (BLM 321-II), Sta 35, 26 Jul 1981, 25°44.8′N, 84°21.0′W, 159 m, thin sand and rubble over rock, triangle dredge, southeastern Gulf of Mexico.—LACM 81-218.1, 1 alcoholic specimen, disc damaged, BLM 321-II, Sta 36, 3 Aug 1981, 25°16.8′N, 83°57.4′W, 127 m, deep sand with some thin sand veneer over rock.

Diagnosis.—With characters of the genus.

Description.—The two specimens from the eastern Gulf of Mexico (southwestern Florida shelf) are not a new species, for they differ from the type material only in minor ways. Arm spines are thornier, many bearing two rows of two or three subapical teeth on opposite sides of the shaft. Fewer arm spines on the type specimens are thorny, and they bear fewer teeth (one or two per row). There are generally three oral papillae per row on the jaws, but the number is highly variable within specimens (Japan specimens, 2–4; Florida, 2–5). The integument also includes white, opaque, irregular granules (Fig. 1) that reach and extend above the surface and appear like icebergs. The granules look imperforate, lacking the typical stereomal-stromal organization of echinoderm ossicles. The granules probably are not calcitic ossicles, for they disaggregate in sodium hypochlorite and do not effervesce in weak acid. Granules of the two specimens from Florida are smaller (84 ± 21.9 μm, $n = 9$; 124 ± 32.8 μm, $n = 10$) than those of the holotype (232 ± 67.8 μm, $n = 34$) and paratype (221 ± 53.8 μm, $n = 21$). Considering the poor condition of the types and new specimens, more rigorous comparisons must await the availability of better material.

Flat, multiperforate plates 111 ± 22 μm ($n = 24$) in diameter are embedded deep in the skin of the ventral interradius of the disc (Fig. 2). They are visible in the type specimens without treatment with sodium hypochlorite and were probably overlooked by Clark (1911), who wrote that the ventral interradius is naked.

Five measurable, prolately spheroidal eggs out of seven removed from an ovary of one specimen (LACM 81-218.1) ranged in greatest diameter from 100 μm to 140 μm. Ossicles of the gonadal wall are irregular perforate plates.

Type locality.—Off the southern coast of Kyushu, Japan.

Distribution.—Japan; eastern Gulf of Mexico.

Habitat.—Type specimens were taken from rocky and stony substrata at 188–278 m in the Pacific Ocean. Stations from which specimens were collected in the eastern Gulf of Mexico at 127–159 m were described by Woodward-Clyde Consultants & Continental Shelf Associates, Inc. (1985). At both stations in the Gulf of Mexico, the bottom was gently sloping, rarely with outcrops of rock or other relief, and mostly covered with a veneer of sand over hard substratum (Station 35) or with deep sand (Station 36). The most diverse benthic taxa in descending order at Station 35 were cnidarians, echinoderms, sponges, and crustaceans; and at Station 36, crustaceans, cnidarians, echinoderms, and sponges. A green encrusting alga dominated the epibenthic cover at Station 35. At Station 36, cover was dominated by sponges in summer and by crinoids in winter.

Etymology.—Given by Clark (1911), in reference to the paired arm spines.

Remarks.—In his original description of *O. disacanthus,* Clark (1911) was uncertain of the identity of one paratype (USNM 26217), which lacked a disc. The specimen clearly is not *O. disacanthus.* Although distal arm spines are glassy and terete, proximal arm spines are flattened, robust, and obtuse, and they do not appear glassy. Most arm segments bear three arm spines, rarely four, and only a few proximal segments bear the two that are the typical number for *O. disacanthus.* Upper arm spines are not webbed. Much of the oral structure is obscured by mud, but the jaws can be seen to carry a vertical row of 3–6 teeth (one jaw has none), an apical cluster of tooth papillae, and 4–8 spiniform oral papillae.

Acknowledgments

The material for this study was provided by K. Spring and was collected during the Southwest Florida Shelf Ecosystems Study, Year 2, under contract 14-12-0001-29144 (formerly AA851-CT1-45) to Continental Shelf Associates, Inc., from the U.S. Department of the Interior, Minerals Management Service. We thank K. Fauchald, Smithsonian Institution, National Museum of Natural History, who approved our distribution of samples between repositories, and R. M. Woollacott, Harvard University, Museum of Comparative Zoology, and D. L. Pawson, C. Ahearn, and M. E. Downey, National Museum of Natural History, for the loan of material in their care. Helpful comments on the manuscript were given by J. H. Dearborn, University of Maine, G. Hendler, Natural History Museum of Los Angeles County, and P. M. Mikkelsen, Delaware Museum of Natural History. We acknowledge with gratitude the collaboration with and encouragement from J. E. Miller (formerly of Harbor Branch Oceanographic Institution) earlier in this study.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(2):298–301. 1995.

Designation of a lectotype for *Crocodilus siamensis* Schneider, 1801 (Reptilia: Crocodylia)

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Abstract.—Schneider (1801) named *Crocodilus siamensis* on the basis of three specimens from Siam that were described and figured (but not named) in an earlier publication (Anon. 1688). None of the three specimens are known to have been preserved. Cuvier (1807) considered the syntypical series composite and proposed the replacement name *Crocodilus galeatus* for one of the included species. Cuvier's (1807) replacement name is assessed and rejected as unjustified. In the interest of nomenclatural stability, a lectotype of *C. siamensis* Schneider is designated. The type locality of *C. siamensis* is shown to be Louvo, Siam (= Ayutthaya, Thailand).

Résumé.—Schneider (1801) a créé l'espèce nominale *Crocodilus siamensis* à partir de trois spécimens du Siam décrits et figurés (sans être nommés) dans un travail publié antérieurement (Anon., 1688). Aucun de ces spécimens n'a été conservé. Cuvier (1807) a considéré que la série-type de *Crocodilus siamensis* était composite, et a proposé en conséquence un nom de remplacement, *Crocodilus galeatus*. La validité de ce nom de remplacement est évaluée, et il est rejeté car étant injustifié. Dans l'intérêt de la stabilité de la nomenclature, un lectotype de *C. siamensis* Schneider est désigné. La localité-type de *C. siamensis* est done fixée à Louvo, Siam (= Ayutthaya, Thaïlande).

Crocodilus siamensis Schneider, 1801, is based on three specimens originally described from Siam (= Thailand) by "les Pères Jésuites François" in a report to the Académie Royale des Sciences, published in 1688. This report, seemingly authored anonymously, is sometimes attributed to Thomas Goüye, and it is so registered in the library of the Muséum National d'Histoire Naturelle, Paris. Pages 1–47 and plates I–III in this report comprise a "Description anatomique de trois crocodiles. Avec les Réflexions de Monsieur du Vernay [sic, = Duverney], de l'Académie Royale des Sciences". This section is a description of three crocodiles from Louvo, the former capital of the Siamese Kingdom, that measured (in French feet; 1 ft. = 324 mm) 10′ 8½″, 9′ 4″, and 1′ 4½″. The greater part of the description is of the largest of these specimens, which also is illustrated in the five figures of plate I, showing the head, anterior snout, and whole body. Plate II shows a ventral dissection and various internal organs of this same specimen; other internal structures and a gecko foot are illustrated in plate III.

Schneider (1801:158) explicitly based *Crocodilus siamensis* on the text description and plates I and III in the 1688 report. Although the "Description anatomique de trois crocodiles . . ." appeared in several other forms (see below), only the original 1688 version has the pagination given by Schneider. The date, 1737, given by Schneider apparently is an error.

Cuvier (1807) discussed the three crocodiles reported by the French missionaries but used a later version of their "Description anatomique de trois crocodiles . . ." found on pages 253–280 and plates 64–66 of Perrault (1733). The text is identical to that in the original (1688) version used by Schneider (1801), but the plates are slightly modified, viz., the figure of a gecko foot originally present on plate III is lacking from plate 66. Besides these editions, other reprints appeared in French, English and German.

Neither Schneider (1801) nor Cuvier (1807) examined the specimens described and figured by the French Jesuits. Schneider (1801) and Cuvier (1807) based their descriptions solely on the text and plates contained in the essentially identical 1688 and 1733 versions of the "Description anatomique de trois crocodiles", respectively. Although Schneider (1801) considered the three specimens to be of the same species, Cuvier (1807:52) argued that the third and smallest specimen described by the missionaries actually represented another species, because it lacked the median cranial crests and small eyes of the larger specimens, described and prominently illustrated in plate 64 (= plate I). There are no records of any of the specimens being sent to a museum, and we suspect that none were preserved.

Although Cuvier (1807:52) recognized flaws in the original figures, commenting on the faulty rendition of the feet and tail, evidently he believed the other details to be correct. Because he considered this material to represent two species, and thus that two species of crocodile occurred in Siam, he rejected Schneider's (1801) name, *C. siamensis,* as inappropriate, and introduced the replacement name *C. galeatus* for the larger specimens and allocated the third and smallest specimen to *C. biporcatus* Cuvier, 1807 (= *C. porosus* Schneider, 1801).

Gray (1862) was the first author to allocate correctly a museum specimen (illustrated by Günther, 1864) to *C. siamensis.* We now know that two specimens of *C. siamensis* from Java, variously misidentified as *Crocodilus raninus* Müller & Schlegel, 1844, *Crocodilus rhombifer* Cuvier, 1807, and *Crocodilus vulgaris* Cuvier, 1807 (= *C. niloticus* Laurenti, 1768), had previously reached Europe (Ross 1992). Gray (1862, 1867, 1872) briefly described the British Museum (Natural History) specimen, collected in "Cambogia" (= Kampuchea) by M. Mouhot (BMNH 61.4.12.22), and, in comparing its head with that figured in the description (plate I) used by Schneider (1801), suggested that (1862:270, 1867: 144, 1872:13) "the two keels which are present in that specimen [i.e., the specimen in plate I] are either an individual peculiarity, or perhaps a character that developed itself as the animal approached old age."

Crocodylus siamensis remained poorly known until the 20th century, when detailed descriptions and analyses were published by Smith (1919) and Müller (1923). These authors and our examination of museum specimens (American Museum of Natural History 28358, 49231; Museum Zoologicum Bogoriense 15; Rijksmuseum van Natuurlijke Historie, Leiden, 7939 and one skull with no number; Natur-Museum Senckenberg 8090) clearly indicate that the original figures used by Schneider (1801) and Cuvier (1807) to formulate their concepts of the species exaggerated the size of the distinctive longitudinal interorbital ridge (which is poorly developed or absent in young animals), depicted a greatly exaggerated crest at the posterior end of the cranial table, and incorrectly showed the eyes to be much smaller than in other crocodile species. Cuvier's (1807) belief that the third and smallest specimen referred to *C. siamensis* by Schneider (1801) was probably *C. biporcatus* (= *C. porosus* Schneider) thus was unfounded, albeit possibly correct.

As no type specimens of *C. siamensis* are known to exist, it is possible Cuvier's (1807) view that the type series included two species might be correct. Because of this confusion, and in the interest of nomenclatural stability, we believe that a lectotype should be designated, and, hereby designate as lectotype of *Crocodilus siamensis* Schneider, 1801, the specimen whose head is figured on plate I of the 1688 "Description anatomique de trois crocodiles . . ." (International Commission on Zoological Nomenclature [ICZN] 1985, Art. 72c(v) and 74c). This specimen was the largest of the three individuals and the subject of the greater part of the text and other figures. The figure of the head of this specimen was reproduced by Cuvier (1807, pl. 2, fig. 9) and by Tiedemann et al. (1817, pl. 11, fig. 2), who also reproduced, with modifications based on Cuvier's comments (1807:52), other parts of plate I of the 1688 "Description anatomique de trois crocodiles . . ." (pl. 11, figs. 1, 3). Following provisions of the International Code of Zoological Nomenclature (ICZN 1985: Art. 72e), this specimen also becomes the lectotype of *Crocodilus galeatus* Cuvier, 1807, which is a junior objective synonym of *C. siamensis* Schneider, 1801.

Few authors subsequent to Schneider (1801) and Cuvier (1807) apparently have examined the original version(s) of the Jesuits' descriptions and accompanying plates. Neither Schneider (1801) nor Cuvier (1807) provided precise locality data for the material described by the missionaries to Siam, and invariably the type locality has been given simply as "Siam" (e.g., Smith 1931; Mertens 1943; Wermuth 1953; Wermuth & Mertens 1961, 1977; King & Burke 1989). Upon examining the original text (Anon. 1688), we were surprised to discover that the Jesuits' gave a precise locality for their three specimens. Accordingly, and following Recommendation 72H of the International Code of Zoological Nomenclature (ICZN 1985), the type locality of *C. siamensis* Schneider can be stated fully as the "Menam qui baigne le pied des remparts de Louvo", Siam (= the Chao Phraya River, at Ayutthaya, Ayutthaya Changwat, Thailand).

Acknowledgments

We would like to thank W. R. Heyer, R. W. McDiarmid, and G. R. Zug for their comments on drafts of this paper and for providing research facilities to CAR and GCM, and M. Hoogmoed, K. Klemmer, G. Foley, and R. G. Zweifel for the loan of specimens.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(2):302–318. 1995.

Description of a new large-bodied species of *Apomys* Mearns, 1905 (Mammalia: Rodentia: Muridae) from Mindoro Island, Philippines

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Abstract.—*Apomys gracilirostris,* a new species in the Philippine endemic murid genus *Apomys,* is described from the Mount Halcon highlands on Mindoro Island. The new species is compared with its larger-bodied congeners: *A. abrae, A. datae, A. sacobianus,* and the two nominal subspecies of *A. insignis, A. i. insignis* and *A. i. bardus.* Twenty-eight cranial, mandibular, and dental measurements were taken on the 83 specimens representing these taxa and the new species. All species examined formed discrete groups in a principal component analysis; there were no apparent differences between the two nominal subspecies of *A. insignis.* The new species differs from congeners in its combination of large body, very long tail, dark pelage, gracile cranium with a long rostrum, and highly compressed upper incisors; the most diagnostic features of the species are the extremely fine upper and lower incisors (with no enamel on the lower), and the degree of molar reduction and simplification.

In 1905, Edgar A. Mearns proposed the generic appellation *Apomys* for representatives of a new species of rodent he had collected on Mount Apo, in southern Mindanao Island, Philippines (Mearns 1905). Different investigators historically have shown considerable flux with respect to the taxonomic placement of the genus (review by Musser 1982). However, since the exhaustive review and diagnosis of *Apomys* by Musser (1982), there has been no doubt as to the validity of these organisms constituting a genus level category. As currently defined (Musser 1982, Musser & Heaney 1992), *Apomys* is restricted to the Philippine Archipelago (excluding the Sunda Shelf island of Palawan and associated peripheral islands).

Eight species are now included in the genus: *A. hylocoetes* and *A. insignis* from Mindanao Island, *A. littoralis* from Mindanao, Leyte, Biliran, and Bohol Islands (Heaney et al. 1989, Musser & Heaney 1992, Rickart et al. 1993), *A. microdon* from southern Luzon and Catanduanes Islands, *A. musculus* from Luzon and Mindoro Islands, and *A. datae* and *A. abrae* from Luzon Island. An additional species, currently undescribed, recently has been reported from a number of islands in the central Visayas group of the Philippine Archipelago (Musser 1982, Musser & Heaney 1992; L. R. Heaney, pers. comm.).

During a biodiversity inventory survey carried out in 1992 on some components of the major Pleistocene island masses (sensu Heaney 1986), one of the localities that was visited was the Mount Halcon massiff, in the northern part of the island of Mindoro. Mount Halcon, reported to reach ca. 2500 m in elevation, had been explored by Edgar A. Mearns in 1906 (Merrill 1907a); however, only 17 of the 496 mammals brought back by him were from Mindoro. Most of his collection from the Mt. Halcon area consisted of *Crocidura*; all told, eight nominal taxa in four orders were collected by him, including the holotypes of five nominal taxa. The object of the current exploration of the Mount Halcon area was to increase sample sizes of some of these taxa in order to arrive at a better assessment of geographic and nongeographic variation, as well as to determine whether additional species, which Mearns may have missed, also existed in the area.

One mammal species found between 1255 m and 1900 m elevation on the north slope of Mount Halcon was a medium-sized rodent, similar to *Apomys* in having a slender rostrum, as opposed to the short, high, blunt rostrum of *Rattus.* The lower incisors were more procumbent than those of *Rattus,* and lacked pigment. The general gestalt, mostly related to how gracile this rodent was, therefore pointed, barring the relatively large size, to its pertenence in the genus *Apomys.* Subsequent examination of cranial morphology, and conversations with colleagues, confirmed this suspicion. Accordingly, individuals collected in that taxon are described below as a new species of *Apomys* from the northern highlands of Mindoro.

Methods

Except for specimens of the new species (at the Cincinnati Museum of Natural History), and those of *Apomys sacobianus* (National Museum of Natural History, USNM), all specimens examined are from the Field Museum of Natural History (FMNH). Terminology referent to molar cusps follows Miller (1912) for upper molars, and Musser and Heaney (1992) for lower molars. Cranial and mandibular measurements were taken with a digital caliper to the nearest 0.01 mm. Twenty-eight cranial, mandibular, and dental measurements, listed below, were taken; the 23 cranial measurements were described and illustrated in Musser (1979); mandibular measurements are defined below. Measurements (abbreviations in parentheses) included: breadth of braincase (BB), breadth across incisive foramina (BIF), breadth across incisor tips (BIT), breadth of palatal bridge at first, and at third molars (BM1, BM3), breadth of mesopterygoid fossa (BMF), breadth of rostrum (BR), breadth of zygomatic plate (BZP), height, and length, of auditory bulla (HB, LB), height of braincase (HBC), interorbital breadth (IB), incisive foramina to M1 (IFM1; modified to be straightline shortest distance, rather than anteroposterior distance), length of diastema (LD), length of incisive foramina (LIF), alveolar length of maxillary toothrow (LMT), length of nasals (LN), length of palatal bridge (LPB), length of rostrum (LR), occipitonasal length (ONL), palatal length (PL), postpalatal length (PPL), and zygomatic breadth (ZB). Five additional measurements not used by Musser (1979) were taken: length of dentary (LMAND), the greatest length of dentary from upper incisive alveolar rim to mandibular condyle; length of mandibular toothrow (LMT), alveolar length of mandibular toothrow; height of mandible (HMC), greatest height of mandible; height of mandibular ramus (HMR), lowest height of ramus in mandibular incisive diastema; and thickness of mandible (TM), measured at thickest point below m2.

Statistical analyses were performed on an 80486 equipped 33 MHz microcomputer using the Statistical Analysis System software, version 6.03 (SAS Institute 1988a, 1988b), generally following Ruedas & Bickham (1992). Univariate statistics, including mean, standard error, moment statistics (skewness, g_1; and kurtosis, g_2) and tests of normality were performed invoking the "normal" option of the UNIVARIATE procedure, which tests for normality using the Shapiro-Wilk statistic, W, and provides the associated probability value. A principal component analysis was carried out to determine whether any group separation occurred using the measurements taken. Such a posteriori grouping methods are preferred herein over a priori grouping methods (mul-

Table 1.—Values for the first through third eigenvectors from the principal component analysis carried out on the correlation matrix of the cranial and mandibular morphometric data of specimens of *Apomys.* Refer to text for character abbreviations. The first four principal components together account for 91.5% of the variation (68.5%, 13.3%, 5.5%, and 2.2%, respectively). Results of the principal component analysis are graphically summarized in Fig. 1.

	Component		
	1	2	3
BB	0.2092	−0.2372	−0.0489
BIF	0.1498	0.3402	0.0601
BIT	0.1244	0.2985	0.4763
BM1	0.1684	−0.0566	−0.5707
BM3	0.1942	−0.2232	−0.1403
BMF	0.0993	0.3870	−0.0400
BR	0.2279	−0.0040	0.2225
BZP	0.2509	0.1233	0.0151
HB	0.1408	0.3926	0.0275
HBC	0.2454	−0.0082	−0.0001
IB	0.0362	−0.1522	0.3550
IFM1	0.1443	−0.3582	0.0222
LB	0.2012	0.0836	−0.2576
LD	0.2465	−0.1715	−0.0298
LIF	0.2353	0.1279	−0.2145
LM13	0.2081	0.2802	−0.1150
LN	0.2610	−0.0246	0.0379
LPB	0.2370	−0.1172	0.1331
LR	0.2453	−0.1326	0.1170
ONL	0.2653	−0.0583	0.0164
PL	0.2651	0.0501	−0.0369
PPL	0.2576	−0.0188	0.0451
ZB	0.1841	−0.2135	0.2830

tiple range tests, canonical discriminant analysis) because there is no prior hypothesis as to the putative identity of the specimens being examined.

Specimens Examined

A. abrae: Philippines: Luzon Island, Ilocos Norte Prov.; Mount Simminublan, 4300–4350 ft. FMNH nos. 92752–92755, males; 92756–92762, females. Abra Prov.; Massisiat, 3500 ft. FMNH 62749, female. Mountain Prov.; Mt. Data, 5300-8000 ft. FMNH 62700, 62724, 62726, 62728, 62738–62740, males; 62719–62723, females.

A. datae: Philippines: Luzon Island, Mountain Prov.; Mount Data, 5300–8000 ft. FMNH 62695, 62696, 62699, 62720, 62741, males; 62706, 62709, 62711, 62712, 62725, 62727, 62731, 62733–62735, 62742, 62744, females. Mountain Prov.; no specific locality. FMNH 62761, female.

A. insignis bardus: Philippines: Mindanao Isl., Zamboanga del Norte Prov.; Grand Malindang Mountains, Dapitan Peak, 6700–7450 ft. FMNH 87568 (young), 87571–87573, males, 87567, 87569, 87570, females.

A. i. insignis: Philippines: Mindanao Isl., Bukidnon Prov.; Malaybalay, Mount Kitanglad, 4200–5000 ft. FMNH 92806, 92808–92812, 92815, 92816, 92818, 92819, 92821, males; 92807, 92813, 92814, 92817, 92820, 92822, females. Davao Prov.; East slope of Mount McKinley, 3500–7100 ft. FMNH 56267, 56270, 56276–56278, males; 56266, 56268, 56269, 56272–56275, 56282, 56285, 56288, females.

A. sacobianus: Philippines: Luzon Isl., Pampanga Prov.; Angeles, Clark Air Base, Sacobia River. USNM 304352, 557717.

Apomys n. sp.: see below, holotype and paratypes.

Results

Descriptive statistics for species of *Apomys* examined in this study are listed in Appendix 1. Results of the principal component analysis (Fig. 1) show considerable, non-overlapping variation among different nominal taxa within *Apomys.* The first four principal components account for 91.5% of the variation (Table 1). Principal component 1 accounts for 68% of the variation and separates *A. insignis* from remaining *Apomys.* Variation is spread fairly evenly over all characters in principal component 1, but characters with heavy loadings include occipitonasal length, palatal length, length of nasals, and postpalatal length. Since *A. insignis* is smaller in all measurements than the *Apomys* considered herein, principal component 1 appears to be constituted

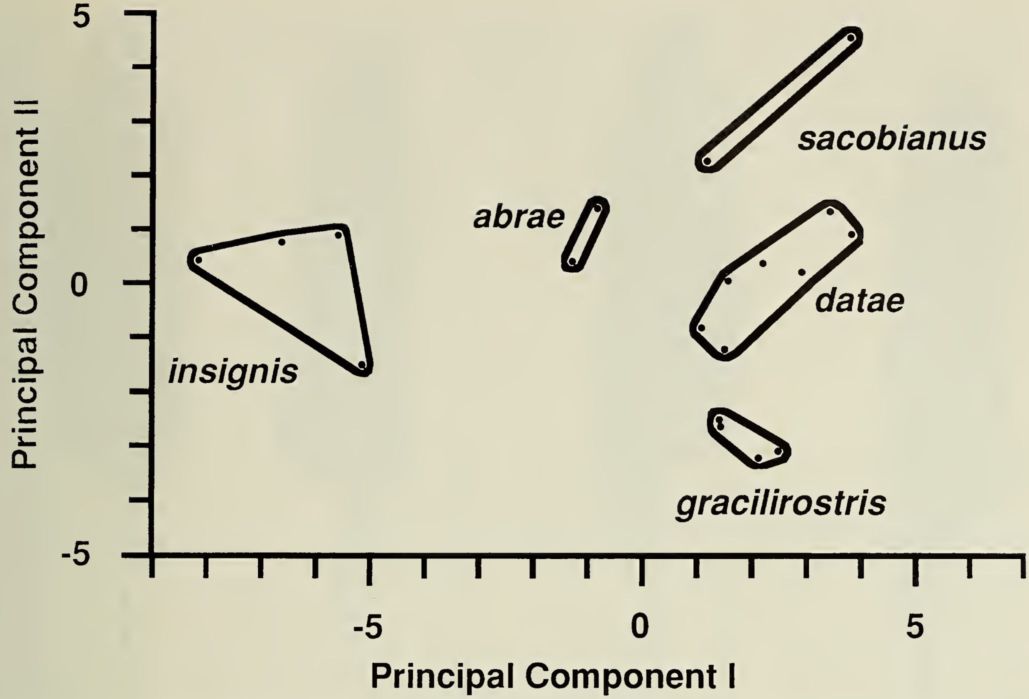

Fig. 1. Plot of principal component scores (PC 1 vs. PC 2) for six species of *Apomys* examined in this study.

primarily on the basis of size. Principal component 2 accounts for 13% of the variation and separates the Mount Halcon taxon from remaining *Apomys.* This principal component shows heavy loadings on height of bulla, breadth of mesopterygoid fossa, straightline distance between incisive foramen and M1, breadth of incisive foramina, breadth of incisor tips, and length of maxillary toothrow. These are measurements in which the Mount Halcon taxon is quite distinct (either larger or smaller) from remaining *Apomys* examined herein; as a consequence, it also appears to be constituted on the basis of magnitude of linear measurements.

Inspection of descriptive statistics (Appendix), of results of principal component analysis, (Table 1 and Fig. 1), and of several discrete characters, clearly identifies the specimens of *Apomys* from the Mindoro highlands as a new species. The species is described below, being named

Apomys gracilirostris, new species
Figs. 2–5

Holotype.—National Museum of the Philippines (NMP) No. 3482 (fide Pedro C. Gonzales; also Cincinnati Museum of Natural History [CMNH] No. 650, and field collection number NMP/CMNH 1136), an adult male snared by Pedro Bangol, a Mangyan native from Lantuyan (= Dulangan Dos); the specimen will be permanently housed at the National Museum of the Philippines. The provenance is: Philippines: Mindoro Island; Mindoro Occidental Province; Municipality of San Teodoro, North Ridge approach to Mount Halcon, ca. 1580 m; ca. 13°16′48″N, 121°59′19″E; this area is known to the Mangyan tribespeople as "Hangló." Date of collection is 12 June 1992. Specimen preserved as a dried skin and skull, in good condition.

Paratypes and localities.—Besides the holotype, an additional 15 specimens are

Fig. 2. Dorsal and ventral views of *Apomys gracilirostris* CMNH 646 (left in each pair) and 649 (right). Specimen 646 is homogeneously colored dorsally and ventrally, while 649 is paler (buffy) in ventral coloration. Length of head and body and tail length (in millimeters) are 147 and 175 (CMNH 646) and 146 and 179 (CMNH 649).

known. Four, snared by Pedro Bangol at the same locality as the holotype, but at elevations ranging between 1675 an 1731 m, are prepared as dried skins with a full skeleton extracted from the left side, body skeleton from the right: CMNH 646 (NMP/CMNH 1119), an adult female (right zygomatic arch broken), 7 Jun 1992; CMNH 647 (NMP/CMNH 1126), young adult male snared 9 Jun 1992; CMNH 648 (NMP 3480; NMP/CMNH 1131), adult male, 10 Jun 1992; and CMNH 649 (NMP 3481; NMP/CMNH 1132), old adult male, 11 Jun 1993. Twelve specimens are fluid preserved, with no skeletal material extracted to date. These are CMNH 642 (NMP/CMNH 1069), a scrotal male collected 28 May 1992, and CMNH 643 (NMP 3479; NMP/CMNH 1100), an adult female collected 1 Jun 1992, from the Dulangan River Valley (Philippines: Mindoro Isl., Mindoro Oriental Province; Municipality of San Teodoro;

Table 2.—Standard external measurements of the holotype of *Apomys gracilirostris,* CMNH 650, and univariate statistics of male and female specimens of *A. gracilirostris.* There were no significant differences between males and females ($P = 0.05$), however, males displayed non-normally distributed measurements in total length ($P = 0.0039$) and mass ($P = 0.0005$). Sample size is four females and 13 males (including holotype) for all measurements except mass, twelve males. All measurements expressed in millimeters except mass, in grams.

Character	Holotype (CMNH 650)	Females		Males	
		Mean ± *SD*	Range	Mean ± *SD*	Range
Total length	294	306.2 ± 23.21	283–330	314.1 ± 30.98	288–398
Tail length	157	161.2 ± 12.61	147–175	159.0 ± 14.50	135–185
Length of hind foot	39	36.5 ± 3.70	33–41	38.8 ± 3.05	34–45
Length of ear	21	19.2 ± 1.26	18–21	18.6 ± 2.72	14–22
Mass	80	88.8 ± 17.97	75–115	87.4 ± 18.28	71–140

North approach to Mt. Halcon, Dulangan River Valley, ca. 1255 m, approx. 13°17′27″N, 121°59′32″W); CMNH 644 (NMP/CMNH 1108), a scrotal male collected 4 Jun 1992, and CMNH 645 (NMP/CMNH 1118), also a scrotal male, collected 7 Jun 1992 from the same locality as the holotype. Seven specimens, CMNH 634, 637 and 639–641 (inclusive), all males, and 635 and 636, females, are from an elevation of ca. 1900 m, an area known to the Mangyan tribespeople as Patok-tok, just above the type locality. All paratypes are in excellent condition except as noted. The following specimens will be permanently housed at the National Museum of the Philippines: CMNH 634 (NMP 3475), 635 (3476), 637 (3477), 641 (3478), 643 (3479), 648 (3480), 649 (3481), and the holotype, CMNH 650, NMP 3482.

Diagnosis.—*Apomys gracilirostris* is distinguished from its congeners by the following combination of traits: with respect to remaining *Apomys,* upper incisors are asulcate and extremely compressed and thin, breadth of incisor tips averaging only 1.56 ± 0.053, versus extremes in the remaining large bodied *Apomys* of 1.66 ± 0.158 (*A .i. insignis* males from Davao Province) to 2.23 ± 0.178 (*A. datae* males); lower incisors unpigmented and elongate. Lower edge of incisive alveolus beginning (in the vertical plane) just in front of m1, whereas the body of the ramus between the first molar and incisor in other species of *Apomys* is much longer. The small width of the incisors becomes even more apparent as a ratio against occipitonasal length; in *A. gracilirostris* this is 0.039 ± 0.002, versus extremes in remaining large bodied *Apomys* of 0.050 (*A. abrae* females from Mountain Province) to 0.061 (a single *A. insignis bardus* female). The skull is gracile, with a long rostrum. The combination of large body (combined head and body length, 143.6 ± 3.97; range 137–147), very long tail (length, 168.2 ± 9.47; range 157–179), dark pelage, gracile cranium, long rostrum (length, 14.11 ± 0.425; range 13.86–14.86), compressed and thin upper incisors (breadth at incisor tips, 1.56 ± 0.054; range, 1.51–1.62) and elongate, unpigmented lower incisors are sufficient to diagnose the species.

Description.—All specimens adults, pelage dark brown on dried skins (Fig. 2), body relatively large for an *Apomys* (external measurements in Table 2), with a long, slender snout, and long tail and feet. Holotype and paratypes similar in dorsal and lateral coloration. Fur silky and soft; proximal part of dorsal hairs light grey, turning pale brown distally; with numerous black guard hairs. Overall color dark brown, although freshly captured specimens with a dark blue/green sheen; some specimens darker along middorsal region. Color somewhat paler laterally. Ventral color variable. One specimen (646; Fig. 2) not differing between dorsal and ventral appearance with respect to tone; 647 and 646 are marginally paler, 647 with silver-tipped grey hairs, 648 with grey hairs tipped with pale brown; 649 and 650 buffy ventrally, (particularly the former; see Fig. 2) with grey hairs tipped to a greater (649) or lesser (650) extent with brown.

Tail generally uniformally dark, however, sometimes paler on ventral surface, some individuals displaying a white extremity, varying from 2 mm in length (637) to 6 mm (640) or 10 mm (639). Scale row counts 14/cm at both base and midsection of tail.

Mystacial vibrissae present; anteriormost ones dark grey, dorsad and caudad ones black, with some fading to grey distally. Ears small relative to size of head; dark brown on inner surface, slightly paler on outer surface.

Hindfeet relatively long (females: mean, 36.5 mm, *SE* 3.70, range, 33–41; males, 38.8 *SE* 3.05, range 34–45), and dark dorsally. Plantar surface also dark, with paler tubercules forming a contrast. Claws relatively long; foreclaws ca. 3 mm in length; hindfoot claws ca. 4 mm long.

Vertebral counts identical except for number of caudal vertebrae: atlas, axis, 5 innominate cervical, 13 thoracic, six abdominal, and three pelvic vertebrae (craniad weakly fused to two, strongly fused caudad vertebrae). Specimen 648 with 32 caudal vertebrae, while 646 and 647 with 35.

Premaxillae projecting approximately 2.5 mm beyond anterior edge of incisive alveoli; top of nasals projecting marginally beyond this. Nasals widest at their anterior extremities, curving somewhat downward to meet premaxillae; nasals narrowing somewhat caudally, narrowest at fronto-nasal suture. Nasals and lower surfaces of premaxillae, maxillae, and palatine almost on same plane, with little tapering towards rostrum when viewed laterally. Incisive foramina long and narrow (4.9 ± 0.102), typically end about 1.3 mm anterior to first molar.

Zygomatic arches and zygomatic plates slender and delicate. As with other members of genus, edges of interorbital and postorbital areas rounded, without the beading characteristic of *Rattus.* Braincase smooth and round, the only protuberances those associated with occipital bone. Caudalmost end of cranium formed by an external occipital protuberance at caudalmost end of interparietal that meets squamous part of occipital (or supraoccipital bone), causing occipital bone to project beyond occipital condyles. Paired protuberances present where caudal ends of squamosal bones meet supraoccipital; without lambdoidal ridge.

Mastoid somewhat inflated. Squamosomastoid foramen present, but not as well developed (as a fenestra) as in *A. insignis,* for example; present only on one side in the holotype (650), 648, and 649 (extremely reduced); on both sides 646 and 647. Large postglenoid fossa separating squamosal from periotic bones.

Foramina of alisphenoid region essentially as described for *Apomys* (Musser 1982), with slight modifications. Lateral strut of alisphenoid bone slender, much more so than illustrated for *A. insignis* (AMNH 207571) by Musser (1982). No separation between anterior opening of alisphenoid canal and coalesced masticatory-buccinator foramina, so that all three are consolidated. Masticatory nerve emerging from posterior end of this consolidated foramen, leaving deep furrow in alisphenoid bone, particularly in region proximal to its point of emergence. From a ventral perspective, auditory bulla separated from alisphenoid bone by middle lacerate foramen, which is only thinly separated from the postglenoid vacuity. Sphenopterygoid vacuity variable in conformation, being single (separating alisphenoid from pterygoid), or consisting of the same, with an additional opening at caudal edge of pterygoid. A varying number of sphenopalatine foramina of varying conformation present. Minute dorsal palatine foramen present in orbital region, above roots of M2. Sphenopalatine foramen, just anterior to dorsal palatine fo-

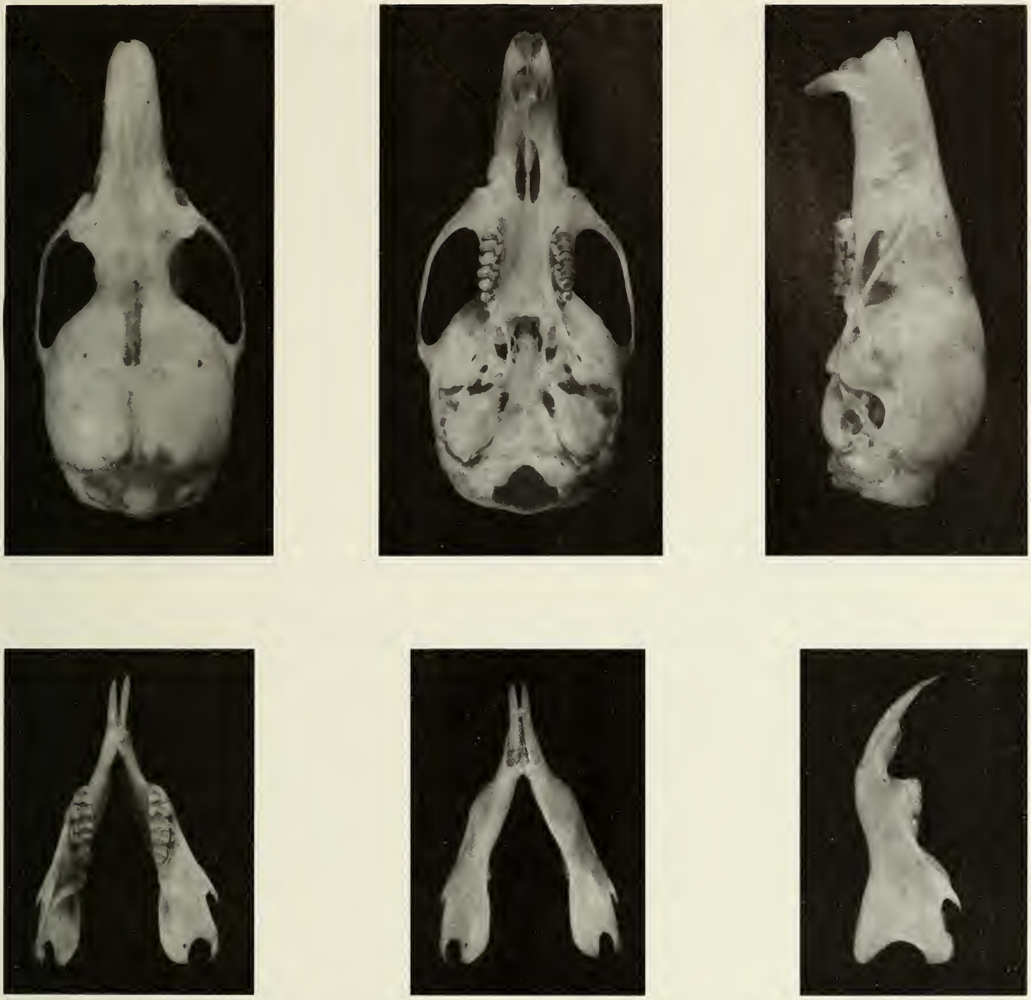

Fig. 3. Dorsal, ventral, and lateral views of cranium and mandibles of the holotype of *Apomys gracilirostris* (CMNH 650). Occipitonasal length 39.4 mm, zygomatic breadth, 17.6 mm, length of dentary, 20.3 mm.

ramen, likewise inconspicuous (in some cases closed); where present, only evident as a depression in maxilla. Sphenoid bone with relatively small optic canal separated by a strut from the much larger orbital fissure.

Dentaries (Fig. 3) with angular process projecting beyond plane of mandibular condyle. Lower edge of incisive alveolus beginning (in the vertical plane) just anterior to m1. With a large protuberance (capsular process sensu Musser & Heaney 1992) forming around end of root of lower incisor, on labial side of dentary, just anterior and ventral to coronoid process, forming narrow shelf that narrows posteriorly into mandibular condyle.

Upper incisors asulcate, extremely compressed and thin, their combined width averaging 1.56 ± 0.053. Enamel pale orange. Lower incisors extremely elongate and slender, also asulcate, and lacking pigment on their enamel surfaces.

Molars (Fig. 5) typical of *Apomys* (refer to fig. 15 in Musser 1982), with a few notable differences. All cusps occupying rela-

Fig. 4. Ventral view of pterygoid and mesopterygoid regions in the holotype of *Apomys gracilirostris*; bottom left is the bony eustachian tube, anterior is to the top.

tively greater area of crown than in other species of *Apomys.* Anterior labial cleft separating the hypothesized front two laminae of m1 not present; as a consequence, antero-lingual or antero-labial cusp not evident. Anterior lamina consisting simply of a large, crescent-moon-shaped ring of enamel surrounding a lacuna of dentine, presumably formed from fusion of anteroconid, protoconid, and metaconid.

All three laminae of M1 relatively broad as well, occupying entire occlusal surface. M1 with a small distinction still evident between cusps t3 and t1/t2, which are continuous. Cusps t8 and t9 occupying almost entire caudad half of M1. No evidence of a

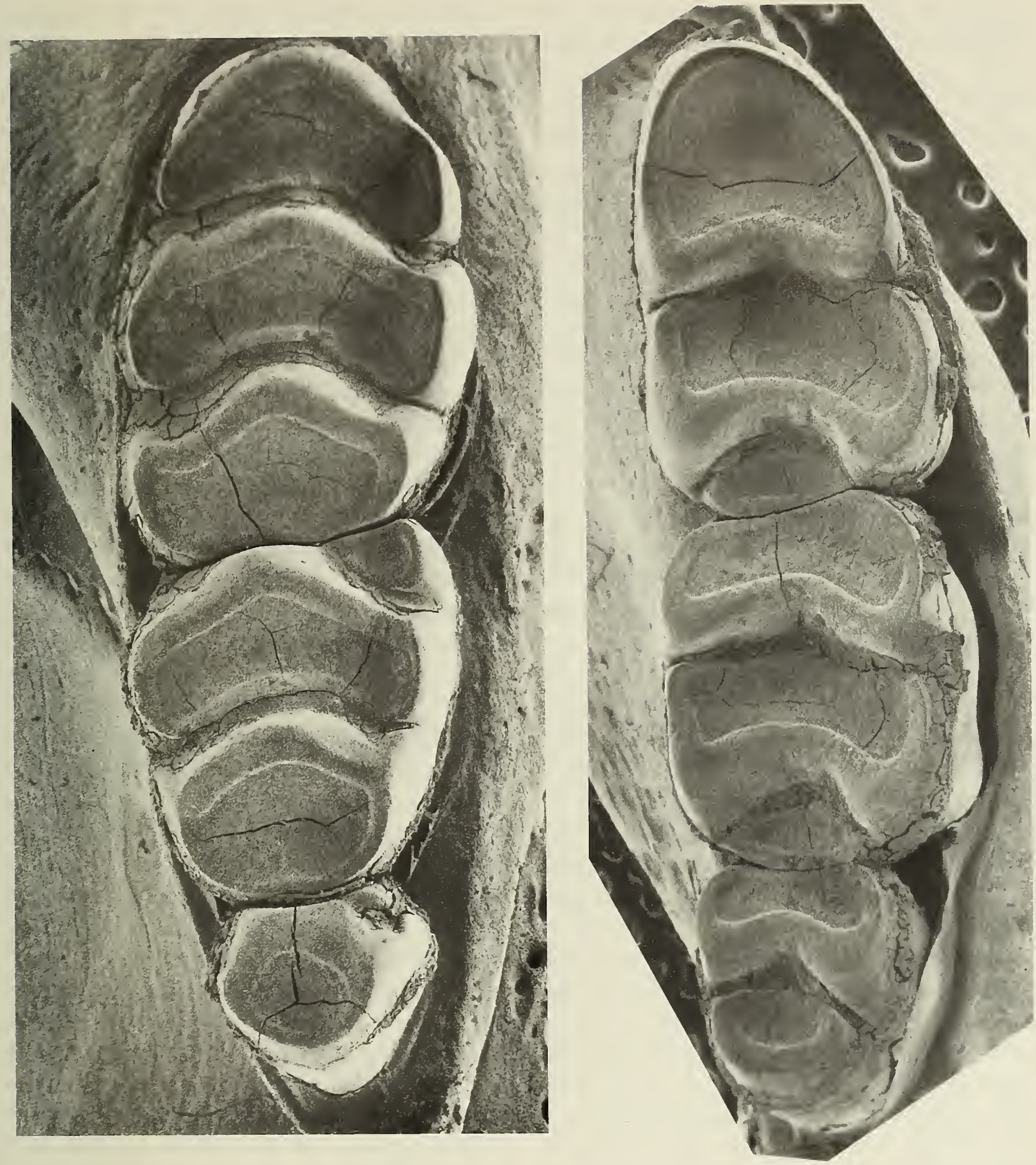

Fig. 5. Upper (left) and lower molar toothrow of the holotype of *Apomys gracilirostris*; length of upper molar toothrow, 6.3 mm, length of lower molar toothrow, 6.4 mm.

posterior cingulum. M2 lacking cusp t1 (vide *A. musculus*), and t3 reduced and tightly compressed between t5 and t6 (continuously fused with t4) and t9 of M1. Cusp t8 large, ovoid, and comprising entire caudad half of M2. M3 with only the slightest trace of t3 existing (more obviously present in other *Apomys*), making this essentially a unicuspid molar. Specimen 649 differs from the other *A. gracilirostris* specimens in having only two upper molars in right maxilla (full complement in left) and two molars in right dentary (full complement in the left).

One female (CMNH 646) had 3 embryos, measuring 2 mm crown–rump length; two of these were on the right horn of the uterus;

636 displayed a swollen uterus with no placental scars. Two of five males from the area surrounding 1900 m were scrotal; males from lower elevations (646–650) all displayed scrotal testes. Testes measurements were 6 × 4 mm (647 and 648) and 7 × 4 mm (649); no measurements were obtained on testes of 650.

Distribution.—*Apomys gracilirostris* is known only from the type locality and general vicinity, with an elevational range of ca. 1250–1950 m; it may occur throughout the highlands of Mindoro, particularly northern Mindoro, where there still remain large tracts of relatively undisturbed montane and midmontane forests.

Etymology.—gracilis + rostrum—a combination of the latin words describing the particularly long and slender rostrum of this species of *Apomys* (with respect to other *Apomys,* and most rodents).

Ecology.—Starting at ca. 1250 m on the north slope of Mount Halcon, the canopy height of the forest (in the general category of Montane Forest) averaged 14–16 m in sheltered areas, with some emergents to 20 m; more exposed areas displayed a canopy height of 6–8 m with emergents to 11 or 12 m. The canopy generally was uneven, allowing considerable light to penetrate in places, although the forest immediately adjacent to the Dulangan River had a very dense canopy. All areas had heavy undergrowth up to 2 m high. Tree ferns *(Cyathea),* birds' nest fern *(Asplenium),* climbing bamboo, palms, and pandans (particularly *Pandanus*) were very common. Also indicative of the extremely wet nature of the area was the heavy growth of moss on trees.

The most dominant trees (typically composing at least 25% of plot surveys) were *Tristania* sp. (Myrtaceae), *Lithocarpus* sp. (Fagaceae) and *Leptospermum flavescens* (Myrtaceae). Important trees (constituting 5–15% of plot surveys) were *Decaspermum paniculatum* and *Tristaniopsis* sp. (Myrtaceae), *Praravinia* sp. and *Psychotria* sp. (Rubiaceae), *Ficus* sp. (Moraceae), *Pinanga* sp. (Arecaceae), *Elaeocarpus* sp. (Elaeocarpaceae) and *Adinandra* sp. (Theaceae). Primary understory trees were *Saurauia* sp. (Actinidiaceae), *Syzygium* sp. (Myrtaceae), *Astronia* sp. (Melastomataceae), and *Symplocos* sp. (Symplocaceae). Numerous herbs and shrubs also abounded. Forest composition in this general area of Mount Halcon also was detailed by Ames (1907), Brotherus (1907), and Merrill (1907b).

From 1600 m to 1950 m, numerous areas were overgrown with bamboo, with the only tree species present being *Agathis philippinensis* ("almaciga"). In areas of closed forest, canopy heights ranged from 7–10 m in most areas, with the tallest trees (in sheltered areas) growing up to ca. 20 m. The canopy was considerably more closed (up to 80% closed) at this elevation that at the lower elevations. Pandans and gingers were so common in some areas as to make passage quite difficult. Leaf litter was approximately 6–8 cm thick. Numerous epiphytic ferns and orchids were present, although none occurred on the almaciga trees.

The gracile skull, long rostrum, reduction in relative size of upper incisors, and extreme elongation of lower incisors of *A. gracilirostris* all point to a diet of soft-bodied invertebrates, although additional, freshly sacrificed specimens will need to be examined to confirm this hypothesis (stomach contents were not readily recognizable). The long tail, and relatively long hind feet with well-developed claws point to a scansorial lifestyle. Much more ecological data, perhaps from mark and recapture studies, still need to be gathered on this little known species.

Comparisons.—The most conspicuous feature of the cranium in *A. gracilirostris* (Fig. 3) is the long and slender rostrum; the length in the five crania examined was 14.11 ± 0.425 (range: 13.86–14.86). Only *A. datae* males exceed *A. gracilirostris* in this respect; for 10 females examined, 13.42 ± 0.702 (12.5–15.0); 7 males, 14.14 ± 0.480 (13.30–14.78); means in other species ranged to a low of 10.45 ± 0.292 for male *A. insignis* from Davao Province. The ratio of rostrum length to skull length is surpassed only by male *A. datae* and female *A. abrae* from Mountain Province, Luzon; for *A. gracilirostris,* 0.354 ± 0.005 (0.348–0.360), versus extremes of 0.329 (female *A. insignis* from Mount Kitanglad, Bukidnon Province, Mindanao) to 0.356 (for 7 male *A. datae* from Davao City Province, Mindanao Island); *A. abrae* females from Mountain Province displayed a mean of 0.355 ± 0.021.

The interorbital region, averaging 6.0 ± 0.233 mm, is relatively the narrowest among *Apomys* species: the ratio of interorbital width to occipitonasal length is 0.150, versus extremes in other *Apomys* of 0.151 (female *A. abrae* from Ilocos Norte, Luzon) to 0.167 (female *A. insignis* from Mt. McKinley, Davao, Mindanao Isl. [this locality may currently be more easy to locate as Mt. Talomo, within the boundary of Davao City Province]).

The conformation of the carotid arterial patterns in *A. gracilirostris* clearly unite this new species in a group with *A. datae* and *A. sacobianus.* The presence of a stapedial foramen in the auditory bulla, together with a relatively large carotid canal for the internal carotid artery, and a prominent furrow between the middle lacerate foramen and the foramen ovale (Fig. 4) for the internal maxillary artery, also is a trait shared by *A. gracilirostris, A. datae* and *A. sacobianus.* It should be noted, however, that this pattern is hypothesized to constitute the ancestral arterial pattern among muroid rodents (Hill 1935, Musser 1982, Musser & Heaney 1992), and as such should not be interpreted as expressing phylogenetic affinity between these *Apomys* species. The minute dorsal palatine foramen present in orbital region, above roots of M2, distinguishes the new species from *A. insignis,* which has an easily visible foramen above the junction between M1 and M2. A more explicit statement of hypothesized relationships among these three species *Apomys,* and among all the members of the genus, will have to await results of an upcoming revision.

The dentaries (Fig. 3) display distinct differences between *A. gracilirostris* and other *Apomys* having to do with the relative length of the angular process and mandibular condyle. When viewed from the side, most *Apomys* (e.g., *A. datae, A. insignis,* and *A. musculus,* as illustrated in fig. 8 of Musser 1982: 24) display a mandibular condyle that projects somewhat beyond the vertical plane of the angular process. In contrast, in *A. gracilirostris,* it is the angular process that projects beyond the plane of the mandibular condyle. Another characteristic distinguishing this species from all other *Apomys* is that the lower edge of the incisive alveolus begins (in the vertical plane) just in front of m1, whereas the body of the ramus between the first molar and incisor in other species of *Apomys* is much longer. A large protuberance (capsular process sensu Musser & Heaney 1992) forms around the end of the root of the lower incisor, on the labial side of the dentary, just anterior and ventral to the coronoid process, forming a narrow shelf that fades back into the mandibular condyle.

The teeth of *A. gracilirostris* are the most diagnostic feature separating the species from its congeners: in fact, the upper and lower incisors are sufficient to diagnose the species, in a museum or in the field. Among *Apomys, A. gracilirostris* likewise displays an increasing degree of molar reduction and simplification of crowns, epitomized by the reduction in number of molars found in *A. gracilirostris* specimen 649. In fact, upon first examination, the extreme reduction of the molars together with the lack of a pigmented enamel on the lower incisors, led me to believe that *A. gracilirostris* constituted a new genus, which it still may, once stricter and more careful analyses are carried out of *Apomys* and potential sister taxa. Outgroup taxa that must be included in such an analysis are the native Philippine shrew rats (*Crunomys, Chrotomys,* and *Rhyncomys).* Inclusion of these taxa will enable testing one of the three hypotheses of generic relationships of *Apomys* proposed by Musser & Heaney (1992): that *Apomys* may be more related to the native Philippine shrew rats than to other Philippine endemics or genera from other archipelagos. The somewhat inflated mastoid bone of *A. gracilirostris* is reminiscent of a condition noted in *Tarsomys apoensis* (Musser & Heaney 1992). It was impossible to determine the homology between the principal cusp comprising the almost unicuspid M3 in *Apomys* and the same structure in other Murinae; Musser and Heaney (1992) hypothesized that the *Apomys* M3 cusp may be homologous with t5 of other murines.

The intent of this work was not to assess the specific status of the two nominal taxa currently included in *A. insignis, A. i. insignis* and *A. i. bardus.* However, it is clear that the lack of morphological differences between these two taxa lends support to the hypothesis that they clearly do not constitute separate species (Musser 1982), and probably not even separate subspecies.

Discussion

Finding a new species of *Apomys* in the Philippines is not as surprising as the fact that it was found in an area that already had been explored by naturalists. Edgar A. Mearns spent some time in the general area, but further east than the new species was collected (Merrill 1907a). This highlights the fact that as good as the turn of the century collectors were, there still are areas in the Philippines that need more thorough study in order to arrive at a fuller understanding of their existing biodiversity. It is even more critical today than before to document the biodiversity in the Philippines, as continuing loss of forest cover leaves ever diminishing pristine habitats available for wildlife. We observed some limited scale logging (with chain-saws and water buffalo) going on up to an elevation of 950 m in the Mount Halcon area, in spite of the fact that the entire area is purportedly protected from exploitation by all save the native Mangyan tribal peoples. These forests harbor a rich endemic fauna, including *Apomys gracilirostris,* the rare endemic *Anonymomys mindorensis* (pers. obv., Musser 1981), very high population levels of *Chrotomys mindorensis* (pers. obv., Musser et al. 1982), and other, as yet undescribed species. The ineluctable conclusion with respect to the conservation of the Mount Halcon Highlands is that the remaining areas of forest must at all costs be protected.

Acknowledgments

I thank most of all Pedro Bangol, the Mangyan tribesman who is responsible for catching the specimens described herein: he had a lot to teach. I thank the Protected Areas and Wildlife Bureau of the Philippine Department of the Environment and Natural Resources for facilitating permits that allowed us to carry out this work. Within these organizations, I especially thank A. Alcala, A. Ballesfin, J. Caleda, C. Catibog-Sinha, C. Custodio, D. Ganapin, and S. Peñafiel. I thank A.-M. and R. Tate, and the Miranda family for extending welcome hospitality during overly long stays in Manila. Assistance in the field was provided by the following CMNH volunteers and uncompensated staff, and NMP staff: R. M. Brown, J. Barcelona, D. T. Busemeyer, R. E. Fernandez, J. W. Ferner, A. Ippolito, and D. D. Keller. Specimens examined in this work kindly were made available by L. R. Heaney and W. T. Stanley, FMNH. Specimens of *A. sacobianus* (USNM) were measured by R. García Perea through the good graces of A. L. Gardner. J. C. Brown assisted with measuring specimens at FMNH. L. R. Heaney, T. A. Munroe, G. G. Musser, and E. A. Rickart reviewed, and greatly improved, preliminary drafts of this manuscript. G. G. Musser kindly diagnosed these creatures as a new species. This work was made possible in part by a grant from the John D. and Catherine T. MacArthur Foundation to P. C. Gonzales (NMP) and R. S. Kennedy (CMNH). This paper constitutes a contribution of the joint National Museum of the Philippines/Cincinnati Museum of Natural History Biodiversity Inventory Project. Electron micrographs courtesy of F. Ezra and D. Jacobs, Miami Valley Laboratories of Procter & Gamble.

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Appendix 1.—Means (plus or minus one standard deviation; sample size in parentheses) and ranges for 28 cranial and mandibular measurements in 12 populations of *Apomys* examined. Superscript 'a' indicates holotype of *A. gracilirostris.*

Taxon: Character	*A. abrae* (♀) (Abra Prov.)	*A. abrae* (♀) (Ilocos Norte Prov.)		*A. abrae* (♂) (Ilocos Norte Prov.)		*A. abrae* (♀) (Mountain Prov.)	
BB	—	14.71 ± 0.52 (3)	14.2–15.2	13.79 ± 0.60 (3)	13.1–14.3	14.86 ± 0.18 (2)	14.7–15.0
BIF	—	2.08 ± 0.09 (7)	2.0–2.2	2.12 ± 0.05 (3)	2.1–2.2	1.89 ± 0.17 (2)	1.8–2.0
BIT	—	1.81 ± 1.34 (7)	1.7–2.1	1.80 ± 0.16 (3)	1.6–1.9	1.74 ± 0.08 (2)	1.7–1.8
BM1	1.9	3.20 ± 0.27 (7)	2.9–3.6	2.70 ± 0.36 (3)	2.3–2.9	3.28 ± 0.08 (2)	3.2–3.3
BM3	—	4.23 ± 0.24 (7)	3.8–4.5	3.98 ± 0.25 (3)	3.7–4.2	4.25 ± 0.10 (2)	4.2–4.3
BMF	—	2.27 ± 0.22 (7)	2.0–2.6	2.74 ± 0.50 (2)	2.4–3.1	2.38 ± 0.20 (2)	2.2–2.5
BR	—	5.93 ± 0.23 (7)	5.5–6.2	5.61 ± 0.21 (3)	5.4–5.8	6.32 ± 0.05 (2)	6.3–6.4
BZP	3.1	2.84 ± 0.16 (7)	2.6–3.0	2.75 ± 0.07 (3)	2.7–2.8	2.67 ± 0.03 (2)	2.6–2.7
HB	4.5	4.61 ± 0.37 (3)	4.2–4.9	4.30 ± 0.02 (2)	—	4.47 ± 0.31 (2)	4.2–4.7
HBC	—	10.60 ± 0.14 (3)	10.4–10.7	10.21 ± 0.71 (4)	9.7–11.3	10.70 ± 0.22 (2)	10.5–10.8
IB	—	5.42 ± 0.16 (7)	5.2–5.7	5.30 ± 0.13 (3)	5.2–5.4	5.40 ± 0.05 (2)	—
IFM1	1.8	1.69 ± 0.16 (7)	1.5–1.9	1.49 ± 0.23 (3)	1.2–1.7	1.62 ± 0.25 (2)	1.4–1.8
LB	5.0	4.96 ± 0.26 (2)	4.8–5.1	4.75 ± 0.11 (2)	4.7–4.8	4.48 ± 0.11 (2)	4.4–4.6
LD	8.8	8.54 ± 0.30 (7)	8.0–8.9	8.66 ± 0.60 (3)	8.0–9.2	8.06 ± 0.52 (2)	7.7–8.4
LIF	4.5	4.73 ± 0.15 (7)	4.6–4.9	4.93 ± 0.23 (3)	4.7–5.1	4.61 ± 0.40 (2)	4.3–4.9
LM13	6.5	6.64 ± 0.24 (7)	6.4–7.0	6.86 ± 0.55 (4)	6.1–7.4	7.00 ± 0.05 (2)	—
LN	13.3	13.05 ± 0.55 (7)	12.3–13.6	13.39 ± 0.54 (3)	12.8–13.8	12.96 ± 1.06 (2)	12.2–13.7
LPB	8.4	7.96 ± 0.08 (7)	7.8–8.1	7.46 ± 0.02 (2)	7.4–7.5	7.40 ± 0.15 (2)	7.3–7.5
LR	11.9	11.96 ± 0.39 (7)	11.4–12.5	11.82 ± 0.63 (3)	11.2–12.5	12.54 ± 1.24 (2)	11.7–13.4
ONL	35.1	35.36 ± 0.95 (4)	34.3–36.3	34.98 ± 1.00 (3)	33.9–35.9	35.24 ± 1.42 (2)	34.2–36.2
PL	18.0	17.52 ± 0.29 (7)	17.1–17.9	16.64 ± 0.51 (3)	16.2–17.2	17.30 ± 1.02 (2)	16.6–18.0
PPL	9.8	10.76 ± 0.60 (3)	10.1–11.3	11.51 ± 1.82 (3)	10.0–13.5	10.70 ± 0.40 (2)	10.4–11.0
ZB	—	17.0 — (1)	—	—	—	—	—
LMAND	19.8	19.16 ± 0.23 (6)	18.9–19.5	19.20 ± 1.21 (4)	17.7–20.5	19.08 ± 1.15 (2)	18.2–19.9
LMT	6.4	6.42 ± 0.36 (7)	6.0–6.9	6.29 ± 0.42 (4)	5.7–6.6	6.46 ± 0.63 (2)	6.0–6.9
HMC	7.4	8.06 ± 0.35 (7)	7.7–8.6	7.80 ± 0.62 (4)	7.0–8.4	7.78 ± 0.25 (2)	7.6–8.0
HMR	2.8	2.65 ± 0.11 (7)	2.5–2.8	2.70 ± 0.10 (4)	2.6–2.8	2.68 ± 0.08 (2)	2.6–2.7
TM	1.8	2.08 ± 0.09 (7)	2.0–2.3	1.96 ± 0.17 (4)	1.8–2.1	1.81 ± 0.11 (2)	1.7–1.9

Taxon: Character	*A. abrae* (♂) (Mountain Province)		*A. datae* (♀) (Mountain Province)		*A. datae* (♂) (Mountain Province)	
BB	14.95 ± 0.55 (7)	13.9–15.6	15.28 ± 0.43 (10)	14.8–16.0	15.46 ± 0.42 (7)	14.7–15.9
BIF	1.98 ± 0.21 (7)	1.8–2.3	2.22 ± 0.15 (10)	2.0–2.5	2.49 ± 0.15 (7)	2.4–2.8
BIT	1.81 ± 0.08 (7)	1.7–1.9	2.02 ± 0.12 (10)	1.8–2.2	2.23 ± 0.18 (6)	2.1–2.6
BM1	3.18 ± 0.14 (7)	3.0–3.4	3.17 ± 0.21 (10)	2.7–3.5	3.40 ± 0.10 (7)	3.2–3.6
BM3	4.12 ± 0.34 (7)	3.4–4.4	4.65 ± 0.27 (10)	4.4–5.1	4.81 ± 0.19 (7)	4.6–5.1
BMF	2.38 ± 0.21 (7)	2.2–2.7	2.39 ± 0.28 (10)	1.8–2.9	2.58 ± 0.17 (6)	2.4–2.8
BR	5.99 ± 0.15 (7)	5.8–6.2	6.59 ± 0.30 (10)	6.3–7.3	6.92 ± 0.35 (7)	6.4–7.4
BZP	2.98 ± 0.21 (7)	2.7–3.3	3.30 ± 0.22 (10)	2.9–3.6	3.45 ± 0.18 (7)	3.2–3.6
HB	4.37 ± 0.33 (7)	3.9–4.7	4.73 ± 0.33 (10)	4.2–5.2	4.79 ± 0.24 (7)	4.5–5.1
HBC	10.41 ± 0.35 (7)	9.7–10.7	11.15 ± 0.41 (10)	10.6–12.0	11.21 ± 0.52 (7)	10.4–11.8
IB	5.65 ± 0.14 (7)	5.4–5.8	5.97 ± 0.13 (10)	5.8–6.2	6.01 ± 0.27 (7)	5.5–6.4
IFM1	1.68 ± 0.10 (7)	1.5–1.8	2.02 ± 0.18 (10)	1.6–2.2	2.14 ± 0.16 (7)	2.0–2.4
LB	4.45 ± 0.19 (7)	4.2–4.6	4.70 ± 0.15 (10)	4.4–5.0	4.76 ± 0.20 (7)	4.4–5.1
LD	8.46 ± 0.51 (7)	7.8–9.4	9.24 ± 0.39 (10)	8.7–10.0	9.72 ± 0.29 (7)	9.4–10.1
LIF	4.68 ± 0.29 (7)	4.2–5.0	4.73 ± 0.41 (10)	3.9–5.2	4.83 ± 0.29 (7)	4.4–5.4
LM13	6.85 ± 0.16 (7)	6.6–7.0	6.92 ± 0.20 (10)	6.7–7.3	7.16 ± 0.15 (7)	7.0–7.4
LN	13.49 ± 0.37 (7)	13.0–14.0	14.66 ± 0.68 (10)	13.6–16.0	15.15 ± 0.67 (7)	14.3–16.3
LPB	8.22 ± 0.41 (7)	7.6–8.8	9.09 ± 0.28 (10)	8.6–9.5	9.38 ± 0.14 (7)	9.1–9.5
LR	12.54 ± 0.44 (7)	11.9–13.0	13.42 ± 0.70 (10)	12.5–15.0	14.14 ± 0.48 (7)	13.3–14.8
ONL	35.62 ± 0.80 (7)	34.4–37.1	38.48 ± 1.04 (10)	36.8–40.5	39.76 ± 0.60 (7)	38.6–40.3

Appendix 1.—Continued.

Taxon: Character	*A. abrae* (♂) (Mountain Province)		*A. datae* (♀) (Mountain Province)		*A. datae* (♂) (Mountain Province)	
PL	17.82 ± 0.66 (7)	17.0–19.1	19.11 ± 0.60 (10)	18.3–20.5	19.91 ± 0.42 (7)	19.4–20.8
PPL	10.36 ± 0.45 (7)	9.8–11.1	11.61 ± 0.46 (10)	10.9–12.2	11.87 ± 0.43 (7)	11.3–12.3
ZB	16.0 — (1)	—	18.03 ± 0.59 (5)	17.1–18.7	18.24 ± 0.26 (4)	18.1–18.6
LMAND	19.20 ± 0.46 (7)	18.3–19.8	20.95 ± 0.59 (10)	20.1–22.0	21.83 ± 0.57 (7)	21.0–22.5
LMT	6.24 ± 0.15 (7)	6.0–6.4	6.42 ± 0.23 (10)	6.1–6.8	6.69 ± 0.13 (7)	6.5–6.9
HMC	7.96 ± 0.18 (7)	7.7–8.3	9.13 ± 0.52 (10)	8.3–9.9	9.49 ± 0.31 (7)	9.1–10.0
HMR	2.67 ± 0.11 (7)	2.5–2.9	3.06 ± 0.14 (10)	2.8–3.3	3.26 ± 0.13 (7)	3.1–3.4
TM	1.85 ± 0.10 (7)	1.7–2.0	2.23 ± 0.08 (10)	2.1–2.3	2.23 ± 0.15 (7)	2.0–2.4

Taxon: Character	*A. i. insignis* (♀) (Bukidnon Province)		*A. i. insignis* (♂) (Bukidnon Province)		*A. insignis bardus* (♀) (Zamboanga del Norte Prov.)	
BB	13.32 ± 0.41 (6)	12.8–13.9	13.48 ± 0.30 (10)	13.0–14.1	13.63 — (1)	—
BIF	1.98 ± 0.22 (6)	1.6–2.3	2.02 ± 0.17 (11)	1.8–2.3	2.20 — (1)	—
BIT	1.69 ± 0.07 (6)	1.6–1.8	1.67 ± 0.10 (11)	1.5–1.8	1.82 ± 0.20 (2)	1.7–2.0
BM1	3.09 ± 0.30 (6)	2.7–3.4	3.06 ± 0.17 (11)	2.8–3.3	3.29 ± 0.04 (2)	—
BM3	4.28 ± 0.10 (6)	4.2–4.5	4.19 ± 0.15 (11)	3.9–4.4	4.23 ± 0.21 (2)	4.1–4.4
BMF	2.38 ± 0.16 (2)	2.3–2.5	2.28 ± 0.15 (8)	2.1–2.5	2.46 ± 0.02 (2)	2.4–2.5
BR	5.43 ± 0.16 (6)	5.3–5.7	5.37 ± 0.26 (10)	5.0–5.9	5.77 — (1)	—
BZP	2.48 ± 0.09 (6)	2.4–2.6	2.41 ± 0.19 (11)	2.1–2.7	2.20 ± 0.29 (2)	2.0–2.4
HB	3.80 ± 0.24 (6)	3.5–4.1	3.58 ± 0.54 (9)	2.7–4.2	3.76 ± 0.02 (2)	3.7–3.8
HBC	9.56 ± 0.13 (6)	9.4–9.8	9.39 ± 0.33 (9)	9.0–9.9	9.74 ± 0.07 (2)	9.7–9.8
IB	4.94 ± 0.16 (6)	4.7–5.2	5.07 ± 0.24 (11)	4.7–5.4	4.84 ± 0.37 (2)	4.6–5.1
IFM1	1.72 ± 0.25 (6)	1.4–2.1	1.65 ± 0.23 (11)	1.3–2.0	1.41 — (1)	—
LB	3.99 ± 0.19 (6)	3.8–4.3	3.78 ± 0.30 (10)	3.2–4.2	3.76 ± 0.00 (2)	—
LD	7.28 ± 0.36 (6)	6.7–7.7	7.31 ± 0.25 (11)	6.8–7.8	7.34 ± 0.16 (2)	7.2–7.4
LIF	3.68 ± 0.49 (6)	3.0–4.3	3.71 ± 0.21 (11)	3.3–4.0	3.78 — (1)	—
LM13	6.02 ± 0.10 (6)	5.8–6.3	5.86 ± 0.16 (11)	5.6–6.2	5.74 ± 0.30 (2)	5.5–6.0
LN	11.49 ± 0.39 (6)	11.0–12.0	11.64 ± 0.70 (11)	10.6–12.9	11.41 — (1)	—
LPB	7.41 ± 0.28 (2)	7.2–7.6	7.18 ± 0.02 (2)	—	7.02 — (1)	—
LR	10.48 ± 0.52 (6)	9.9–11.4	10.51 ± 0.58 (11)	9.3–11.5	10.72 — (1)	—
ONL	31.86 ± 0.60 (6)	31.2–32.9	31.68 ± 0.63 (10)	30.7–32.7	32.29 — (1)	—
PL	15.75 ± 0.44 (2)	15.4–16.1	15.41 ± 0.20 (2)	15.3–15.6	15.49 ± 0.25 (2)	15.3–15.7
PPL	9.71 — (1)	—	9.3 — (1)	—	9.13 ± 0.54 (2)	8.8–9.5
ZB	— — (0)	—	— — (0)	—	14.70 — (1)	—
LMAND	17.26 ± 0.21 (6)	17.0–17.6	17.06 ± 0.44 (10)	16.1–17.6	16.54 ± 0.35 (2)	16.3–16.8
LMT	5.38 ± 0.30 (6)	5.0–5.9	5.43 ± 0.17 (11)	5.2–5.7	5.24 ± 0.16 (2)	5.1–5.4
HMC	7.25 ± 0.24 (6)	6.9–7.5	7.29 ± 0.29 (11)	6.8–7.7	6.71 ± 0.16 (2)	6.6–6.8
HMR	2.46 ± 0.14 (6)	2.2–2.6	2.42 ± 0.13 (11)	2.1–2.7	2.45 ± 0.40 (2)	2.2–2.7
TM	1.78 ± 0.10 (6)	1.6–1.9	1.75 ± 0.13 (11)	1.5–1.9	1.65 ± 0.06 (2)	1.6–1.7

Taxon: Character	*A. insignis bardus* (♂) (Zamboanga del Norte Prov.)		*A. gracilirostris*					
			1136^a (♂)	1126 (♂)	1131 (♂)	1132 (♂)	1119 (♀)	Means (±SD)
BB	13.29 — (1)	—	15.6	16.1	15.3	15.6	15.6	16.05 ± 0.471
BIF	1.94 ± 0.06 (2)	1.9–2.0	1.8	2.0	2.1	2.1	1.9	1.98 ± 0.145
BIT	1.83 ± 0.03 (3)	1.8–1.9	1.6	1.5	1.6	1.5	1.5	1.56 ± 0.054
BM1	3.01 ± 0.07 (2)	3.0–3.1	3.5	3.5	4.4	4.3	4.5	4.05 ± 0.486
BM3	4.32 ± 0.09 (2)	4.2–4.4	4.7	5.0	5.5	—	5.7	5.24 ± 0.465
BMF	2.63 ± 0.21 (2)	2.5–2.8	1.9	2.1	2.0	2.2	2.3	2.09 ± 0.176
BR	5.72 ± 0.28 (2)	5.5–5.9	6.6	6.3	6.7	6.6	6.4	6.53 ± 0.145
BZP	2.36 ± 0.26 (2)	2.2–2.5	3.3	3.0	3.2	3.6	3.0	3.21 ± 0.223
HB	3.74 — (1)	—	4.2	4.0	3.4	4.2	3.8	3.92 ± 0.307
HBC	9.15 — (1)	—	11.1	11.3	10.5	10.4	11.1	10.88 ± 0.404
IB	4.91 ± 0.20 (2)	4.8–5.0	5.8	6.3	5.5	6.0	6.2	6.00 ± 0.233

Appendix 1.—Continued.

Taxon: Character	*A. insignis bardus* (♂) (Zamboanga del Norte Prov.)		*A. gracilirostris*					
			1136[a] (♂)	1126 (♂)	1131 (♂)	1132 (♂)	1119 (♀)	Means (±SD)
IFM1	1.82 ± 0.12 (2)	1.7–1.9	2.4	2.2	2.4	2.9	2.5	2.49 ± 0.241
LB	3.99 — (1)	—	5.1	5.0	4.8	5.2	5.0	5.03 ± 0.151
LD	7.62 ± 0.42 (2)	7.3–7.9	9.8	10.1	10.2	10.8	10.4	10.22 ± 0.450
LIF	3.80 ± 0.08 (6)	3.7–3.8	4.8	4.8	4.9	5.0	4.9	4.87 ± 0.102
LM13	5.54 ± 0.39 (3)	5.2–6.0	6.3	6.3	6.6	6.2	6.5	6.39 ± 0.246
LN	11.96 ± 0.46 (2)	11.6–12.3	14.8	14.8	14.5	16.0	14.9	15.00 ± 0.566
LPB	7.44 ± 0.15 (2)	7.3–7.6	9.2	8.8	9.1	9.5	9.0	9.14 ± 0.259
LR	10.70 ± 0.11 (2)	10.6–10.8	13.9	13.9	14.0	14.9	13.9	14.11 ± 0.425
ONL	32.06 — (1)	—	39.4	39.7	39.0	41.6	39.8	39.89 ± 0.997
PL	15.75 ± 0.07 (2)	15.7–15.8	19.1	19.0	19.4	19.9	19.4	19.35 ± 0.344
PPL	9.21 — (1)	—	11.9	11.6	11.6	12.3	12.1	11.92 ± 0.310
ZB	— — (0)	—	17.6	17.6	18.0	18.6	18.1	17.98 ± 0.389
LMAND	16.25 ± 1.13 (2)	15.4–17.0	20.3	19.5	20.2	21.5	20.8	20.47 ± 0.750
LMT	5.42 ± 0.11 (2)	5.4–5.5	6.4	6.2	6.2	6.6	6.2	6.32 ± 0.183
HMC	6.70 ± 0.40 (2)	6.4–7.0	8.5	8.6	8.2	9.0	8.9	8.64 ± 0.298
HMR	2.40 ± 0.20 (2)	2.2–2.5	2.9	2.8	2.9	3.0	2.8	2.88 ± 0.090
TM	1.56 ± 0.06 (2)	1.5–1.6	1.9	1.7	1.8	1.8	1.8	1.80 ± 0.062

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(2):319–337. 1995.

A review of the spiny mouse genus *Scolomys* (Rodentia: Muridae: Sigmodontinae) with the description of a new species from the western Amazon of Brazil

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Abstract.—Included within a collection of mammals assembled during a year-long vertebrate survey of the Rio Juruá in the western Amazon Basin of Brazil is a series of specimens of a new spiny mouse of the genus *Scolomys.* This genus is one of the more highly-localized and poorly-known murid rodents of the neotropical forests. Prior to the collection reported here, there were two recognized species known from a total of 15 specimens. One of these, *S. melanops* Anthony, 1924, is known only from three closely spaced localities in eastern Ecuador; the second, *S. ucayalensis* Pacheco, 1991, is known from only one locality in north-central Perú. We provide a revised diagnosis and description of the genus while describing the third species, suggest phylogenetic affinities of the genus within the tribe Oryzomyini, and summarize aspects of the ecology and life history of the new species.

Resumo.—Um novo catito de espinho (gênero *Scolomys*) foi coletado durante um levantamento da fauna de vertebrados realizado no rio Juruá, no oeste da Amazônia brasileira. Este gênero de roedores murídeos neotropicais foi pouco estudado e possui uma distribuição geográfica muito restrita. Somente duas espécies eram até então conhecidas: uma do leste do Equador (*S. melanops* Anthony, 1924; 13 espécimes provenientes de três localidades) e outra do norte do Peru (*S. ucayalensis* Pacheco, 1991; dois espécimes provenientes de uma localidade). Neste estudo nós descrevemos uma terceira espécie e apresentamos uma revisão aumentada da diagnose e descrição do gênero. Também sugerimos afinidades filogenéticas dentro da tribo Oryzomyini, além de sumarizarmos pela primeira vez aspectos da ecologia e história natural desses animais.

The genus *Scolomys* contains small-bodied and strongly spinose mice of the tribe Oryzomyini Vorontsov, 1959 (sensu Voss & Carleton 1993) of the South American Sigmodontinae (Muridae) rodents. Each of the two known species has a very localized distribution in the forests of western Amazonia. The genus was described in 1924 by H. E. Anthony and the type species, *S. melanops,* is known from a total 13 specimens from three nearby localities in east-central Ecuador. A second species, *S. ucayalensis,* was recently described by Pacheco (1991) based on two specimens from a single locality in north-central Perú.

We have obtained a series of 23 specimens from four localities along the Rio Juruá in the lowland Amazonian forest of western Brazil (states of Amazonas and Acre) that represents a third species of this poorly-known genus. Based on these new materials and an examination of most other specimens, we provide an expanded diagnosis and description of the genus and describe the new species here. We also compare *Scolomys* to the sympatric and superficially similar oryzomyine genus *Neacomys* as well as to other oryzomyine genera, provide remarks on phyletic relationships based on morphological characters and comparative DNA sequences, and summarize what few facts are available on life history and ecology.

Scolomys Anthony, 1924

Type species.—*Scolomys melanops* Anthony (1924:2).

Emended diagnosis.—Members of the tribe Oryzomyini (sensu Voss & Carleton 1993) of the murid rodent subfamily Sigmodontinae (sensu Carleton & Musser 1984) with 3 pairs of mammae (1 thoracic, 1 abdominal, and 1 inguinal [following position designations given by Voss & Carleton 1993; Anthony (1924) recorded mammae as 1 pectoral, 2 inguinal]). Pelage comprised of short, stiff spines on both dorsum and venter with equal-length normal hairs interspersed throughout, giving general spiny appearance over entire body. Skull with short and blunt rostrum flanked by shallow zygomatic notches; supraorbital margins rounded, forming a moderately-developed shelf overhanging posterior half of orbit, and extending onto braincase as ridges; braincase rather globular in shape; interparietal large and well-developed; palate long and wide, with well-developed and complex posterolateral pits, but with rather short and posteriorly broadened incisive foramina; alisphenoid strut absent; carotid arterial circulation of Pattern 3 (of Voss 1988); subsquamosal fenestra reduced to totally occluded, tegmen tympani either not in contact with or only touches, but does not overlap, squamosal; incisors small, narrow, proodont to orthodont; upper and lower molars small, pentalophodont, but with low cusps that wear quickly with age; procingulum of M1 undivided by anteromedial flexus; labial flexi deeply penetrating in all molars; lingual flexi reduced in size in M1 and M2 and obsolete in M3; upper and lower molars with well-developed mesoloph(id)s; stomach unilocular and hemiglandular; male phallus cylindrical with incomplete crater rim, terminally exposed urethral flaps, lateral mounds of distal baculum hidden by tissue of crater rim, and an epidermis with small and widely-spaced spines.

Description.—Body pelage short and close, with texture markedly spinose both above and below; color ranges from grizzled pale reddish-black to nearly totally black dorsally and gray ventrally; dorsal hairs of two types: (1) long (averaging 12 mm), stout, flat, and broad (averaging 0.6 mm) spines with a medial trough on both surfaces, with the terminal ⅓ to ¼ increasingly dark to the tip and proximal portion clear; and (2) long, thin hairs of length equal to spines and with tips reddish or blackish; ventral hairs of both types uniformly gray from base to tip. Mystacial, superciliary, genal I, submental, interramal, and carpal vibrissae present. Pinnae small, appearing somewhat thickened and thus stiff, and, while appearing naked from a distance, are clothed externally and internally with short reddish-brown hairs. Manus with five large, fleshy plantar pads (two carpal and three interdigital); toes pale in color; digit I reduced but with a small nail, digits II through V long and well-developed with short, stout, and curved claws. Pes rather short and broad, although metatarsus is nearly twice as long as digit III; the heel is haired and the naked sole begins at about ¼ the length of the plantar surface (not including the digits); outer digits shorter than the middle three (with the claw of I extending to or just past the base of II and that of V to the proximal phalax of IV); conspicuous tufts of long, silvery hairs present at dorsal bases of claws extending past the tips, but the claw is visible from above;

Fig. 1. Photograph of a living *Scolomys juruaense*, new species (INPA 2490, Barro Vermelho, left bank Rio Juruá, Amazonas, Brazil).

claws short, stout (about twice as long as deep) and strongly curved along their dorsal surface; plantar pads five to six (thenar and four interdigital pads large, fleshy, and always present; hypothenar pad either absent or only weakly developed). Tail shorter than head-and-body, appearing sparsely haired, without a terminal tuft or pencil of long hairs; 15–18 scale annuli per cm at midlength; annular hairs broad, blackish, and 2.5–4 scale rows in length, but sparsely distributed so that the tail scales are conspicuous. The overall impression is of a small-bodied, short-tailed, and short-eared mouse with a broad head, but short and pointed rostrum and very spiny fur (Fig. 1).

Skull, in dorsal view, with short and broad or tapering rostrum flanked by shallow, barely perceptible zygomatic notches; nasolacrimal capsules expanded (especially so in *S. melanops*, Fig. 2); interorbital region broad and hourglass-shaped, with well-defined beaded ledges overhanging margins from middle of frontals, continuing along posterior margins of orbit and onto braincase just above the squamoso-parietal suture as weakly to moderately-developed temporal ridges. Braincase distinctly rounded and globular in appearance, dominating dorsal aspect of skull (length of braincase ½ length of skull). Nasals somewhat expanded and taper posteriorly to a median point that terminates well behind the premaxillary-frontal sutures. Interparietal large, ½ to ⅓ as deep as wide.

In lateral view, nasals extend only to or just barely beyond anterior curvature of incisors. Zygomatic plate narrow, vertical to slightly angled posteriorly from base, and without distinct, free dorsal edge (thus, the zygomatic notch is shallow when viewed from above). Zygomatic arch thin with jugal reduced. Postglenoid foramen moderate to small; hamular process of squamosal stout;

Fig. 2. Dorsal, ventral, and lateral views of cranium, lateral view of left mandible of *Scolomys melanops* Anthony, USNM 513581, adult male. Scale bar equals 10 mm.

subsquamosal foramen reduced to totally occluded; mastoid fenestra very small to lacking. Tegmen tympani of periotic either does not contact or abuts, but does not overlap, the squamosal. Tympanic bullae small and inflated ventrally only to level of molar series.

In ventral view, incisive foramina moderate in size (occupying about 60% of diastemal distance) and distinctly tear-drop in shape, pointed anteriorly with diverging sides and expanded, rounded posterior margins; premaxillary-vomerine septum greatly swollen and nearly filling the entire cavity when viewed ventrally. Bony palate long and wide (sensu Hershkovitz 1962), without a medial ridge or palatal excrescences, with only weakly evident lateral folds, but with large and complex posterolateral pits. The mesopterygoid fossa wide with parallel sides and a rounded or squared anterior margin, ending well behind the third molars; bony roof of fossa complete, or perforated only by barely perceptible sphenopalatine vacuities along the presphenoid. Parapterygoid fossae well developed, with lateral margins straight to slightly convex and strongly divergent towards the bullae, devoid of vacuities except for a small foramen ovale, and moderately excavated, certainly not flat in appearance. Alisphenoid strut absent, but only foramen ovale is present laterally; without anterior opening of alisphenoid canal. A shallow trough where the masticatory-buccinator branch of the maxillary nerve courses visible; it emanates from anterior margin of the foramen ovale and obliquely crosses the alisphenoid onto the squamosal. Facial circulation apparently derived only from the internal carotid artery (Pattern 3, of Voss, 1988), as indicated by a greatly reduced to absent stapedial foramen, no squamoso-alisphenoid groove along interno-lateral wall of braincase, and no sphenofrontal foramen (signs of supraorbital branch of stapedial artery).

Mandible short and stout; coronoid process short with a weakly to moderately-curved posterior projection; capsular processes of lower incisor alveoli weakly developed; lower incisors thin, elongate, with enamel essentially devoid of pigment. Upper incisors ungrooved, with yellow to pale yellow enamel; small, deeper than wide, and proodont (*S. melanops,* Fig. 2) to orthodont (*S. ucayalensis* and the new species described below).

Maxillary tooth rows slightly convergent posteriorly, and angled obliquely downward and outward at about a 40 degree angle. Teeth of nearly all known specimens moderately to well-worn, and, as the cusps are low, even a little wear obscures surface topography. Molars small, always longer (anteriorly–posteriorly) than wide, and forming a graded series with the third molar greatly simplified. Upper teeth pentalophodont with principal cusps arranged transversely and slightly obliquely; labial and lingual reentrant folds do not interdigitate, or contact, with major labial folds of M1 and M2 (paraflexus and metaflexus) deep, extending at least ⅔ across the tooth, lingual folds reduced, with protoflexus only evident as a shallow lateral indentation in M1 and not visible at all in M2. Procingulum of M1 and m1 well-developed but not divided into separate anterolabial and anterolingual conules (no anteromedial flexus [-id]); anteroflexus on M1 absent so that anteroloph not separated from labial anteroconule; anteroloph of M2 well developed; distinct mesolophs present and extending to labial margin of all three molars; posteroloph well developed on M1 but barely perceptible on M2 and absent on M3. Paracone and metacone of M1 and M2 tall and well developed with protocone and hypocone proportionately reduced in size and much lower in topography; only paracone and weakly-developed protocone present on M3.

Content and distribution.—The genus *Scolomys* comprises two described species, the known ranges of which are geographically restricted within the western Amazon Basin (Fig. 3). The type species, *S. melan-*

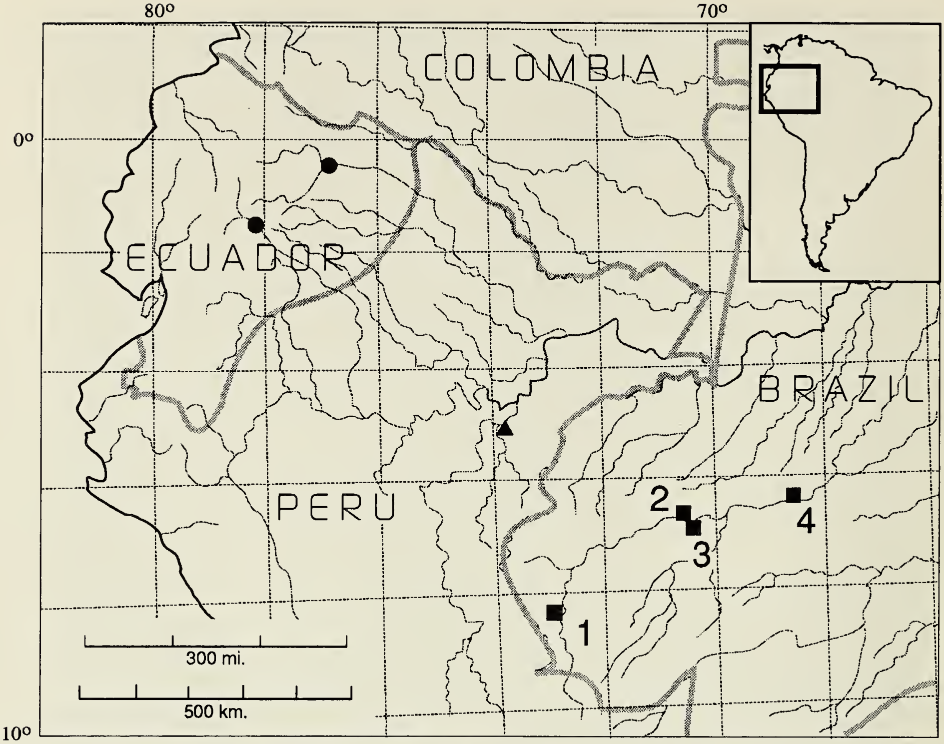

Fig. 3. Distributional records of spiny mice, genus *Scolomys*. Circles = *S. melanops* Anthony, triangle = *S. ucayalensis* Pacheco, and squares = *S. juruaense* new species (numbered as in list of specimens; see text).

ops, is known from three localities in eastern Ecuador: the type locality at Mera, 1160 m, Pastaza Province (holotype and five paratypes in the American Museum of Natural History, New York [AMNH], and three topotypes in the Natural Museum of Natural History, Washington D.C. [USNM]); Huamaní, Volcán Sumaco, Napo Province (above Mera, one specimen in the collection of the Escuela Politécnica Nacional, Quito [Albuja, 1991]), and Limoncocho, 250 m, Napo Province (3 specimens in USNM). *Scolomys ucayalensis* Pacheco is known from two specimens from its type locality, Centro de Investigaciones "Jenaro Herrera," 2.8 km E Jenaro Herrera, Depto. Loreto, right bank of Río Ucayali, Perú, 135 m. A third species from four localities in western Amazonia of Brazil is described here; it may be known as

Scolomys juruaense, new species

Holotype.—MPEG 23824 (Museo Paraense Emilio Goeldi, Belém, Pará, Brazil), adult female, collected on 19 September 1991 by J. L. Patton (original number 15570); skin with skull and mandibles, in good condition, plus liver tissue preserved both deep frozen and in ethyl alcohol. Tissues are maintained in the collections of the Museum of Vertebrate Zoology, University of California, Berkeley.

Type locality.—Seringal Condor, left bank Rio Juruá, Amazonas, Brazil 70°51′W, 6°45′S. Obtained in tree-fall slash disturbance in otherwise primary terra firme (or upland, non-seasonally flooded) forest.

Paratypes.—The total known sample of *S. juruaense* consists of the holotype and 22 additional specimens that are deposited in the Coleção de Mamíferos, Instituto Nacional de Pesquisas da Amazônia (INPA); Museu Paraense Emilio Goeldi (MPEG); and Museum of Vertebrate Zoology, University of California at Berkeley (MVZ), listed here by locality (numbered as in the map, Fig. 3): Brazil—Acre: (1) Sobral, left bank Rio Juruá, 72°49′W, 8°22′S—INPA 2485, adult female, skin with skull, carcass in fluid plus karyotype; INPA 2486, adult male, in fluid plus karyotype; MPEG 24023, adult female, skin with skull, carcass in fluid plus karyotype; MPEG 24024, adult female, in fluid plus karyotype; MVZ 183172, juvenile female, in fluid plus karyotype. Amazonas: (2) type locality—MPEG 24019, adult male, skin and skull; MPEG 24020, adult male, skin and skull plus karyotype; MVZ 183167, adult female, skin and skull; MVZ 183168, adult male, skin and skull plus karyotype; (3) Penedo, right bank Rio Juruá, 70°45′W, 6°50′S—INPA 2487, adult male, skin and skull; INPA 2488, adult male, body in fluid with skull extracted; MPEG 24022, adult female, body in fluid with skull extracted; MVZ 183165, adult male, body in fluid with skull extracted; MVZ 183166, adult female, skin and skull; and (4) Barro Vermelho, left bank Rio Juruá, 68°46′W, 6°28′S—INPA 2489, subadult male, skin and skull plus karyotype; INPA 2490, adult female, skin and skull plus karyotype; INPA 2491, adult female, skin and skull plus karyotype; INPA 2492, adult male, skin and skull, karyotype; MPEG 24021, adult male, skin and skull plus karyotype; MVZ 183169, subadult male, skin and skull plus karyotype; MVZ 183170, adult male, in fluid plus karyotype; and MVZ 183171, adult male, in fluid. Liver tissues preserved in 95% ethyl alcohol and frozen at −76°C are available for all specimens and are deposited in the Museum of Vertebrate Zoology, as are chromosome slides for all karyotyped specimens.

Distribution.—Known from three localities on the left and one on the right bank in the central and upper reaches of the Rio Juruá in the Brazilian states of Acre and Amazones (Fig. 3); all localities are below 400 m in elevation.

Etymology.—The name refers to the known distribution along the Rio Juruá, the largest white-water tributary of the Rio Amazonas with an origin extralimital to the Andean cordillera.

Diagnosis.—A small-bodied mouse (Table 1) with short, nearly naked tail (83% of body length); short, broad head with pointed snout (Fig. 1); short and relatively broad hindfeet; hypothenar pad greatly reduced to absent (minutely present in 15 of 23 specimens) but thenar and interdigital pads well-developed; small and rounded ears; dorsal color varying from a grizzled pale reddish-brown (Sudan Brown to Antique Brown; capitalized color terms from Ridgway 1912) to dark reddish-black (Raw Umber) finely streaked with black; with rounded and inflated braincase; short, basally-broad rostrum that tapers distally; narrowed and straight zygomatic arches; narrow but long orbital openings; subsquamosal fenestra totally occluded by stout hamular process of squamosal; short and distally broad incisive foramina with sides distinctly 'stepped'; wide mesopterygoid fossa with parallel sides and squared, as opposed to rounded, anterior margin (Fig. 4); and 2N = 50. Other characteristics are as listed above for the genus.

Measurements of holotype.—Measurements are in millimeters and weight (mass) in grams; external measurements are those recorded on the specimen label and bilateral measurements were taken on the right side with digital calipers: Total length, 160; head and body, 86; tail, 76; hind foot (with claws), 21; ear (from notch), 16; condyloincisive length (CIL), 21.21; zygomatic breadth (ZB), 12.42; braincase breadth (BB), 11.59; least interorbital breadth (IOC), 5.84; rostral length (RL, taken from anterior orbit to tip of nasals), 7.98; nasal length (NL), 8.60; rostral width-1 (RW-1, across nasolacrimal capsules), 4.86; rostral width-2 (RW-2, at premaxillo-maxillary suture), 3.61; orbital

Table 1.—Selected measurements of spiny mice of the genus *Scolomys* (mean ± one standard error and range, with sample size).

Variable	*S. melanops*	*S. ucayalensis*	*S. juruaense*
Total length	153.9 ± 3.01 (138–167) *n* = 10	144.0 *n* = 1	152.4 ± 1.9 (142–163) *n* = 11
Tail length	62.8 ± 2.06 (55–77) *n* = 10	60.0 *n* = 1	69.0 ± 1.50 (26–76) *n* = 11
Hind foot length	20.9 ± 0.31 (20–23) *n* = 10	18.0 *n* = 1	20.6 ± 0.20 (19–22) *n* = 16
Ear height	15.0 *n* = 3	13.0 *n* = 1	15.6 ± 0.18 (15–17) *n* = 16
Condyloincisive length	19.87 ± 0.30 (18.51–20.67) *n* = 7	19.41 ± 0.47 (18.94–19.89) *n* = 2	20.43 ± 0.22 (18.60–21.97) *n* = 16
Zygomatic breadth	12.42 ± 0.18 (11.37–12.90) *n* = 8	11.52 ± 0.25 (11.27–11.77) *n* = 2	12.13 ± 0.13 (11.18–13.30) *n* = 16
Braincase breadth	11.12 ± 0.07 (10.82–11.41) *n* = 8	11.41 ± 0.13 (11.29–11.54) *n* = 2	11.39 ± 0.11 (10.54–12.33) *n* = 16
Least interorbital constriction	4.96 ± 0.07 (4.77–5.45) *n* = 9	5.58 ± 0.09 (5.49–5.68) *n* = 2	5.59 ± 0.09 (4.55–6.13) *n* = 16
Rostral length	6.92 ± 0.16 (6.34–7.78) *n* = 9		7.86 ± 0.11 (6.93–8.48) *n* = 15
Nasal length	7.64 ± 0.10 (7.16–8.14) *n* = 9	7.69 ± 0.27 (7.42–7.96) *n* = 2	8.31 ± 0.11 (7.83–9.34) *n* = 15
Rostral width—1	4.78 ± 0.07 (4.47–5.10) *n* = 9		4.81 ± 0.07 (4.36–5.40) *n* = 16
Rostral width—2	3.48 ± 0.08 (3.21–3.84) *n* = 9		3.64 ± 0.06 (2.79–4.05) *n* = 16
Orbital length	6.90 ± 0.10 (6.45–7.21) *n* = 8		7.38 ± 0.09 (6.67–7.89) *n* = 16
Diastema length	5.84 ± 0.09 (5.50–6.34) *n* = 9	5.59 ± 0.21 (5.38–5.80) *n* = 2	6.23 ± 0.09 (5.73–6.75) *n* = 16
Maxillary tooth row length	2.70 ± 0.05 (2.49–2.93) *n* = 9	2.81 ± 0.13 (2.69–2.94) *n* = 2	2.66 ± 0.04 (2.31–2.88) *n* = 16

Table 1.—Continued.

Variable	*S. melanops*	*S. ucayalensis*	*S. juruaense*
Incisive foramen length	3.76 ± 0.09 (3.31–4.19) *n* = 9	3.765 ± 0.001 (3.76–3.77) *n* = 2	3.94 ± 0.07 (3.17–4.32) *n* = 16
Palatal bridge length	9.03 ± 0.19 (8.42–9.69) *n* = 6	8.65 ± 0.05 (8.60–8.70) *n* = 2	9.14 ± 0.12 (8.28–9.87) *n* = 16
Alveolar width	4.41 ± 0.07 (4.15–4.74) *n* = 8	4.475 ± 0.001 (4.47–4.48) *n* = 2	4.62 ± 0.05 (4.29–4.96) *n* = 16
Occipital condyle width	5.82 ± 0.07 (5.54–6.14) *n* = 7		6.01 ± 0.06 (5.64–6.46) *n* = 16
Mastoid breadth	10.28 ± 0.15 (9.67–10.70) *n* = 7		10.29 ± 0.08 (9.70–10.73) *n* = 16
Basioccipital length	3.19 ± 0.06 (2.98–3.38) *n* = 7		3.23 ± 0.05 (2.83–3.60) *n* = 16
Mesopterygoid fossa length	3.30 ± 0.18 (2.98–3.68) *n* = 4		3.61 ± 0.05 (3.35–3.92) *n* = 16
Mesopterygoid fossa width	1.79 ± 0.09 (1.38–2.15) *n* = 7		1.97 ± 0.03 (1.78–2.20) *n* = 16
Zygomatic plate width	1.59 ± 0.06 (1.42–1.81) *n* = 7		1.71 ± 0.03 (1.54–1.93) *n* = 16
Cranial depth	8.32 ± 0.12 (7.87–8.72) *n* = 7		8.89 ± 0.09 (8.18–9.49) *n* = 16

length (OL), 7.74; maxillary diastema length (D), 6.43; maxillary tooth row length (MTRL), 2.82; incisive foramen length (IFL), 4.00; palatal bridge length (PBL), 9.68; alveolar width (AW, outside of M1), 4.58; occipital condyle width (OCW), 6.46; mastoid breadth (MB), 10.73; basioccipital length (BOL), 3.44; mesopterygoid fossa length (MPFL), 3.48; mesopterygoid fossa width (MPFW), 2.13; zygomatic plate width (ZPW), 1.66; cranial depth (CD), 8.97; mass, 26 grams.

Additional measurements.—See Table 1 for additional measurements of adult specimens of *S. juruaense* and of *S. melanops* and *S. ucayalensis*.

Description.—Dorsal coloration uniform from snout to rump, but individuals vary both within and among localities from grizzled pale reddish-brown to dark reddish-black; ventral coloration uniformly clear gray. Fore and hindfeet clothed dorsally with stiff white hairs; ungual tufts of thin, silvery hairs extend to or just beyond tip of claws. Otherwise as described for the genus, above.

Most features of cranial morphology (Fig. 4 and Table 1) are given above in the diagnosis, or detailed under the extended de-

Fig. 4. Dorsal, ventral, and lateral views of cranium, lateral view of left mandible of the holotype of *Scolomys juruaense,* new species, MPEG 23824, adult female (original number JLP 15570). Scale bar equals 10 mm.

Fig. 5. Occlusal views of left upper maxillary tooth row (from left to right) of *S. melanops,* USNM 513581 and *S. juruaense,* new species, MVZ 183169, INPA 2487, INPA 2485. Scale bar equals 1 mm.

scription of the genus above. Features of particular note include a short rostrum distally tapering from a broad base; relatively long nasals; shallow zygomatic notches; wide interorbital region with well-developed ledges extending posteriorly as ridges onto temporal region; narrow, rather straight, and nearly parallel zygomatic arches with reduced jugals; elongated and narrow orbital openings; short (about ⅔ diastemal length) but posteriorly-widened incisive foramen with distinctly "stepped" lateral margins; broad mesopterygoid fossa with parallel sides and a flat, squared anterior margin; orthodont upper incisors; and short and stout hamular process of squamosal totally occluding subsquamosal fenestra.

Maxillary and mandibular molar teeth are as described above for the genus (Fig. 5). The general lack of specimens with unworn molars precludes the determination of structural differences in occlusal morphology that may characterize each of the three recognized species.

Phallus (Fig. 6) small, elongated, and narrow (averaging 4.2 mm in length and 1.6 mm in width), with a distinctly cylindrical shape and straight sides. External surface of the glans rugose, sparsely covered with small spines (averaging 7 per mm) buried in irregular pits from the lip of the terminal crater (excluding a narrow non-spinous rim) to the prepuce; without a dorsal groove or lateral notches, but with a thickened, spine-free midventral ridge extending from prepuce to crater rim. A distinct, corrugated and non-spinous crater rim present, low in profile ventrally, enlarged laterally, but incomplete at dorsal midline and not circumscribing entire crater; crater rim distinctly separated from spinous epithelium of proximal glans by a distinct fold or groove. Medial bacular mound visible distally beyond the crater rim; distinctly shorter and round-

Fig. 6. Ventral, lateral, and dorsal views of the male phallus of *S. juruaense,* new species (MVZ 183171). CR, crater rim; MBM, medial bacular mound; MVR, midventral ridge; P, prepuce; SE, spinous epithelium; UF, urethral flaps. Scale bar equals 2 mm.

ed lateral mounds buried under laterally expanded crater rim. Dorsal papilla lacking spines and thickened, spatulate, and triangular in shape, with its tip extending just above crater rim. Urethral flaps lacking spines, but well developed, tapering distally, and varying in length but always visible above crater rim at ventral base of medial bacular mound. Distal baculum cartilaginous and tridigitate; proximal baculum with a stout straight shaft and laterally flared base.

Stomach unilocular and hemiglandular, with a moderately deep incisura angularis (extending about one-third the depth of the corpus and antrum), with rather short but thick bordering fold, and an expanded corpus with a moderately small antrum (terms from Carleton 1973).

Chromosome preparations are available from nine males and five females (see specimens examined above). The diploid number is 50 and the fundamental number is 68. The karyotype (Fig. 7A) is comprised of an acrocentric X-chromosome, the largest element of the complement, a small acrocentric Y-chromosome, and 24 pairs of autosomes of the following size and morphology: 2 pairs of large subtelocentric

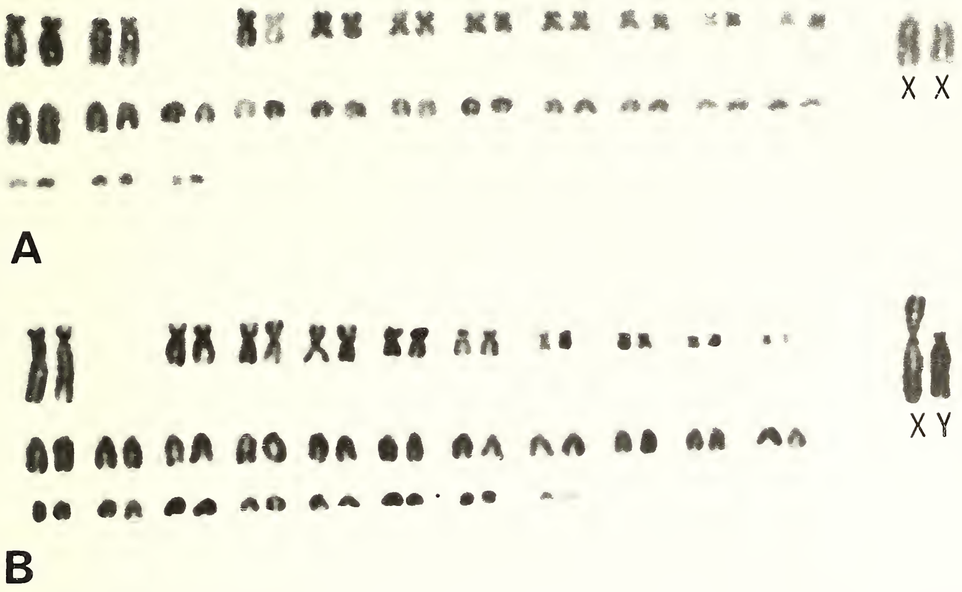

Fig. 7. Karyotypes of (A) *S. juruaense,* new species (MVZ 183172; female, 2N = 50, FN = 68) and (B) *S. melanops* (USNM 513583; male, 2N = 60, FN = 78).

chromosomes, 8 pairs of meta-submetacentric chromosomes grading in size from medium to small, and one large and 13 medium to small pairs of acrocentric chromosomes.

Comparisons.—From *S. melanops* (see Table 1 and Figs. 2 and 4), *S. juruaense* averages larger in all cranial dimensions except maxillary tooth row length and zygomatic breadth; and it differs by virtue of orthodont versus proodont upper incisors; longer and distally tapering rostrum; less expanded nasolacrymal capsules when viewed from above; narrow, rather straight, and nearly parallel zygomatic arches enclosing a narrow and elongated orbital opening; occluded as opposed to open subsquamosal fenestra; more gracile mandible with longer, more curved, and narrower coronoid process; usually present but minute hypothenar pad on sole of hind foot; and 2N = 50 rather than 2N = 60 karyotype. *Scolomys juruaense* is also larger in all cranial dimensions (except maxillary tooth row length, least interorbital constriction, and braincase breadth) than *S. ucayalensis,* although proportionally their skulls are more similar to one another than either is to *S. melanops* (ratio diagram, Fig. 8). These two species can be distinguished by the following combination of characters: pale reddish-brown to reddish-black dorsal coloration as opposed to uniformly dark gray to brownish-black (Pacheco 1991), longer hind foot, longer ear, greater breadth across the zygomatic arches, longer nasals, longer diastema, "stepped" lateral margins of the incisive foramen, and squared (rather than distinctly rounded) anterior margin of the mesopterygoid fossa. The karyotype of *S. ucayalensis* is not known.

Little comparison can be made in relation to the occlusal surfaces of the cheek teeth. These details are not given in the original description of *S. ucayalensis* and the teeth are too worn in most available specimens of both *S. melanops* and *S. juruaense* (Fig. 5). Similarly, no comparison can be made in soft anatomical structures, as none have been described for species other than what we provide here for *S. juruaense.* The karyotype of *S. melanops* (Fig. 7B) is grossly sim-

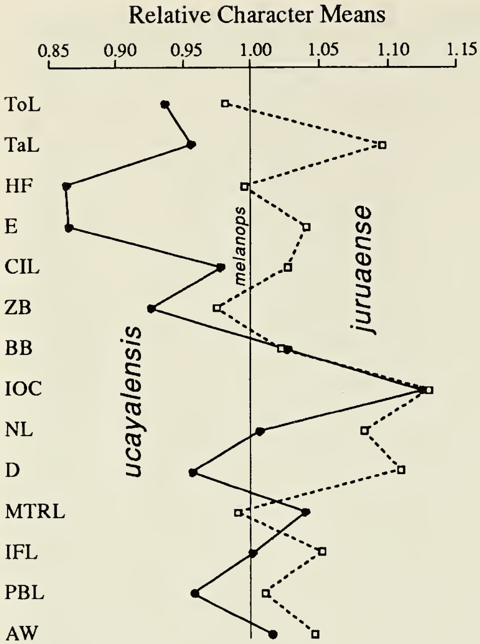

Fig. 8. Ratio diagram comparing averages of external and cranial dimensions for *Scolomys ucayalensis* (solid circles) and *S. juruaense* (open squares) in relation to those of *S. melanops* (vertical line).

ilar to that of *S. juruaense* (Fig. 7A), with a diploid number of 60 and fundamental number of 78. Its karyotype is composed of one pair of large subtelocentric, 9 pairs of medium-sized to minute meta-and submetacentric, and 19 pairs of acrocentric autosomes grading evenly from medium-sized to small. The X is a large submetacentric chromosome, the largest element of the complement, and the Y is a subtelocentric element as large as the autosomal pair.

The phenotypic similarity (especially orthodont incisors, distally tapering rostrum, less-flared and parallel zygomatic arches, long and narrow orbital openings, and more elongated braincase) of *S. juruaense* and *S. ucayalensis* suggest a closer genetic relationship between them relative to *S. melanops.* This hypothesis remains to be tested, however.

Habitat.—All specimens of *S. juruaense* were obtained in primary terra firme (upland, non-seasonally flooded) forest in Sherman live traps placed on the ground and baited with a combination of ground whole oats, raisins, and peanuts. As all individuals were live-trapped, stomach contents consisted only of the bait used (ground whole oats, raisins, and peanuts) and a few insect parts which may have been ingested accidentally. An equal number of Sherman traps placed in the trees at heights of 10–15 meters failed to secure any specimens of this species, although species of the sigmodontine genera *Oecomys* and *Rhipidomys* were taken. Other sigmodontines found sympatric with *S. juruaense* include *Oryzomys capito, Oryzomys yunganus, Oryzomys macconnelli, Neacomys spinosus, Neacomys* sp. (a smaller-bodied form sympatric with *N. spinosus,* with proportionally longer tail, shorter tooth row, and 2N = 35/36 as opposed to 2N = 64 karyotype), *Nectomys squamipes, Oecomys trinitatus, Oecomys roberti, Oecomys superans, Oecomys bicolor,* and *Rhipidomys leucodactylus.*

Reproduction.—*Scolomys juruaense* apparently breeds in both wet and dry seasons as pregnant or perforate females were taken in March (wet season), and in August, September, and October (dry season). Two of the three female specimens of *S. melanops* from the type locality were pregnant when collected in March. Litter sizes (maximum number of embryos 3 in both *melanops* [Anthony 1924] and *juruaense* [range 1–3]) are somewhat low in comparison to other sympatric small-bodied oryzomyines, notably *Oligoryzomys microtis* (modal litter size 5, range 2–8) and *Neacomys spinosus* (modal litter size 3, range 2–4).

Phylogenetic Affinities

Voss & Carleton (1993) provided a phylogenetic diagnosis of the Oryzomyini Vorontsov, 1959, defining the tribe by the following combination of characters: (1) a pectoral pair of mammae (with mammary counts of eight or more); (2) a long palate with prominent posterolateral pits; (3) no alisphenoid strut separating the buccinator-masticatory and accessory oval foramina; (4) no posterior suspensory process of the squamosal attached to the tegmen tympani; and (5) no gall bladder. They included one extinct and 14 Recent genera within this diagnosed unit: *Scolomys* along with *Holochilus, Lundomys, †Megalomys, Melanomys, Microryzomys, Neacomys, Nectomys, Nesoryzomys, Oecomys, Oligoryzomys, Oryzomys, Pseudoryzomys, Sigmodontomys,* and *Zygodontomys.* While the placement of *Scolomys* within the Oryzomyini has never been challenged, to our knowledge, this genus possesses only four of these five diagnostic characters. Among oryzomyines, *Scolomys* apparently is unique with a reduced mammary count, lacking both pectoral and postaxial pairs.

No hypothesis of phylogenetic relationships among the member genera of the Oryzomyini has as yet been proposed and a sufficient understanding of character variation in the soft and hard anatomy within the tribe is, at present, too limited for such to be developed here. *Scolomys* and *Neacomys* are the only neotropical sigmodontines with strongly spinose fur, and they are superficially similar in overall small size, relatively short and naked-appearing tail, and apparently strictly terrestrial habits as well. This resemblance is apparently not due to immediate common ancestry, however. For example, we could score 21 of the 25 characters listed by Voss & Carleton (1993: 23–27) in both genera. Of these, the two differ in mammary count (6 in *Scolomys,* the presumptive ancestral state of 8 in *Neacomys*), carotid circulation (*Scolomys* has the derived Pattern 3, *Neacomys* the ancestral Pattern 1), anteroloph on M1 (present [=ancestral state] in *Neacomys,* confluent with anterolabial conule in *Scolomys*), and protoflexus of M2 (absent in *Scolomys,* present [=ancestral state] in *Neacomys*). The two genera do share 17 characters in common, but all are apparently shared-primitive traits either for sigmodontines as a whole (11 characters; numbers 1, 2, 3, 4, 6, 9, 13, 14, 15, 16, and 24 of Voss & Carleton 1993) or for oryzomyines in particular (6 are shared broadly by other genera in the tribe; characters 7, 8, 10, 12, 21, and 25). *Scolomys* does share the derived carotid circulation pattern with *Oligoryzomys* (Carleton & Musser 1989), some but not all *Oryzomys* (Gardner & Patton 1976), *Nectomys,* and *Holochilus* (Voss & Carleton 1993), which might suggest a relationship among this group of genera.

As a means to assess relationships within the Oryzomyini, we examined the sequence of 801 base pairs (267 codons) of the mitochondrial cytochrome-b gene for 17 species of seven oryzomyine genera (*Microryzomys minutus*; *Neacomys spinosus* and two undetermined species; *Nectomys squamipes*; *Oecomys bicolor, roberti, superans, trinitatus,* and an undetermined species; *Oligoryzomys longicaudatus* and *microtis*; *Oryzomys capito, macconnelli, nitidus,* and *yunganus*; and *Scolomys juruaense*). The thomasomyine taxa *Thomasomys aureus* and *Rhipidomys leucodactylus* were used as out-groups. Methods for DNA extraction, amplification by the polymerase chain reaction (PCR), and sequencing, as well as oligonucleotide primers used in the PCR reactions follow those given in Smith & Patton (1993). All sequences are available in GenBank; those for *Nectomys squamipes, Oligoryzomys longicaudatus, Oryzomys capito,* and the two thomasomyine outgroups were presented in Smith & Patton (1993). Table 2 provides a matrix of average sequence divergence distances, corrected for multiple replacements (Brown et al. 1982), and of the average number of transversions at the 3rd position of codons. Distances between these genera of oryzomyines are substantial, averaging 33.99% in corrected sequence divergence (range 25.6% [*Oecomys* versus *Oryzomys*] to 40.8% [*Microryzomys* versus *Scolomys*]). Moreover, *Scolomys* is consistently the most divergent, with an av-

Table 2.—Above the diagonal: average pair-wise divergence estimates of 801 base pairs of the mitochondrial cytochrome-b gene among seven genera of oryzomyine rodents, and between them and two thomasomyine out-group taxa, corrected for multiple hits by the method of Brown et al. (1982). Below the diagonal: average number of 3rd position transversions (with estimates of times of divergence, in millions of years, in parentheses). Averages for both sequence divergence and numbers of 3rd position transversions among species within a given genus are given on the diagonal.

Taxon[a]	*Microryzomys*	*Neacomys*	*Nectomys*	*Oecomys*	*Oligoryzomys*	*Oryzomys*	*Scolomys*	*Thoasomys*	*Rhipidomys*
Microryzomys	—	29.6	28.5	30.3	34.0	36.4	40.8	40.5	44.4
Neacomys	46.0 (7.5)	22.4/25.0	31.2	35.6	35.4	37.3	38.5	43.4	44.3
Nectomys	36.3 (5.9)	39.0 (6.4)	—	31.1	33.6	30.7	36.9	43.7	40.4
Oecomys	34.5 (5.6)	41.2 (6.7)	38.4 (6.3)	14.8/18.0	32.4	25.6	38.5	37.7	42.3
Oligoryzomys	45.0 (7.3)	44.8 (7.3)	42.5 (6.9)	37.8 (6.2)	17.5/20.0	30.0	39.3	37.2	36.0
Oryzomys	43.3 (7.1)	44.5 (7.3)	39.0 (6.4)	31.1 (5.1)	34.9 (5.7)	24.9/30.0	38.0	36.9	41.2
Scolomys	35.0 (5.7)	43.3 (7.1)	45.0 (7.3)	44.6 (7.3)	44.5 (7.3)	46.0 (7.5)	—	48.6	41.7

[a] *Microryzomys minutus* (Peru: MVZ 173957), *Neacomys spinosus* (Brazil: MNFS 1262), *Neacomys* sp. 1 (Brazil: MNFS 1395), *Neacomys* sp. 2 (Brazil: JLP 15365), *Nectomys squamipes* (Peru: MVZ 166700), *Oecomys bicolor* (Brazil: MNFS 1499), *Oecomys* sp. (Brazil: J354), *Oecomys roberti* (Brazil: JLP 15241), *Oecomys superans* (Brazil: JLP 15517), *Oecomys trinitatus* (Brazil: MNFS 1250), *Oligoryzomys longicaudatus* (Argentina: MVZ 155842), *Oligoryzomys microtis* (Brazil: MNFS 1321), *Oryzomys capito* (Peru: MVZ 166676), *Oryzomys macconnelli* (Brazil: MNFS 156), *Oryzomys nitidus* (Brazil: MNFS 1419), *Oryzomys yunganus* (Brazil: MNFS 1101), *Scolomys juruaense* (holotype, MPEG 23824), *Thomasomys aureus* (Peru: MVZ 170076), and *Rhipidomys leucodactylus* (Peru: MVZ 168938).

erage of 38.67% divergence in all pair-wise comparisons.

The mtDNA sequences were analyzed both by the minimum evolution tree estimate (using the METREE version 1.2 program; Rzhetsky & Nei 1992), based on Kimura 2-parameter molecular distance matrices (Kimura 1980), and maximum parsimony (using PAUP 3.1.1; Swofford 1993). While both approaches provide strong support for the monophyly of the oryzomyine genera examined (at a confidence limit value of 99% in the distance phenogram [Fig. 9A] and a bootstrap value of 95% in the parsimony cladogram [Fig. 9B]) relative to the thomasomyine out-group genera, neither view provides much resolution among the oryzomyine genera or in the specific placement of *Scolomys* among them. All terminal branches are very long and internodal distances are short. As a result, nearly all internodes linking the oryzomyine genera have either confidence limits (Fig. 9A) or bootstrap values (Fig. 9B) below 50%. However, with the exception of *Oryzomys*, both measures are above 90% in the linkage of species within polytypic genera. *Scolomys* appears as a weakly supported sister taxon to a clade composed of *Nectomys, Oryzomys,* and *Oecomys* (with a confidence of only 46%) in the distance tree and to *Nectomys* in the parsimony tree (but at a bootstrap value <50%).

While the mtDNA sequence data do not provide strong support for relationships among this group of oryzomyine genera, these data are significant for two reasons. For one, the very short internodal distances suggest that divergence among taxa was nearly simultaneous and that, as a consequence, resolution of relationships by any set of characters is likely to be difficult. It may not be surpising, therefore, that *Scolomys* combines a few uniquely derived morphological characters with others that are apparently primitive for the tribe. This general lack of resolution is opposite to that observed among members of the tribe Akodontini of the South American sigmodontines, based on variation over the same sequence of cytochrome-b (Smith & Patton 1993). Consequently, difficulties in resolv-

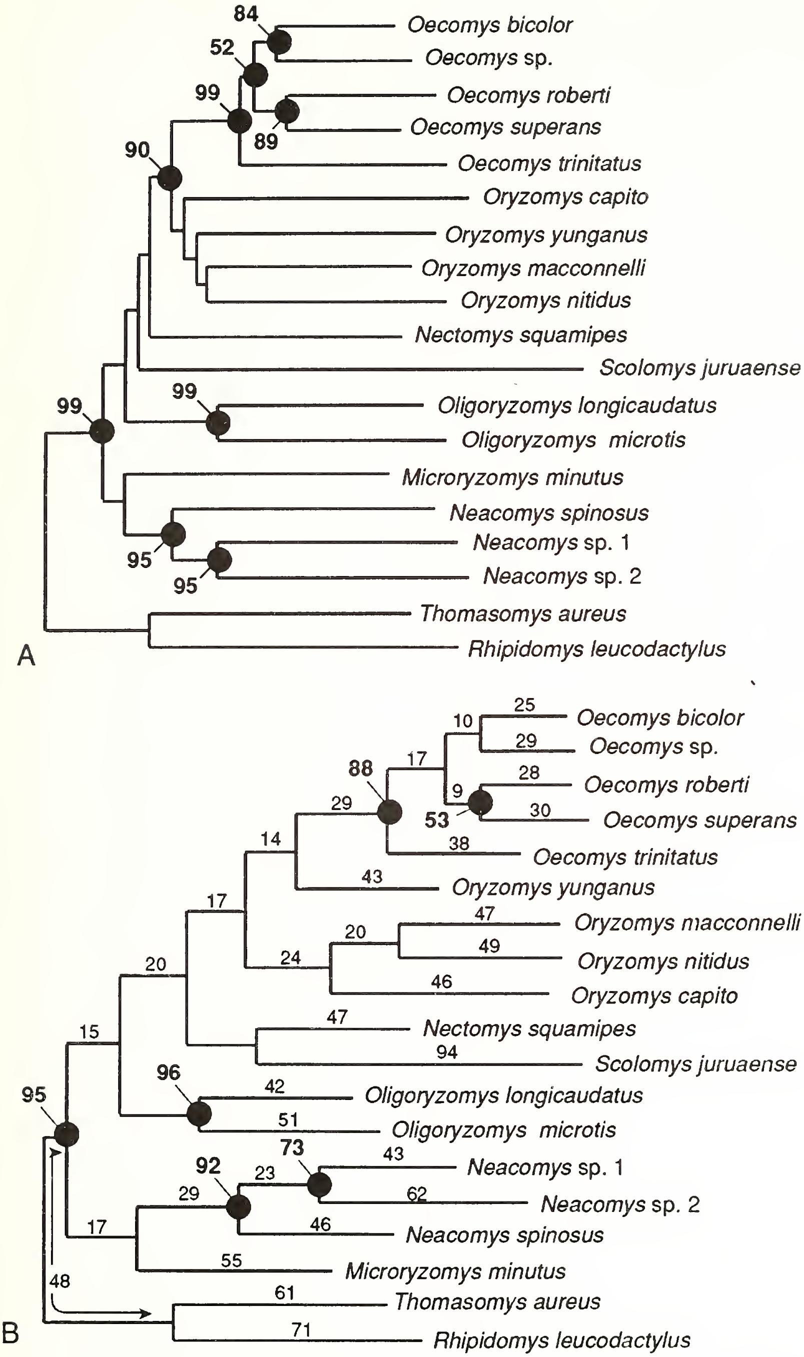

Fig. 9. Hypotheses of phyletic relationship between exemplar species of seven genera of the tribe Oryzomyini, with the thomasomyine genera *Thomasomys* and *Rhipidomys* as out-groups, based on 801 base pairs of the mitochondrial cytochrome-b gene. (A) Minimum evolution tree based on a Kimura 2-parameter distance matrix (METREE version 1.2; Rzhetsky & Nei 1992); branch lengths are proportional and circled numbers at each node are confidence limits. (B) Maximum parsimony cladogram, excluding 3rd position transitions (PAUP version 3.1.1; Swofford 1993); the number of character changes along each branch is indicated and circled numbers at specific nodes are bootstrap values (based on 500 iterations) above 50%.

ing relationships among oryzomyine genera are likely to reflect true patterns and timing of diversification rather than inadequacies of the sequence used in comparisons. Secondly, the long terminal branches and overall extensive degree of sequence divergence suggest that divergence times within the oryzomyines are deep. Based on the rate estimate of 2.3% per million years for third position transversions of the cytochrome-b gene (Table 2; rate calculation from Smith & Patton [1993] for the Akodontini), times of divergence among the examined genera of oryzomyines average about 6.6 million years (range 5.1 to 7.5). These numbers are in general accordance with estimates of times of divergence for the Sigmodontinae as a monophyletic lineage, based on DNA-DNA hybridization analyses (reviewed in Catzeflis et al. 1993). However, they also suggest that divergences within the oryzomyines were nearly simultaneous with the divergence between members of that tribe and at least the Akodontini (Catzeflis et al. 1993: their fig. 12.4), if not for other sigmodontines as well.

Acknowledgments

Specimens were collected as part of the Projeto Rio Juruá, sponsored by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) and financed by grants from the Wildlife Conservation Society, the National Geographic Society, and the Museum of Vertebrate Zoology. We are grateful to J. M. Ayres, who served as project coordinator; A. L. Gardner, who shared information on *S. melanops,* including its karyotype; G. G. Musser and M. D. Carleton, who permitted access to specimens in their respective collections; S. Marques for assistance in cataloging specimens into the MPEG collection; V. Pacheco for examining *S. juruaense* and for commenting upon the manuscript; K. Klitz for preparation of some figures; our colleagues of the Juruá project for field aid; and the people of the Rio Juruá for their generous hospitality. The editorial comments of R. S. Voss, A. L. Gardner, and an anonymous reviewer greatly improved the paper, although none should be held responsible for its final contents. MNFS was supported by a fellowship from CNPq.

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Systematic studies of oryzomyine rodents (Muridae: Sigmodontinae): definition and distribution of *Oligoryzomys vegetus* (Bangs, 1902)

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Abstract.—Morphological and distributional evidence is presented to document the specific stature of *Oligoryzomys vegetus* (Bangs, 1902) and to clarify its identification with respect to Central American populations of *O. fulvescens.* The geographic range of *O. vegetus* covers not only the mountains of western Panama but also the cordilleras de Tilarán, Central, and Talamanca of Costa Rica, generally above 1000 meters elevation and within lower montane and montane biotic zones. Within southern Central America, populations of *O. fulvescens* usually occur from sea level to 1000 meters in wet tropical and subtropical associations, but numerous instances of sympatry with *O. vegetus* are recorded in the 1000–1500 meter zone. Two species-group taxa, both described from Costa Rica, are allocated to subjective junior synonymy under *O. vegetus,* namely *Oryzomys fulvescens creper* Goodwin, 1945 and *Oryzomys fulvescens reventazoni* Goodwin, 1945. With improved understanding of its taxonomy and geographic range, *Oligoryzomys vegetus* emerges as another species of small terrestrial mammal restricted to the highlands of Costa Rica and western Panama, a region which has formed a modest center for mammalian endemism in southern Central America.

In 1902, Outram Bangs reported two species of *Oligoryzomys* occurring together at Boquete and its vicinity, on the southeastern slopes of Volcán de Chiriquí between 3800 and 4800 ft in western Panama. Five specimens, ranging in age from young to old adults, were identified as Allen's (1893) *Oryzomys costaricensis*; 13 others, however, about the same in age span, were larger-bodied with darker fur, bigger hindfeet, and longer, monocolored tails. The latter Bangs (1902) described as a new species, *Oryzomys* (*Oligoryzomys*) *vegetus.* To Bangs, the collection of *Oligoryzomys* from Volcán de Chiriquí was clearly separable into two species, and the comparative data he listed support this view.

Two years later, Allen (1904a) examined seven additional specimens from Boquete, collected by J. H. Batty in 1901, and compared them with Bang's original material. Allen (1904a:69) at first did not appreciate the distinctions between the forms Bangs had identified as *costaricensis* and *vegetus*: "The type and 12 topotypes of *O. vegetus,* kindly sent me for examination by Mr. Bangs, do not differ appreciably from the type, 3 topotypes, and additional Costa Rica specimens of *O. costaricensis.* They also agree with the 7 Boquete specimens collected by Mr. Batty, which I unhesitatingly refer to *O. costaricensis.*" In a brief commentary on previously described forms of *Oligoryzomys,* Allen later stated (1916:526):

"The Mexican and Central American forms[1] [His footnote listed *fulvescens* Saussure, 1860, *costaricensis* Allen, 1893, *vegetus* Bangs, 1902, and *nicaraguae* Allen, 1910] that have been recognized are probably only geographic races of *O. fulvescens* (Saussure). A reexamination of *vegetus,* of Chiriquí, proves it to be quite easily separable from either *fulvescens* or *costaricensis.*" The context of Allen's remarks suggests that he had reappraised *vegetus* and would consider it valid at least as a subspecies, a viewpoint thereafter formalized by Goldman (1918).

Goldman (1918), in his revision of North American *Oryzomys,* concurred with Allen's (1904a) original doubt about the specific separation of *vegetus* from *costaricensis.* Nevertheless, he considered the Boquete form sufficiently distinct to retain it as a subspecies of *Oryzomys fulvescens,* and he did likewise for *costaricensis.* Goldman's formal action considerably expanded the morphological definition of *Oryzomys* (*Oligoryzomys*) *fulvescens* to embrace populations distributed geographically from northeastern Mexico, throughout Middle America, to eastern Panama, and ranging altitudinally from near sea level to over 3000 m (Fig. 1). The trinomial recognition of *vegetus* has been subsequently observed both in regional geographic treatments (Goldman 1920, Goodwin 1946, Handley 1966) and in authoritative classifications of North American Mammalia (Miller 1924, Miller & Kellogg 1955, Hall & Kelson 1959, Hall 1981).

The experience and observations of other museum and field workers have cast some doubt on Goldman's (1918) interpretation of the relationship and status of *Oligoryzomys* populations in western Panama. In the Field Museum of Natural History, a penciled note—in the script of Wilfred H. Osgood (fide P. Hershkovitz and B. Patterson), dated 7 November 1932, and found in a tray of Panamanian *Oligoryzomys*—reads: "Goldman makes *vegetus* a subspecies of *fulvescens,* but its larger skull and longer tail, darker coloration etc. seem to make this doubtful." In the Academy of Natural Sciences, Philadelphia, Robert K. Enders deposited large series of *Oligoryzomys* that he collected from the Chiriquí region of Panama in the 1930s. The extensive erasing and overwriting of identifications (*fulvescens costaricensis* or *f. vegetus*) penciled on the skin tags suggest the confusion Enders encountered in trying to reconcile the variation in his samples with Goldman's taxonomy. For example, at Río Gariche, around 1600 m, Enders identified the two "subspecies" *costaricensis* and *vegetus* as occurring at the same locality (ANSP 18408-9). In like manner, recent samples taken from western Panama have impressed field workers of the morphological distinction and sympatric overlap of *vegetus* and *fulvescens costaricensis* (USNM series from NE San Felix, collected by Ronald H. Pine in June–July, 1980).

Such examples, together with our earlier restudy of the critical series in the Museum of Comparative Zoology, have led us to agree with Bangs's (1902) original assessment of *Oligoryzomys* in western Panama (Carleton & Musser 1989, Musser & Carleton 1993). Bangs presented data from what are clearly samples of two species of *Oligoryzomys, O. fulvescens costaricensis* and *O. vegetus.* The purposes of this report are: 1) to consolidate the evidentiary basis for the specific recognition of *O. vegetus* (Bangs, 1902); 2) to more fully document the geographical and altitudinal distribution of *O. vegetus* based on larger samples of museum specimens; and 3) to attribute *Oryzomys fulvescens reventazoni* Goodwin, 1945 and *Oryzomys fulvescens creper* Goodwin, 1945 as subjective junior synonyms of *Oligoryzomys vegetus.*

Materials and Methods

Specimens reported herein consist principally of skins with their associated skulls from the following institutions and muse-

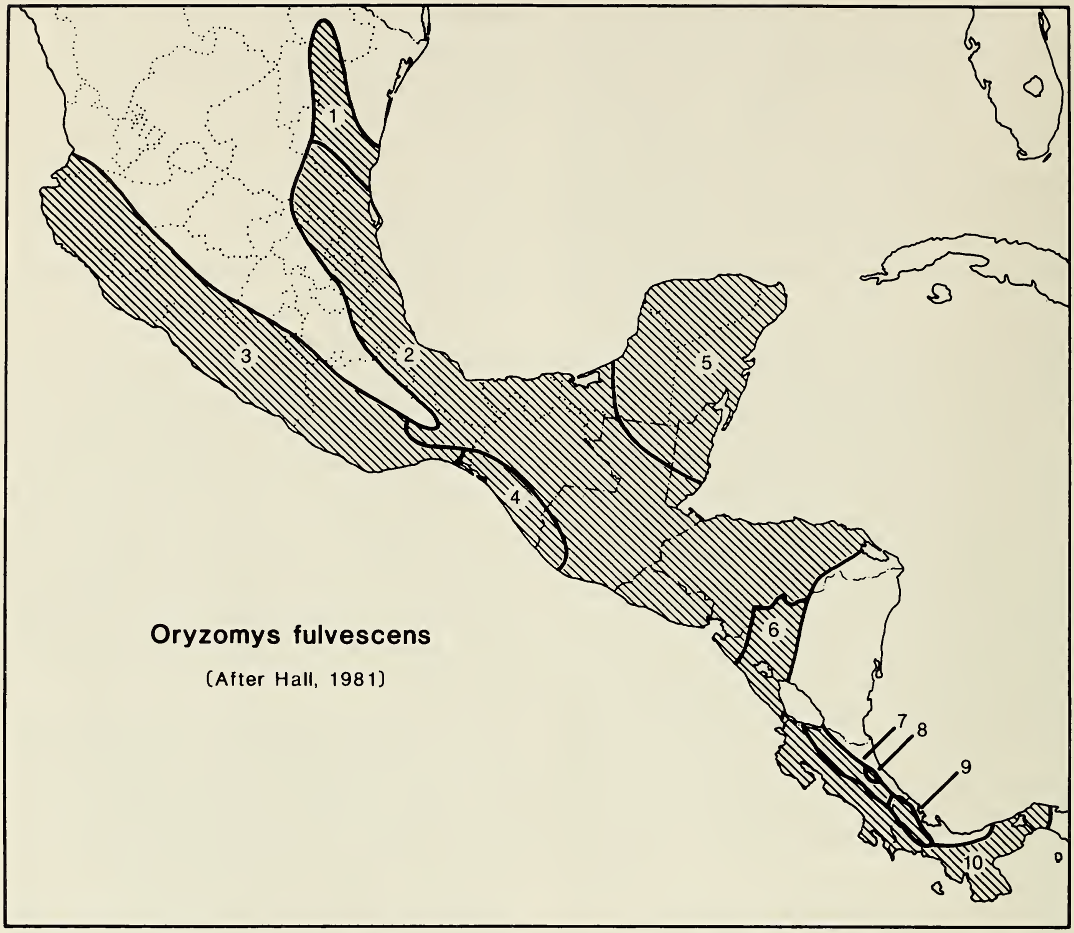

Fig. 1. Central American distribution of *Oryzomys* (*Oligoryzomys*) *fulvescens* as set forth by the revision of Edward A. Goldman (1918). Geographic races included (adapted from Hall 1981): 1) *O. f. engraciae* Osgood, 1945; 2) *O. f. fulvescens* (Saussure, 1860); 3) *O. f. lenis* Goldman, 1915; 4) *O. f. pacificus* Hooper, 1952; 5) *O. f. mayensis* Goldman, 1918; 6) *O. f. nicaraguae* Allen, 1910; 7) *O. f. creper* Goodwin, 1945; 8) *O. f. reventazoni* Goodwin, 1945; 9) *O. f. vegetus* Bangs, 1902; 10) *O. f. costaricensis* Allen, 1893.

ums: Academy of Natural Sciences, Philadelphia (ANSP); American Museum of Natural History, New York City (AMNH); Field Museum of Natural History, Chicago (FMNH); Louisiana State University Museum of Zoology, Baton Rouge (LSUMZ), Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museum of Natural History, University of Kansas, Lawrence (KU); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Type specimens and original series of *costaricensis* Allen (1893), *creper* Goodwin (1945), *nicaraguae* Allen (1910), *pacificus* Hooper (1952), *reventazoni* Goodwin (1945), and *vegetus* Bangs (1902) were studied firsthand.

Approximately 800 museum specimens of *Oligoryzomys* were examined (see full locality information in Taxonomic Summary), though only some 550 were measured, of which still smaller geographically cohesive subsets were identified for the various numerical analyses. Relative age was coarsely indexed by degree of molar wear to the four age-classes (juvenile, young-, full-, and old-adult) recognized by Carleton & Musser (1989). Emphasis was placed on accruing samples from Costa Rica and Panama to illuminate the morphological differentiation and distribution of *O. vegetus* and *O. fulvescens costaricensis,* but representatives of certain northern subspecies—namely, *O. f. fulvescens, O. f. nicaraguae,* and *O. f. pacificus* (according to range limits as given by Hall 1981)—were included for comparative purposes. These operational taxonomic units (OTUs), their sample sizes, and specific localities are recognized as follows.

Oligoryzomys vegetus

CR1: *n* = 13, from Costa Rica, Limon, Valle El Silencio.
CR6: *n* = 12, from Costa Rica, Alajuela, Villa Quesada and Tapesco.
CR7: *n* = 17, from Costa Rica, Puntarenas, Monteverde.
PA4: *n* = 19, from Panama, Chiriquí, Boquete (type locality of *vegetus* Bangs, 1902).
PA5: *n* = 35, from Panama, Chiriquí, localities along the upper valley of the Río Chiriquí Viejo (Boquete Trail, Casa Tilley, Cerro Punta and environs, Finca Martinz).
PA6: *n* = 68, from Panama, Chiriquí, Siola.
PA8: *n* = 12, from Panama, Chiriquí, Río Chebo and Cerro Pando.

Oligoryzomys fulvescens costaricensis

CR2: *n* = 24, from Costa Rica, Puntarenas, Cañas Gordas.
CR3: *n* = 5, from Costa Rica, Puntarenas, El General (type locality of *costaricensis* Allen, 1893).
CR4: *n* = 25, from Costa Rica, San José, San Geronimo de Pirrís.
CR5: *n* = 26, from Costa Rica, Cartago, localities along the upper valley of the Río Reventazón (Cartago, Cervantes, El Muñeco, Santa Teresa Peralta, Turrialba and environs).
PA1: *n* = 16, from Panama, Panama, Cerro Azul.
PA2: *n* = 19, from Panama, Cocle, El Valle and vicinity.
PA3: *n* = 20, from Panama, Chiriquí, Colorado Camp.
PA7: *n* = 28, from Panama, Chiriquí, Finca Santa Clara and Río Santa Clara.

Oligoryzomys fulvescens fulvescens

FUL: *n* = 57, from Mexico, Veracruz, various localities including the restricted type locality (Orizaba) of *fulvescens* (Saussure, 1860).

Oligoryzomys fulvescens nicaraguae

NI1: *n* = 23, from Nicaragua, northcentral highland localities (following Jones & Engstrom 1986).
NI2: *n* = 7, from Nicaragua, southwest coastal localities (following Jones & Engstrom 1986).

Oligoryzomys fulvescens pacificus

PAC: *n* = 19, from Mexico, Chiapas, Arriaga, Maspastepec (type locality of *pacificus* Hooper, 1952), and Pijijiapan.

To assist verification of place-names and geographic coordinates used in preparation of the distribution map, we consulted gazetteers and-or maps provided in revisionary and faunal works, principally those in Fairchild & Handley (1966), Goldman (1920), Hooper (1952), McPherson (1985), and Slud (1964).

Three external and 16 skull dimensions

(values in millimeters, mm) were recorded and analyzed to summarize patterns of variation within and between the populations sampled. Total length (TOTL), tail length (TL), and hindfoot length (HFL) are those recorded by a collector on the skin label. Crania were viewed under a dissecting microscope when measuring the 14 cranial and two dental variables to 0.01 mm using handheld digital calipers accurate to 0.03 mm. These measurements, and their abbreviations as used herein, include (see Fig. 2 for landmarks): occipitonasal length (ONL); zygomatic breadth (ZB); breadth of braincase (BBC); breadth across the exoccipital condyles (BOC); least interorbital breadth (IOB); length of rostrum (LR); postpalatal length (PPL); length of bony palate (BPL); length of upper diastema (LD); length of incisive foramen (LIF); maximum breadth across incisive foramina (BIF); breadth across bony palate (BBP); breadth of zygomatic plate (BZP); coronal length of maxillary toothrow (LM1–3); coronal width of first upper molar (WM1); and length of auditory bulla (LAB). Anatomical terminology follows Carleton & Musser (1989) for general features of the oryzomyine skull.

Univariate and multivariate computations were restricted to specimens assigned to the three adult cohorts (young, full, and old). Standard descriptive statistics (mean, range, standard deviation) were derived for the OTUs. One- and two-way analyses of variance, discriminant functions, and principal component analyses were computed using the three external and 16 craniodental variables, all of which were first transformed to natural logarithms. Principal components were extracted from the variance-covariance matrix, and loadings are expressed as Pearson product-moment correlation coefficients of the components with the original external and cranial variables. All analytic procedures were carried out using Systat (Version 5.0, 1992), a series of statistical routines programmed for microcomputers.

Comparisons of *Oligoryzomys fulvescens costaricensis* (Allen, 1893) and *O. vegetus* (Bangs, 1902)

External and craniodental variation.—In diagnosing *vegetus,* Bangs (1902) drew attention to its longer hindfoot and larger, heavier skull, especially with wider zygomatic span, as compared to examples of *costaricensis* (then recognized as a species). The better sample sizes now available bolster Bangs's impression of their salient contrast in size, with specimens of *vegetus* consistently averaging greater in most univariate comparisons (Appendix). Lengths of tail (TL) and hindfoot (HFL) provide key characters for first-approximation identification in the field, with TL usually exceeding 110 mm in adult *vegetus* (usually <110 mm except in oldest *fulvescens*) and with HFL typically 22 mm or greater in adult *vegetus* (usually ≤22 mm in *fulvescens*).

Two constellations of points, which correspond to our independent identification of species, are apparent within the plane of the first two principal components extracted for all intact specimens of *Oligoryzomys* from Costa Rica and Panama (Fig. 3). The first two components together account for 68 percent of the variation in the original variable data (Table 1); whereas, the amount explained for components three through 19 is five percent or less for each, and bivariate plots of these disclose no meaningful discrimination of taxa. The 95% confidence ellipse for scores of *vegetus* on PC I versus PC II contains not only specimens from Panama but also those from many localities in Costa Rica. Moreover, each species ellipse circumscribes many specimens taken at the same collecting locality—such as Boquete, Río Chebo, and Finca Santa Clara in Panama, and El Muñeco and Santa Teresa Peralta in Costa Rica (see Specimens Examined). Although individuals from sympatric localities are not identified in Fig. 3 due to visual congestion, certain specimens that do bear on our taxonomic interpreta-

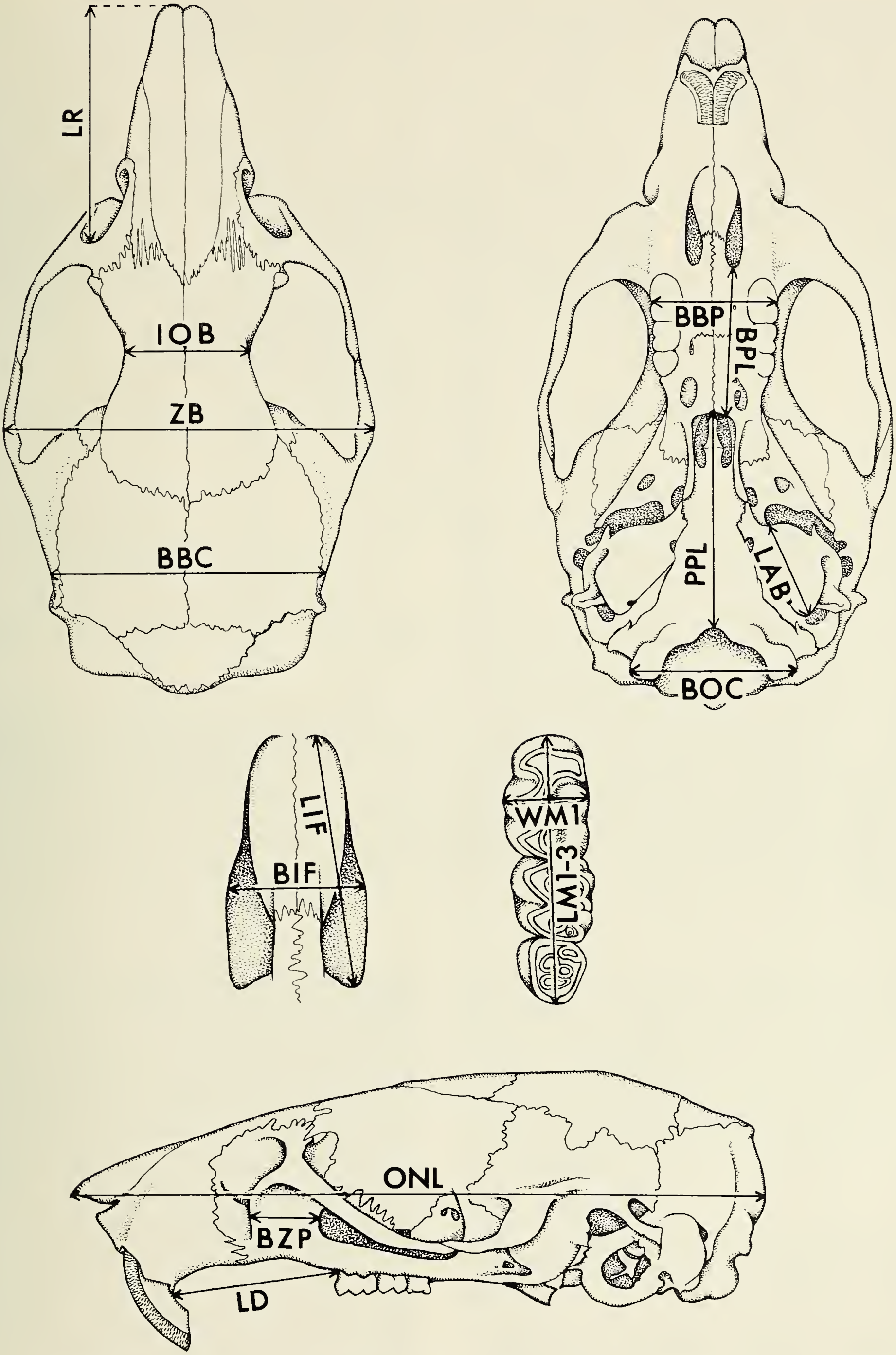

Fig. 2. Schematic views of the cranium (dorsal, ventral, lateral), right maxillary molar row, and incisive foramina of an adult *Oryzomys alfaroi* illustrating the limits of the 16 craniodental measurements recorded for specimens of *Oligoryzomys* (see Materials and Methods for abbreviations).

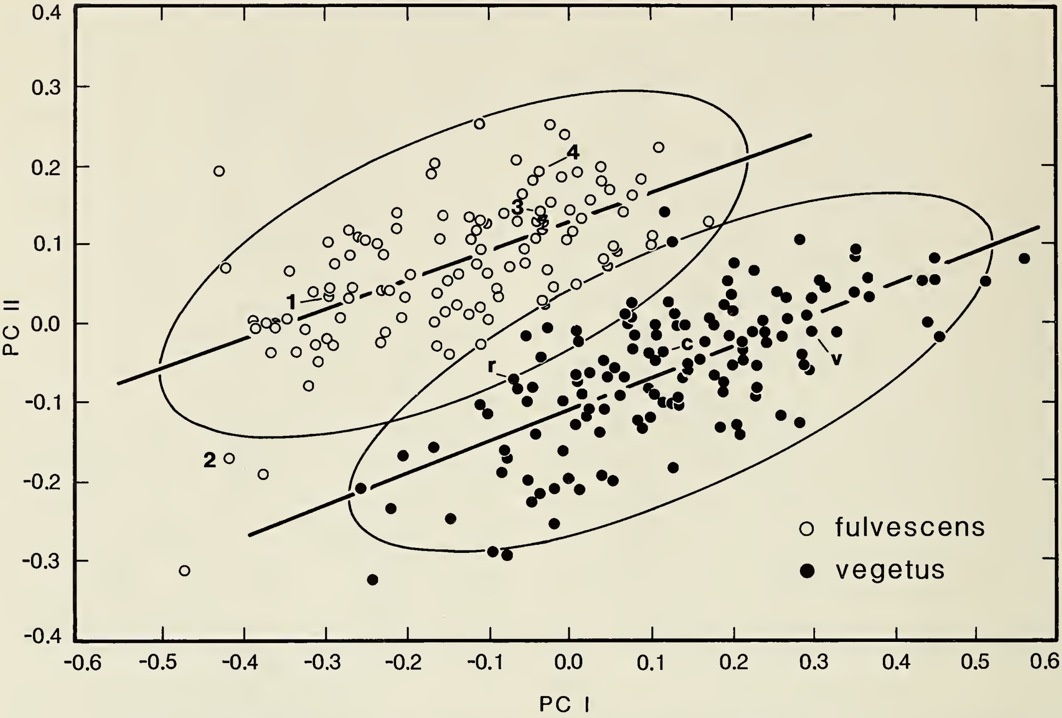

Fig. 3. Projection of individual specimen scores, based on log-transformed external (3) and craniodental (16) variables, onto the first two principal components for samples of *Oligoryzomys fulvescens costaricensis* (n = 115) and *O. vegetus* (n = 134) from Costa Rica and Panama with complete measurements (see Table 1). Lowercase letters correspond to holotypes of *creper* (c), *reventazoni* (r), and *vegetus* (v); numbered dots depict two paratypes (1–2) of Goodwin's (1945) *reventazoni,* here reassigned to *O. fulvescens,* and topotypes (3–4) of Allen's (1893) *costaricensis.* Ellipses circumscribe 95% confidence limits for specimen scores of each species; regression lines of PC II on PC I differ significantly between species in their Y-intercepts ($P < 0.001$) but not their slopes ($P = 0.556$).

tions are indicated. These include the holotypes of *Oryzomys fulvescens creper* and *O. f. reventazoni,* which cluster among samples of *vegetus* from Costa Rica and Panama, and two topotypes each of *costaricensis* and *reventazoni,* which fall among or nearer to examples of *fulvescens.* Mahalanobis distances derived from two-group discriminant function analysis associate the two holotypes as *vegetus* and classify all four topotypes as *fulvescens* (even outlier number two of *reventazoni*) according to their posterior probabilities of group membership.

Even though juveniles were omitted from our multivariate analyses, postweaning growth undoubtedly accounts for much of the scatter observed within each species sample and for the oblique orientation of specimen scores on the first and second principal components. A similar pattern of multivariate dispersion has been recovered for other closely related, congeneric species of Muroidea (Voss & Marcus 1992), and its ontogenetic causality explicated using laboratory-raised animals in which parentage, age, sex, and equality of sample sizes have been rigorously controlled (Voss et al. 1990). Such influences on variability within and between samples, particularly balanced age and sex representation, are seldom achieved with the museum series normally accessible to an investigator. Proportion of the sexes among our samples is notably biased toward males (64% of all *f. costaricensis*; 68% of all

Table 1.—Results of principal component analysis and one-way *ANOVAs* performed on all intact specimens of *Oligoryzomys fulvescens* ($n = 115$) and *Oligoryzomys vegetus* ($n = 134$) from Panama and Costa Rica (see Fig. 3).

Variable	Correlations PC I	Correlations PC II	*f* (species)
TOTL	0.94	−0.08	145.2***
TL	0.92	−0.23	225.8***
HFL	0.81	−0.32	247.8***
ONL	0.92	0.17	121.8***
ZB	0.86	0.04	151.5***
BBC	0.76	−0.33	439.5***
BOC	0.73	−0.12	131.2***
IOB	0.09	0.29	6.4**
LR	0.81	0.23	68.8***
PPL	0.82	0.27	54.5***
BPL	0.39	0.38	0.0
LD	0.83	0.13	76.3***
LIF	0.25	0.69	19.1***
BIF	0.23	0.56	11.9***
BBP	0.78	−0.06	125.4***
BZP	0.14	0.88	60.0***
LM1-3	−0.07	0.45	57.9***
WM1	0.33	0.13	3.7
LAB	0.66	−0.11	123.7***
Eigenvalue	0.041	0.013	
% Variance	52.0	16.1	

** = $P \leq 0.01$; *** = $P \leq 0.001$.

Table 2.—Results of two-way *ANOVAs* for 3 external and 16 cranial measurements of 91 specimens (63 ♂, 28 ♀) of *Oligoryzomys vegetus* from the valley of the Río Chiriquí Viejo, Chiriquí, Panama.

Variable	*f*(Sex)	*f*(Age)	*f*(interaction)
TOTL	1.8	12.9***	0.5
TL	0.5	8.8***	0.8
HFL	0.6	2.6	0.6
ONL	1.4	29.7***	0.2
ZB	1.3	23.8***	1.1
BBC	6.9**	4.1*	0.3
BOC	0.3	8.3**	0.5
IOB	0.7	2.4	0.7
LR	0.5	21.9***	0.0
PPL	0.0	31.2***	0.2
BPL	0.2	5.7**	1.0
LD	2.1	37.1***	0.7
LIF	3.3	12.9***	0.0
BIF	0.2	8.6***	1.0
BBP	1.4	19.5***	0.2
BZP	1.2	10.1***	0.1
LM1-3	0.2	0.7	0.2
WM1	0.8	2.3	0.2
LAB	5.2*	1.5	1.1

* = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$.

vegetus), and the number of specimens in young-, full-, or old-adult age classes does vary from OTU to OTU.

In the largest, most geographically and temporally homogeneous sample available to us (91 *vegetus* collected by R. K. Enders in Chiriquí, Panama), consistent age-related size differences are apparent, but classification by sex and sex-age interaction reveals negligible influence on mean differences (Table 2). Total length and tail length, as expected, increase among the three adult age-classes and yield highly significant mean differences, but hindfoot length does not. Among the 16 craniodental variables, the magnitude and significance levels of *f*-values for age-class effects are typically highest for those dimensions measured on the facial region (ZB, LR, LD, LIF), intermediate for measurements across the neurocranium (BBC, BOC, IOB), and lowest on the molars (LM1–3, WM1). These results generally parallel the patterns of covariation and growth allometry of the muroid skull documented for other species of Sigmodontinae (Voss & Marcus 1992). Although relative age may sometimes confuse the identification of individual specimens, the contribution of age-related effects is minor compared to the magnitude of interspecific differentiation between *O. vegetus* and *O. fulvescens,* for example as observed in principal component analysis (Table 3).

Table 3.—One-way *ANOVAs* generated for various group effects on results of principal component analysis (see Fig. 3).

Variable	*f*(sex)	*f*(age)	*f*(species)
PC I scores	0.6	28.3***	188.5***
PC II scores	0.5	26.3***	140.7***

*** = $P \leq 0.001$.

Fig. 4. Dorsal, ventral, and lateral views of adult crania and mandibles of: left, *Oligoryzomys fulvescens costaricensis* (USNM 541183; Panama, Chiriquí, 24 km NNE San Felix; ONL = 21.9 mm); and right, *Oligoryzomys vegetus* (USNM 541186; Panama, Bocas del Toro, 3.5 km E Escopeta; ONL = 23.5 mm).

The overall larger body size and more robust skull of *vegetus* relative to *fulvescens costaricensis* are corroborated by results of the principal component ordination. The three external and most cranial measurements exhibit high and positive correlations with the first principal component, which suggests a general size factor (Table 1), and higher scores were generated on average for specimens of *vegetus* ($\bar{X} = 0.12$) along this axis than for those of *f. costaricensis* ($\bar{X} = -0.14$). Dimensions that contribute to the separation along PC II emphasize the smaller body size (TL, HFL) and narrower skull (BBC, BOC) of *f. costaricensis,* but also reveal its relatively wide interorbit and zygomatic plate (IOB, BZP), longer and wider incisive foramina (LIF, BIF), and more robust molars (LM1–3) as compared to examples of *vegetus* (Fig. 4). The comparatively strong loadings of LIF and BIF on PC II were unexpected, but closer examination of crania confirmed that the incisive foramina typically span about three-quarters of the diastema in *f. costaricensis* in contrast to about two-thirds in *vegetus.*

In view of the small absolute size of the skull and toothrows in *Oligoryzomys,* the magnitude of mean differences between the two species is not conspicuous (Appendix), even for dimensions where population variances are low and *f*-ratios for species effects are high (Table 1). Thus, simple univariate range limits, such as employed in keys, may

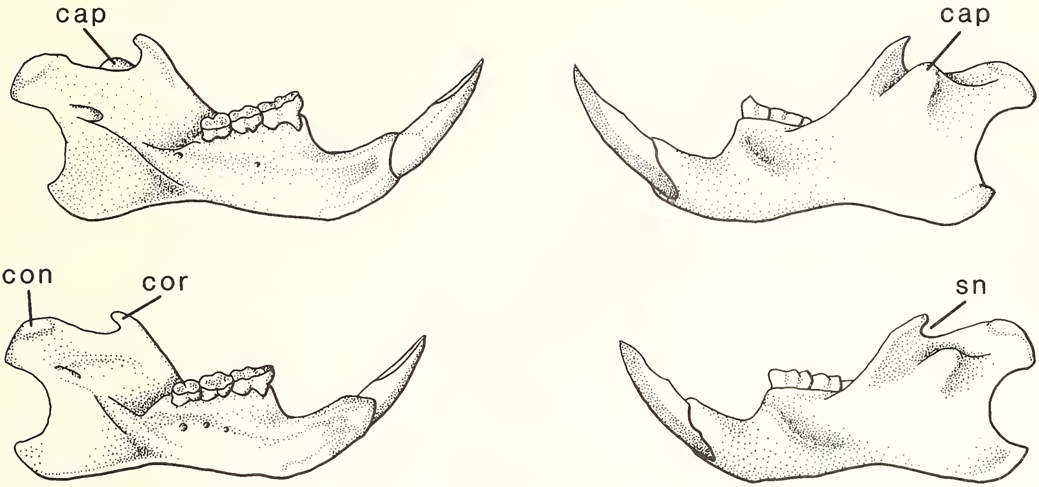

Fig. 5. Lateral and medial views of the mandibles illustrating typical development of the capsular process of: top, *O. vegetus* (USNM 541186); and bottom, *Oligoryzomys fulvescens costaricensis* (USNM 541183). Abbreviations: cap, capsular process of the lower incisor; con, condyloid process; cor, coronoid process; sn, sigmoid notch.

be uninformative for practical segregation of the species. Of the variables quantified, the larger size of *vegetus* is best appreciated in cranial length (ONL) and especially in certain width measurements (ZB, BBC, BBP). Differences in overall form and proportion, such as those reflected along PC II, are easier to grasp visually. Hence, adult specimens of *vegetus* typically exhibit a narrower interorbital constriction accentuated by laterally flaring zygoma, a slimmer zygomatic plate and hence a shallower zygomatic notch, a broader braincase and longer rostrum, more delicate molars for the size of skull, and shorter-narrower incisive foramina as compared to those of *fulvescens* (Fig. 4).

Development of the capsular process, among the few qualitative osteological traits which may serve to separate closely related muroid species, provides some discrimination of *vegetus* and *fulvescens costaricensis*. This process, which represents the posterior alveolar terminus of the lower incisor, arises from the lateral surface of the dentary. In specimens of *vegetus*, the capsular process forms a distinct knob that, with the ascending ramus oriented in a horizontal plane, is typically observed to extend above the ventral rim of the sigmoid notch, whether viewed from a lateral or medial aspect (Fig. 5). In examples of *fulvescens*, this process is weakly pronounced, forming a lateral mound or bulge that usually ends below the ventral rim of the sigmoid notch.

This distinction is not absolute, for some specimens (16%) of *vegetus* lack the strong dorsal projection of the capsular process and a minority (7%) of *fulvescens* possess one. In approximately 20% of both species, the process terminates about level with the sigmoid notch (Fig. 6). Expression of the capsular process may correlate with age of the animal. For all individuals of *vegetus* scored ($n = 167$), there exists a strong positive association between age-class (juvenile through old-adult) and dorsal projection (below, even, above) of the capsular process (Kruskal-Wallis statistic = 38.0; $P < 0.001$). That is, individuals with the capsular process below or even with the sigmoid notch are predominantly restricted to the juvenile and young-adult age groups, whereas a capsular process extending above the notch oc-

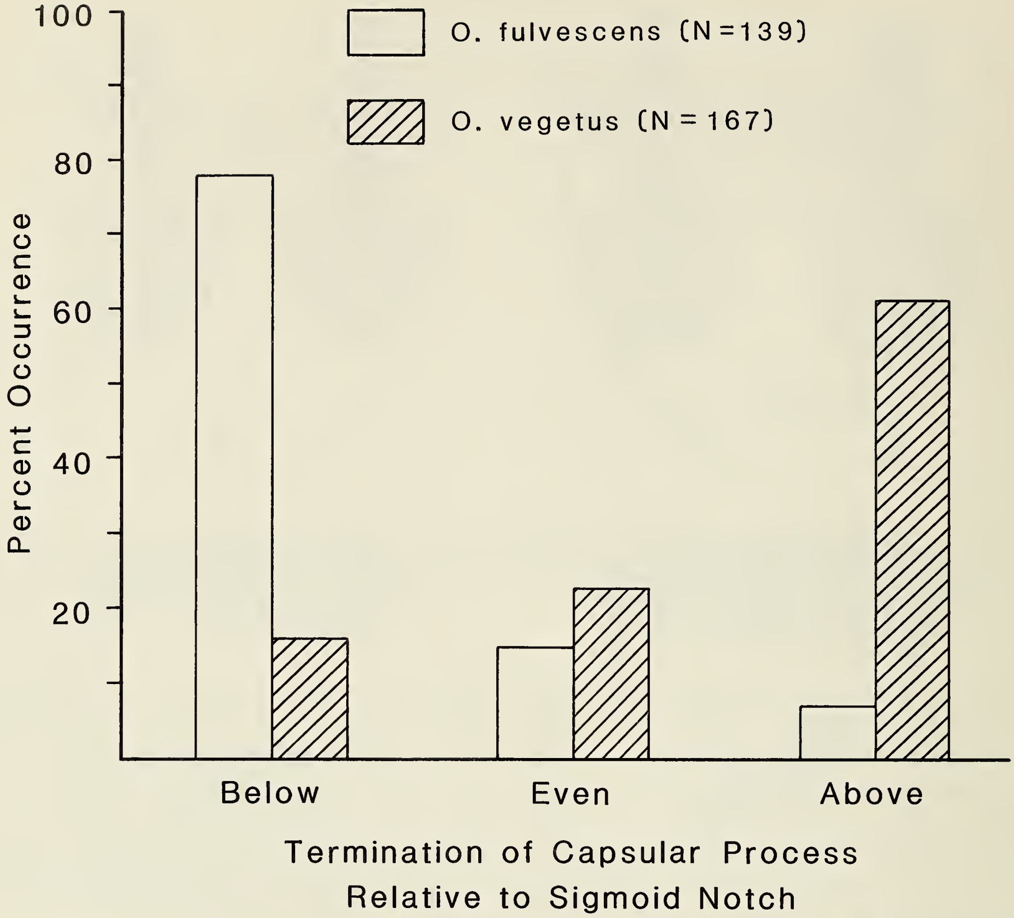

Fig. 6. Distribution of character state development of the capsular process in samples of *Oligoryzomys fulvescens costaricensis* and *O. vegetus* from Costa Rica and Panama (see Fig. 5 and text).

curs almost exclusively in full- and old-adults. Enigmatically, the parallel relationship is not supported by the same nonparametric *ANOVA* for all *fulvescens costaricensis* ($n = 139$; Kruskal-Wallis statistic = 4.98; $P = 0.18$). As with the utility of other distinguishing features employed at the species level, conformation of the capsular process must be considered in concert with other traits to render confident identification.

Bangs (1902) also cited the color of the incisor enamel as a diagnostic trait of *O. vegetus.* The difference—that is, pale yellowish orange in *f. costaricensis* and medium orange in *vegetus*—does seem valid as an average impression, but the contrast is subtle and best appreciated when comparing series.

Pelage texture and color.—The two species differ in fur texture and coloration, essentially evident as a harsh and pale coat contrasted to a softer and darker one. These qualitative distinctions, although fine, are easily appreciated in freshly collected material but are less readily grasped with extremely old and faded, dust-covered museum skins.

The dorsum of *O. fulvescens* is pale tawny to reddish brown, flecked with bright buffy and dark hairs that convey a more streaked or variegated appearance (somewhat like *Reithrodontomys fulvescens*). The streaked visual impression results from admixture of the densely black guard hairs and tricolored overhairs, which have a pronounced middle buffy band accentuated by a narrow basal plumbeous band and a very short fuscous tip. Overall, the dorsum presents a bright but pale tone and the fur is somewhat harsher to the touch.

Examples of *O. vegetus* possess more somber upperparts, evenly colored dark brown and lacking conspicuous streaking. In each overhair, the basal plumbeous band is discernably long relative to the middle buffy band, which is subdued, and the terminal tip is dusky. The resultant tone is appreciably darker than observed in typical *O. fulvescens,* and the fur is soft and fine rather than harsh. The nose, forehead, and cheeks are also darker in *O. vegetus,* and the eye ring dusky and better defined than is common in *O. fulvescens.*

A light versus dark venter distinguishes the two species. The underparts of *O. fulvescens* are pale, a whitish gray; the overhairs may be entirely white to their base, especially on the throat and chest, or with a light gray basal band. The ventral fur of *O. vegetus,* on the other hand, is dark gray in appearance, the hairs possessing a well-defined basal plumbeous band and a clear or whitish tip. A buffy overwash may occur in some specimens of either species but is more commonly encountered among samples of *O. fulvescens.* In like manner, both species have lateral ochraceous stripes but those on the sides and flanks of *O. fulvescens* are generally more prominent.

Coloration of the feet does not offer any distinguishing trait. The tops of the tarsus and metatarsus are covered with hairs that range from white to translucent and basically present a whitish appearance in both *Oligoryzomys.*

In summary, qualitative features of the skin and skull, augmented by the spatial structure inherent in multivariate summaries of the 19 mensural characters, convincingly sustain Bangs's (1902) original perception of the existence of two morphologically similar but nonetheless distinct and separable species in western Panama. Inclusion of samples of *Oligoryzomys* from Costa Rica demonstrates the occurrence of the same two morphologies and the broader distribution of the species that we recognize as *O. vegetus.*

Relationships of *costaricensis* and *vegetus* to Other Central American *Oligoryzomys*

At the time Bangs (1902) reported his new species *Oryzomys vegetus,* previously named forms of Central American pygmy rice rats were also recognized as full species, namely *fulvescens* Saussure (1860) and *costaricensis* (Allen, 1893). In his revision of North American *Oryzomys,* Goldman (1918) established the precedent for treating all Middle American populations of *Oligoryzomys,* which he ranked as subgenus, as members of the single polytypic species *fulvescens,* and subsequent twentieth-century descriptive activity has transpired within his taxonomic framework (see subspecies and ranges, Fig. 1). In particular, systematists have routinely classified Panamanian populations of the shorter-tailed, pale-bellied form as *fulvescens costaricensis* (Goldman 1918, 1920; Hall 1981; Handley 1966).

Set against this systematic background, we naturally interpreted the morphological differentiation and sympatry of *costaricensis* and *vegetus* as indicative of the latter's specific status and continued to view the former as a subspecies of *fulvescens* (Carleton & Musser 1989, Musser & Carleton 1993). However, our casual presumption was somewhat disquieted by Joel A. Allen's (1904a:69) provocative comment in a paper that we had initially overlooked.

> "Mr. Bangs informs me [given as in litt.] that he inadvertently placed the name *vegetus* on the dark form (= *costaricensis* vera) instead of on the light form, after

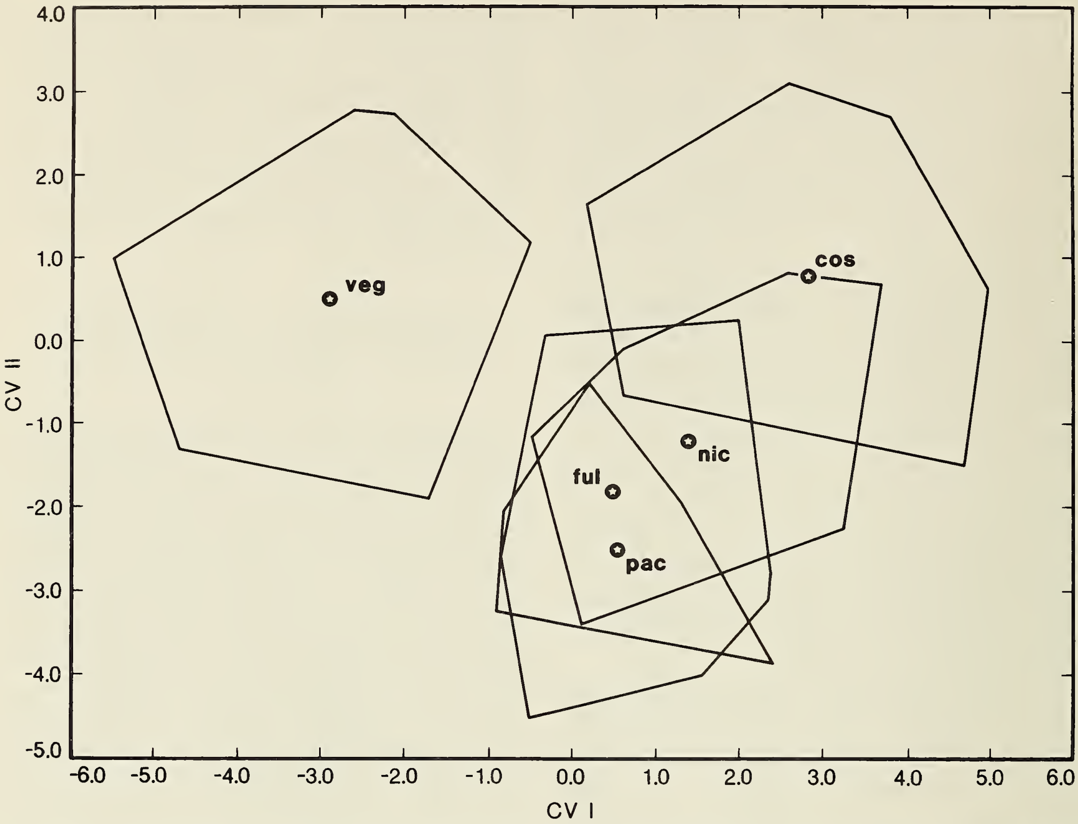

Fig. 7. Plots of first two canonical variates extracted from discrimination function analysis performed on five Central American taxa of *Oligoryzomys* and using all specimens with complete external and craniodental measurements ($n = 332$). Polygons enclose maximal dispersion of individual specimen scores around group centroids for each of five taxa (see Table 4): cos, *O. fulvescens costaricensis* ($n = 115$); ful, *O. f. fulvescens* ($n = 47$); nic, *O. f. nicaraguae* ($n = 21$); pac, *O. f. pacificus* ($n = 15$); veg, *O. vegetus* ($n = 134$).

> having returned the specimens of *O. costaricensis* borrowed from this Museum [that is, AMNH], so that *vegetus* = *costaricensis* and the light form was left unnamed [emphasis ours]."

In other words, Bangs confessed to having inadvertently applied an extraneous name, *vegetus,* to the Boquete rodent that he considered identical to Allen's (1893) *costaricensis,* while the Boquete form that he had meant to describe as new has been, by default, allocated to and subsequently known as *fulvescens costaricensis* (for example, Goldman 1920, Hall 1981, Handley 1966). Curiously, Goldman supplied no indication that he was aware of the supposed mix-up with regard to the naming of *vegetus,* either in his revision of *Oryzomys* (1918) or in his publication on the mammals of Panama (1920).

Allen's (1904a) allusion to an unfortunate lapsus by Mr. Bangs reopens the issue of which taxon, *costaricensis* or *vegetus,* if either, intergrades with northern populations of *Oligoryzomys fulvescens,* to which problem we now turn. In assessing these relationships, we included specimens from Veracruz, Mexico, as a comparative standard for Saussure's (1860) *fulvescens* s. s. Representatives of other northern subspecies were selectively sampled: *nicaraguae* Allen

(1910) because of its contiguous geographic position to *costaricensis*; and *pacificus* Hooper (1952) because of Jones & Engstrom's (1986) suggestion that it may link with more southerly-distributed, Pacific-coast populations of *fulvescens.*

Goldman (1918) formally recognized, aside from the nominate race, four subspecies of *Oryzomys* (*Oligoryzomys*) *fulvescens*: *costaricensis* Allen (1893) (with *nicaraguae* Allen, 1910, in full synonymy), *lenis* Goldman (1915), *mayensis* Goldman (1918), and *vegetus* Bangs (1902). His remarks under the various subspecific accounts clearly affirm that he viewed *costaricensis* as most similar to the nominate form *fulvescens.*

Our morphometric evaluations reinforce Goldman's (1918) general estimation of phenetic resemblance and support a hypothesis of consanguinity among Central American races currently arranged under *Oligoryzomys fulvescens* (that is, excepting *O. vegetus*). Although much variation exists within and among geographic representatives of *O. fulvescens,* these subspecific taxa considerably overlap one another in multivariate space, and all four are wholly set apart from specimens of *O. vegetus* (Fig. 7). In group assignments according to posterior probabilities of membership, specimens of the four subspecies were variously distributed among one another, but none was misclassified with *vegetus,* or vice versa. Clustering of OTU means also emphasizes the integrity of samples of *O. vegetus* as distinct from those representing the four geographic races of *O. fulvescens* (Fig. 8).

The three external measurements and most cranial variables contribute more or less equally to the hiatus along the first canonical variate and, by the sign and magnitude of their loadings (Table 4), underscore the fundamentally larger size of *vegetus* as contrasted to specimens of *fulvescens,* including *costaricensis.* Certain cranial dimensions (BZP, IOB, LM1–3), as divulged in the PCA, depart from this pattern and appear relatively, in some OTUs absolutely, greater in certain examples of *fulvescens.* For instance, Goldman (1918), in comparing *costaricensis* to *fulvescens* proper, cited the wider and longer molar rows of the former as its most distinctive character and one that approached *vegetus* in size. Although the correctness of Goldman's assessment does hold in simple univariate comparisons, a multivariate perspective demonstrates the proportionally large molar rows possessed by individuals of *costaricensis,* a shape feature which clearly aligns it with other representatives of *O. fulvescens,* not *O. vegetus.*

Table 4.—Results of discriminant function analysis performed on all intact specimens of *Oligoryzomys f. fulvescens* ($n = 47$), *O. f. costaricensis* ($n = 115$), *Q. f. nicaraguae* ($n = 21$), *O. f. pacificus* ($n = 15$), and *Oligoryzomys vegetus* ($n = 134$) (see Fig. 7).

Variable	CV I	CV II	*f*(taxon)
TOTL	−0.63	0.41	62.0***
TL	−0.69	0.44	89.1***
HFL	−0.73	0.18	77.5***
ONL	−0.58	0.39	55.8***
ZB	−0.62	0.32	54.7***
BBC	−0.81	0.36	139.4***
BOC	−0.55	0.49	56.1***
IOB	0.03	0.75	35.3***
LR	−0.48	0.33	31.3***
PPL	−0.37	0.28	20.5***
BPL	−0.09	0.53	17.8***
LD	−0.48	0.29	27.6***
LIF	0.17	0.24	5.5***
BIF	0.16	−0.03	2.7*
BBP	−0.59	0.46	61.3***
BZP	0.38	0.20	17.3***
LM1-3	0.29	0.64	34.8***
WM1	−0.19	0.51	21.3***
LAB	−0.56	−0.07	35.9***
Canonical correlations	0.93	0.73	

* = $P \leq 0.05$; *** = $P \leq 0.001$.

Qualitative agreements too—like cranial shape and proportions and pelage color and texture—support the affiliation of *costaricensis* with *fulvescens* and other northern races. Termination of the incisor capsule below the sigmoid notch is the common

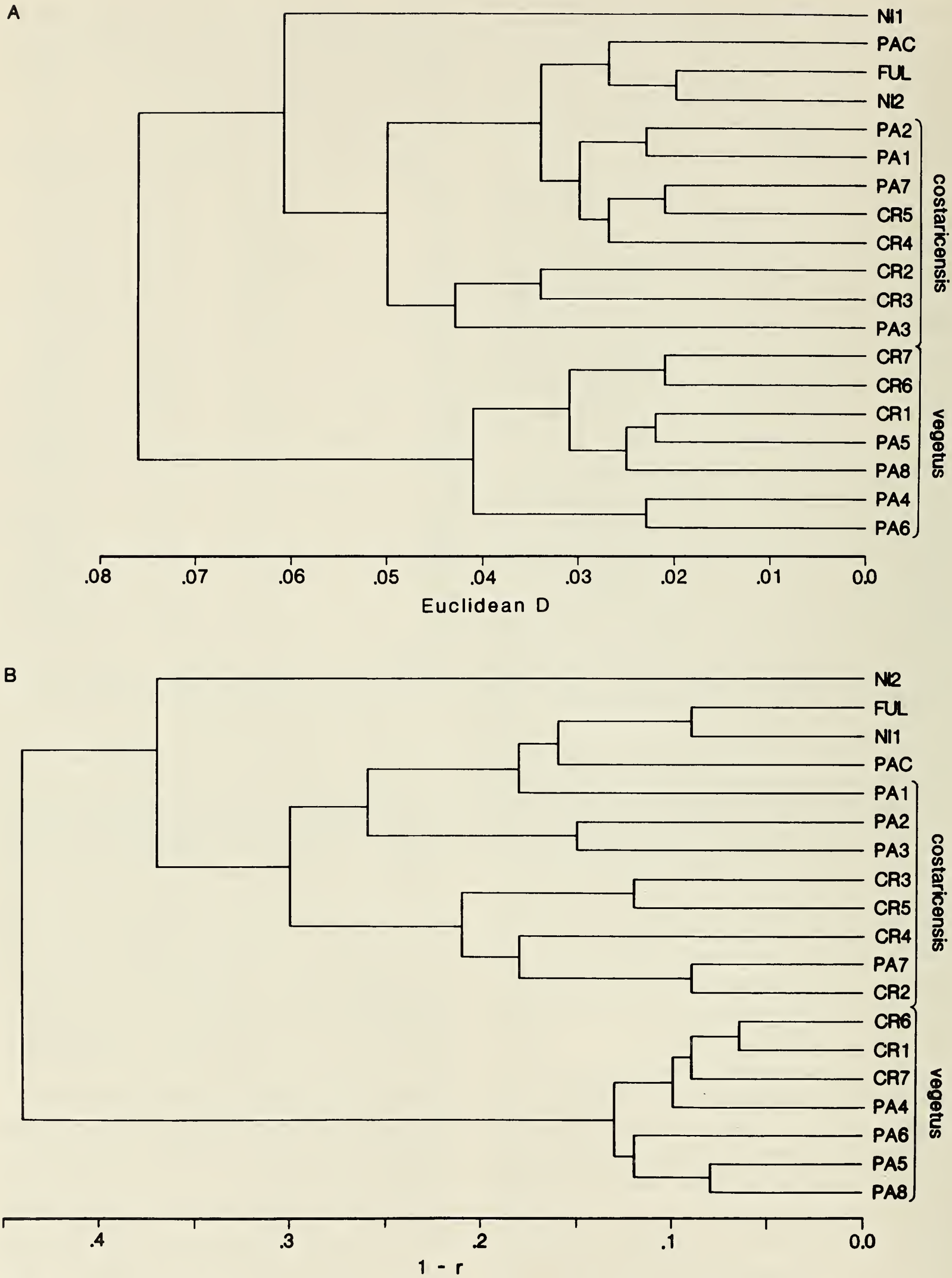

Fig. 8. UPGMA clustering of log-transformed samples means for the 19 OTUs of Central American *Oligoryzomys* identified in the Materials and Methods, using both a Euclidean distance coefficient (A) and the Pearson correlation coefficient (B).

condition in *f. fulvescens* (56% of 36 specimens scored) and *f. nicaraguae* (67% of 33 specimens), but these percentages are lower than that derived for our larger sample of *f. costaricensis* (78% of 139 specimens). Thus, the development of the capsular process in the former populations, while in the direction of agreement with *f. costaricensis,* is less decisive as a basis for discrimination from *O. vegetus.*

In summary, both morphometric comparisons and discrete character traits indicate the close kinship and probable conspecificity of *costaricensis* with northern *O. fulvescens.* Although we advise the continued affiliation of *costaricensis* as a subspecies of *O. fulvescens,* we stress the need for stronger empirical analyses of relationship and status among populations of *fulvescens* (see discussion below). Aside from such uncertainties involving *O. fulvescens,* and whether intended or not, Bangs (1902) did not err in selecting an individual of the "dark form" as the type of his new species *Oligoryzomys vegetus.*

Distribution and Zoogeography

In reinstating *vegetus* as a valid species of *Oligoryzomys,* Carleton & Musser (1989) at the time viewed its distribution as restricted to the highlands of western Panama, principally in the region of Volcán de Chiriquí. Although zoogeographically plausible, they, and later Musser & Carleton (1993), overlooked its presence in the contiguous mountain systems of Costa Rica. Such a distributional picture is confirmed by the renewed study of museum specimens, including evidence provided below for the junior synonymy of certain *Oligoryzomys*—namely *creper* Goodwin (1945) and *reventazoni* Goodwin (1945)—described from the middle and upper highlands of Costa Rica.

The species *Oligoryzomys vegetus,* or sprightly pygmy rice rat as christened by Bangs (1902), inhabits the rugged, mountainous spine of central Costa Rica and western Panama (Fig. 9). Specimens at hand document its geographic range from the northernmost extent of the Cordillera de Tilarán (Monteverde and environs), through the cordilleras Central and Talamanca, to the Cordillera de Chiriquí (at least to the vicinity of Cerro Bollo). We have searched for examples of *O. vegetus* among other museum series of *O. fulvescens* (in addition to those listed herein) from the highlands of Nicaragua, Guatemala, and southern Mexico but have found only *fulvescens* proper in these regions. We therefore believe that our locality records circumscribe the principal geographic distribution of *O. vegetus* (Fig. 9), although it may be expected farther east in westcentral Panama and may be sought on the highest peaks of the Cordillera de Guanacaste in northern Costa Rica (but see below).

The known altitudinal occurrence of *Oligoryzomys vegetus* extends from 840 m (valley of the Río Peñas Blanca, Costa Rica) to over 3000 m (below the summits of Volcán Irazú and Cerro de la Muerte, Costa Rica). Most collecting localities lie between 1000 and 2000 m. *Oligoryzomys vegetus* does not penetrate the tropical lowlands of Costa Rica and Panama where *O. fulvescens* commonly occurs (Fig. 9). Within these countries, the latter species is found from near sea level to approximately 2000 m. Although most localities of *O. f. costaricensis* occur from 750 m to 1500 m, as portrayed in Fig. 10, the low incidence of records below 750 m is biased by the infrequency of elevational notation by collectors (for example, the numerous lowland localities in eastern Panama and northern Costa Rica); whereas, collecting stations in the middle and upper highlands more commonly bear, for whatever reason, altitudinal information. Thus, histograms of altitudinal occurrence (Fig. 10) are dominated by the long history of mammalogical field work in the mountains of central Costa Rica and western Panama.

These regions, not unexpectedly, also contain most locations of documented sym-

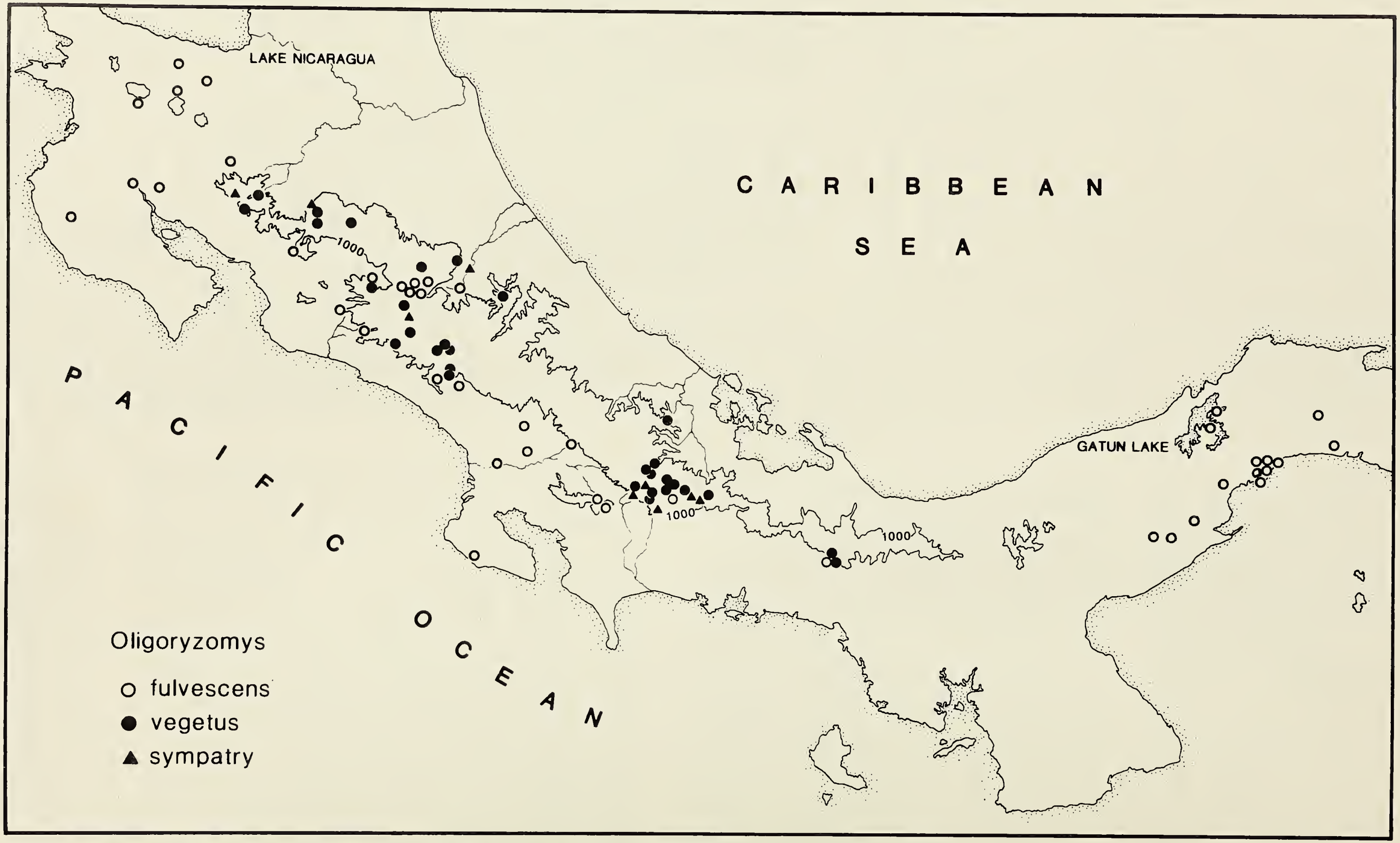

Fig. 9. Geographic distribution of *Oligoryzomys fulvescens* and *O. vegetus* in Costa Rica and Panama based on specimens examined herein. Solid line corresponds to the 1000-meter contour.

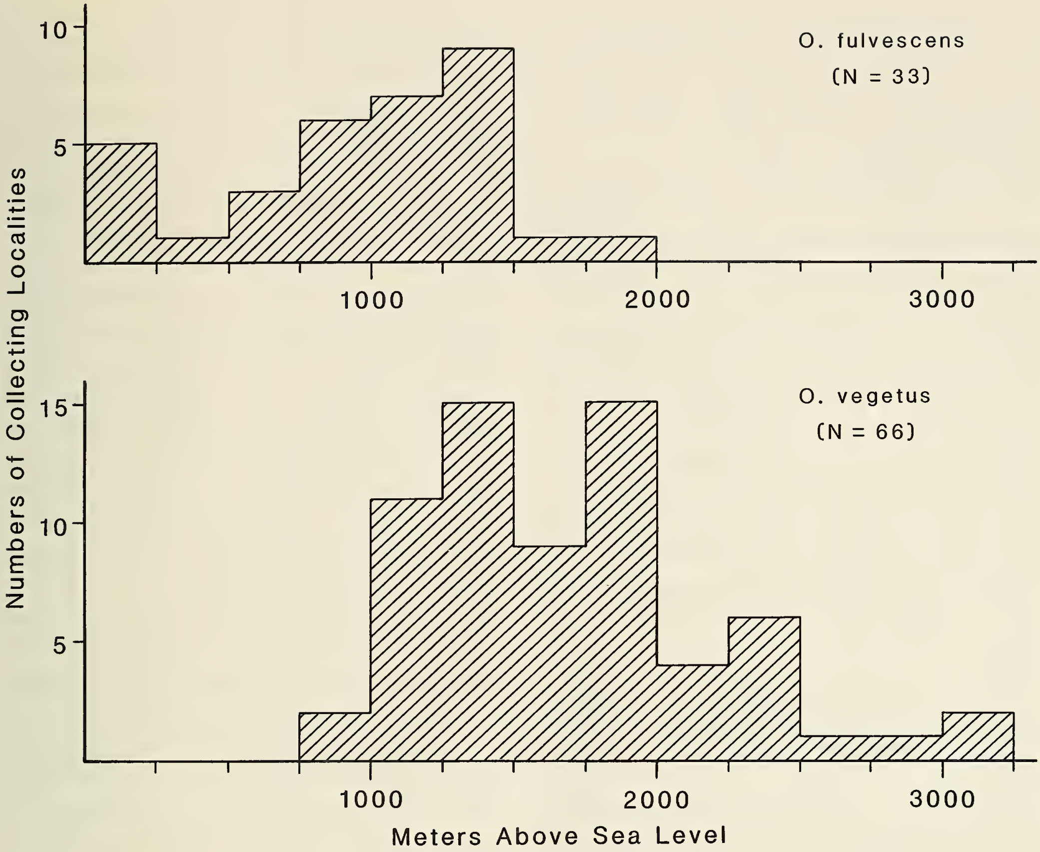

Fig. 10. Frequency distributions illustrating occurrence of collecting localities with recorded elevations for samples of *Oligoryzomys fulvescens* and *O. vegetus* from Costa Rica and Panama.

patry of *O. vegetus* and *O. f. costaricensis,* especially along the upper drainage basins of the Río Reventazón, Costa Rica, and the Río Chiriquí Viejo, Panama. In addition to Bangs's (1902) original discernment of sympatry at Boquete, Panama, we have encountered examples of *O. vegetus* and *O. f. costaricensis* intermixed at several other sites, both in Costa Rica (El Muñeco, Monteverde, Lajas) and in Panama (Río Chebo, Río Gariche, Finca Lerida, Finca Santa Clara, Río Santa Clara). Indeed, as argued below, Goodwin's (1945) type series of *Oryzomys fulvescens reventazoni,* from Santa Teresa Peralta, Costa Rica, is itself a composite, the holotype synonymous with *O. vegetus* and the four paratypes referrable to *O. fulvescens.* Almost all sites of sympatry or contiguous allopatry lie within the elevational zone from 1000 to 1500 m.

In his insightful biogeographic study of Costa Rican rodents, McPherson (1985:224) characterized *fulvescens* as virtually ubiquitous within the country, occurring throughout most biotic zones, and having "geographical and elevational distributions . . . greater than those of any other species in Costa Rica." His geographical and ecological summation, like the earlier erroneous definition of "*Oryzomys fulvescens,*" was a misleading composite based on data from two biological species. In fact, reassortment of McPherson's, and our own, Costa Rican localities by correct specific identifications reveals far narrower altitudinal and ecological occurrences of the two *Oligoryzomys* that correspond intelligibly with well-defined climatic, vegetational, and physiographic associations. Populations of *O. fulvescens costaricensis* predominantly occur within Tropical and Premontane life zones (sensu Holdridge 1967); whereas, those of *O. vegetus* are principally confined to Lower Montane and Montane formations. Most instances of sympatry involve sites classified as Premontane Wet Forest and Premontane Rain Forest, although overlap at lower (Tropical Wet Forest-Upper Transition) and higher (Lower Montane Wet Forest) life zones does occur. The deeper, softer pelage of *O. vegetus* is consistent with its higher-elevation affinity and presumably confers greater insulative properties for a small rodent living in wet, cool environments.

Within these broadly characterized forest domains, pygmy rice rats prefer grassy or shrubby microhabitats placed within forest clearings or at woodland edges, often along small streams or near other aquatic settings. Specific habitat notations on skin tags commonly reference "dense grass at edge of clearing near stream," "second-growth scrub at edge of clearing," "dense grass beside small stream in forest," and "under tall weeds and raspberry bushes." In view of their proclivity for early successional stages, both species of *Oligoryzomys* seem to adapt readily to a variety of second-growth habitats and to prosper around active or abandoned agricultural fields and pasturelands. We cannot glean suitably detailed information from field catalogs and skin labels that would suggest microhabitat segregation of the two *Oligoryzomys* at localities of sympatry, perhaps because field workers were seldom aware that two species might be encountered in their traplines. At one such place, El Muñeco in Costa Rica (1100–1200 m), Austin Smith trapped five specimens of *Oligoryzomys,* all initially identified as *O. fulvescens costaricensis.* Two of these prove to be *O. fulvescens,* both caught in "Caribbean rain forest in brush," and three are *O. vegetus,* one each trapped in "Caribbean rain forest in sugar cane," "pasture in cloud forest zone," and "Caribbean cloud forest." *Oligoryzomys,* species indeterminate, has been described both as terrestrial (e.g., Handley 1966) and as semi-arboreal (e.g., Timm et al. 1989), and has been observed to climb nimbly upon small limbs and branches in dense undergrowth (McPherson 1985). The larger hindfeet and relatively longer tail of *O. vegetus* predict more highly developed scansorial abilities in this species. Beyond these natural history anecdotes and generalities, detailed field studies must be conducted to shed light on specific ecological requirements and habits of the two *Oligoryzomys* in areas of syntopy.

Although the morphological similarity between *Oligoryzomys vegetus* and Central American *O. fulvescens* has engendered years of taxonomic confusion, the two may not prove to be sister species. In fact, the closest specific relative of *O. vegetus* may inhabit the northern Andes of South America. In his description, Bangs (1902:36) speculated that *vegetus* "may prove to be only a northern subspecies of *O. dryas humilior* Thomas of Colombia, Bogota region to Santa Marta region." The forms *dryas* and *humilior,* however, are junior synonyms of *Microryzomys minutus,* a species of a very distinctive oryzomyine genus related to *Oligoryzomys* (see Carleton & Musser 1989). A more plausible candidate is suggested by Osgood (1912), who named a new pygmy *Oryzomys, O. griseolus,* from the Páramo de Tama in westernmost Venezuela. Osgood, who had available samples of geographically contiguous *Oligoryzomys* like *navus* and *tenuipes,* thrice mentioned *O. vegetus* of western Panama as bearing the greatest resemblance to his new species. The question of their phylogenetic stature to one another, like the need for improved delimitation of species and phylogenetic systematics of South American *Oligoryzomys* in general, still warrants much basic investigation (see Carleton & Musser 1989). However, biogeographic consideration of other mammals, as well as other vertebrates, restricted to these Costa Rica-Panamanian mountains suggests that such a northern Andean connection is reasonable.

The distribution of *Oligoryzomys vegetus*, as now understood, accords closely with a region of Middle American topography already recognized by zoogeographers and variously labeled the Costa Rica-Chiriquí Highlands (Slud 1964), the Talamancan Province (Savage 1966), or the Cordilleran Faunal Area (McPherson 1985, 1986). (Middle America is here understood to include Central America north of the Panamanian isthmus and most of Mexico exclusive of the Mesa Central.) The middle- to high-elevation mountains in Costa Rica and western Panama, harboring cool and perennially moist forests, have figured prominently in the historical zoogeography and phyletic diversification of Central American amphibians and reptiles (Savage 1966, 1982) and birds (Slud 1964, Stiles 1983), vertebrate groups which contain a large number of species and genera endemic to the region. Small terrestrial mammals do not exhibit such high degrees of endemism as these other vertebrates; nonetheless, the area has played an important role in their phylogenetic history as well, especially as demonstrated for Rodentia by McPherson (1985, 1986). Many rodent species either reach their southern or northern limits of distribution in the Cordilleran Faunal Area or are hypothesized to have originated there in situ.

Review and enhancement of McPherson's (1985) taxonomic and distributional data indicate that at least one genus (*Syntheosciurus*), 14 species, and two strongly differentiated subspecies of small mammal are limited to the mountains of Costa Rica and western Panama and their humid forest associations (Table 5). Most of these taxa occur in both the Chiriquí region of western Panama and the Talamancas of southcentral Costa Rica. Fewer species are known to occur throughout the four highland areas, but there is reason to doubt that they necessarily would. Geological evidence (summary in Castillo-Muñoz 1983) supports the greater antiquity (Oligocene-Miocene) of the Talamanca-Chiriquí ranges as compared to the younger Central and Tilarán cordilleras (late Pliocene-Pleistocene). Some have attributed the high endemism to the possible isolation of the Talamanca-Chiriquí region as an island, or series of islands, within the Panamanian portal prior

Table 5.—Insectivora, Lagomorpha, and Rodentia endemic to highlands of Costa Rica and western Panama.

	Cordilleras			
Taxon	Tilarán	Central	Talamanca	Chiriquí
Soricidae				
Cryptotis endersi[a]			?	X
C. gracilis[b]	X	X	X	X
C. nigrescens[c]	X	X	X	X
Leporidae				
Sylvilagus dicei[d]			X	X
Sciuridae				
Syntheosciurus brochus[e]		X	X	X
Geomyidae				
Orthogeomys cavator[f]			X	X
O. heterodus[f]		X	X	
Heteromyidae				
Heteromys oresterus[g]			X	
Muridae				
Rheomys raptor hartmanni[h]	X	?	X	X
R. underwoodi[i]		X	?	X
Oryzomys devius[j]		X	X	X
Oligoryzomys vegetus[k]	X	X	X	X
Sigmodontomys aphrastus[l]			X	X
Reithrodontomys b. brevirostris[m]		X	X	
R. creper[n]	X	X	X	X
R. rodriguezi[o]		X	X	
Scotinomys xerampelinus[p]		X	X	X

Sources.—a: Choate (1970); b: Woodman & Timm (1992), N. Woodman (pers. comm.); c: Woodman & Timm (1993); d: Diersing (1981); e: Enders (1980); f: Hafner (1991); g: Rogers & Rogers (1992); h: Reid & Langtimm (1993), Voss (1988); i: Voss (1988); j: Gardner (1983); k: This study; l: Musser & Carleton (1993); m: Hooper (1952), McPherson (1985); n: Hooper (1952), Timm et al. (1989); o: McPherson (1985), Timm et al. (1989); p: Hooper (1972).

to complete closure and late-Pliocene formation of the landbridge (McPherson 1985, 1986; Slud 1964; Stiles 1983). Vouchered evidence for the expected occurrence of some species within certain mountain ranges is yet lacking, an omission that prescribes the continuing need for basic faunal survey. Also lacking is recent systematic investigation of other mammalian groups with highly disjunct Middle American distributions and distinctive geographic races limited to these southern highlands. Renewed revisionary focus on taxa such as *Cryptotis parva, Peromyscus mexicanus, Reithrodontomys mexicanus, R. sumichrasti,* and *Scotinomys teguina* will likely augment the amount of endemism thus far apparent among small mammals.

Most of the 17 species-group taxa (Table 5) represent genera that are either wholly endemic to Middle America (*Syntheosciurus, Orthogeomys, Heteromys, Rheomys,* and *Scotinomys*), or genera whose species diversity persuasively implicates a Middle American origin and subsequent radiation into temperate North America and northwestern South America (*Cryptotis, Reithrodontomys*—see Choate 1970, and Hooper 1952, respectively). Except for *Rheomys* (see Voss 1988), these Middle American endemics have tribal-, subfamily-, or family-level phyletic affinity with species that are otherwise North American in distribution and origin. However, like *Rheomys,* the three species of Oryzomyini (sensu Voss & Carleton 1993) appear to represent Central American elements of groups that are essentially South American in origin and principal differentiation. *Oryzomys devius* is the northernmost outlier of the *albigularis* species-group, a complex which is predominantly northern Andean in diversity and distribution (for example, see Patton et al. 1990) and whose morphology exhibits generic-level differentiation from other oryzomyines. Musser & Carleton (1993) provisionally associated the poorly known species *aphrastus* with the genus *Sigmodontomys,* whose type species *alfari* is distributed over lowland forest in southern Central America and northwestern South America, where it reaches western and northern Andean slopes but not eastern ones. The form *aphrastus* actually may bear closer kinship to another enigmatic, little known species, *Oryzomys hammondi* of northwestern Ecuador (for example, see Hershkovitz 1948). And the putative sister species of *Oligoryzomys vegetus* may be plausibly sought, as suspected by Osgood (1912), among northern Andean members of the genus. Biogeographic evaluations of other vertebrates lend support to the possibility that the vicariant sister-groups to many taxa endemic to the Costa Rica-Chiriquí highlands occur in South America (Savage 1966, 1982; Slud 1964).

The conjectural tone of the previous paragraph exposes the weaknesses of our current systematic understanding of many neotropical rodents—confusion over their morphological identity, meagre specimen-based knowledge of their distributions, and absence of explicitly defended statements of their phylogenetic relationships. Such systematic and biogeographic speculation should be tested by character data and viewed from a cladistic perspective. Improved species definition of forms like *Oligoryzomys vegetus* is an elemental step toward these goals.

Taxonomy

Oligoryzomys vegetus (Bangs)

Oryzomys (*Oligoryzomys*) *vegetus* Bangs, 1902:35 (type locality—Panama, Volcán de Chiriquí, Boquete, 4000 ft; holotype—MCZ 10298).—Miller, 1912:177.

Oryzomys costaricensis.—Allen, 1904a:69.

Oryzomys fulvescens vegetus.—Goldman, 1918:93.—Goldman, 1920:102.—Miller, 1924:363.—Goodwin, 1946:396.—Miller & Kellogg, 1955:441.—Hall & Kelson, 1959:568.—Handley, 1966:781.—Hall, 1981:622.

Oligoryzomys vegetus.—Carleton & Musser, 1989:71.—Musser & Carleton, 1993: 718.

Oryzomys fulvescens creper Goodwin, 1945:2 (type locality—Costa Rica, Cartago, Volcán Irazú, 9400 ft; holotype—AMNH 141199).—Goodwin, 1946: 396.—Miller & Kellogg, 1955:440.—Hall & Kelson, 1959:568.—Musser & Carleton, 1993:718.

Oryzomys fulvescens reventazoni Goodwin, 1945:3 (type locality—Costa Rica, Cartago, Santa Teresa Peralta; holotype—AMNH 141891).—Goodwin, 1946: 397.—Miller & Kellogg, 1955:440.—Hall and Kelson, 1959:568.—Musser & Carleton, 1993:718.

Emended diagnosis.—A species of *Oligoryzomys* characterized by relatively soft and fine pelage, dorsum a somber, dark brown, without prominent streaking or grizzling, and underparts dark gray; tail dusky, monocolored for most of its length except slightly paler near the ventral base; size medium (HFL ca. 22–25 mm, ONL ca. 22–24 mm) for the genus with relatively long tail (usually >110 mm in adults), about 140% of head-and-body length; skull relatively broad across zygomatic arches (ca. 11.3–12.5 mm) and braincase (ca. 10.5–11.0 mm), zygomatic plate and interorbital constriction correspondingly narrow; molar toothrows (2.7–3.0 mm) appear delicate for size of skull; capsular process of dentary well developed.

Distribution.—Intermediate to high elevations (840 to <3000 m) in the mountains of Costa Rica (cordilleras Tilarán, Central, and Talamanca) and western Panama.

Remarks.—Goodwin (1945) named two Costa Rican subspecies of *Oryzomys fulvescens* that we herein reallocate to *Oligoryzomys vegetus.* He (1945:2) characterized *creper* as "A rather small, dark-colored, long-tailed *Oligoryzomys,* smaller than *vegetus* Bangs, with noticeably smaller feet and darker color." Examples of *vegetus* from Costa Rica do average smaller than our samples from western Panama but not inordinately so (Appendix), and they unambiguously cluster with Panamanian OTUs of *vegetus* as opposed to geographically proximate representatives of *fulvescens costaricensis* (Fig. 8). Craniodental proportions and qualitative features, including development of the capsular process, of the type specimen of *creper* inarguably place it within the morphological range observed for Bangs's (1902) *vegetus* (see Fig. 3), which condition supports their synonymy. Except for our disagreement over specific assignment and status, Goodwin's description and comparisons of *creper* are apt, and most AMNH specimens from the central highlands of Costa Rica that he (1945, 1946) referred to the subspecies we accept as *vegetus.*

Oryzomys fulvescens reventazoni, Goodwin's other Costa Rican subspecies, presents a less clearcut interpretation, in part due to the uniformly young age of the five specimens composing the type series. Defining characters, as stated by Goodwin (1945:3), recall those of *creper*: "A very small, dark-colored pygmy rice rat. Similar in general appearance to *O. f. creper* but much smaller and tail shorter." Goodwin (1945, 1946) repeatedly emphasized the striking resemblance, except for size, between the type specimen of *reventazoni* and that of *creper.* In fact, many distinctions he ascribed to the two holotypes can be reasonably attributed to age-related size differences, for the holotype of *creper* is a very old adult with flatly worn molars, whereas that of *reventazoni* is a much younger animal in fresh adult pelage. Goodwin simultaneously noted the still smaller size and paler coloration, with white underparts, of his four topotypes of *reventazoni*; their size and pelage impress us only as young individuals of *fulvescens,* which is known to occur with *vegetus* elsewhere in the upper valley of the Río Reventazón (see Specimens Examined). Finally, results of principal component analysis substantiate the closer morphometric agreement of the type of *reventazoni* to examples of *vegetus* and of the two measureable topotypes to those of *fulvescens* (Fig. 3). We conclude that Goodwin's type series is a composite. The identity of the type specimen (AMNH 141891), as name bearer of the taxon, dictates the relegation of *reventazoni* to subjective junior synonymy under *O. vegetus*; the four topotypes (AMNH 140364–5, 141890, 141892) are reassigned to *O. fulvescens costaricensis.*

Specimens examined.—352, as follows.

Costa Rica: Provincia de Alajuela, Cataratos San Carlos (AMNH 141941–2); Monteverde Cloud Forest Reserve, valley of Río Peñas Blancas, La Esperanza, 840 m (KU 143399); Lajas Villa Quesada (AMNH 139736–43, 140363); Tapesco (AMNH 139804–6); Volcán Poas, 2000 m (UMMZ 123200); Zarcero, 6500 ft (FMNH 43990). Provincia de Cartago, Estrella de Cartago, 4500 ft (UMMZ 64131–2); Volcán Irazú, 9400 ft (AMNH 141199); Volcán Irazú, 0.25 mi N Hotel Robert, 2575 m (UMMZ 116903); Moravia, 1116 m (UMMZ 111983, 112283–4); El Muñeco, 10 mi S Cartago, Río Navarro, 3700, 3800, and 4000 ft (UMMZ 67310, 67312–3); El Muñeco, 13 km S Cartago (KU 27017); Salsipuedes, Pan Am Hwy, 2730 m (UMMZ 123380); El Sauce Peralta (USNM 250394–5); Santa Teresa Peralta (AMNH 141891). Provincia de Limon, Río Teribé, Valle El Silencio, Río Cotón, 8000 ft (USNM 539895–907). Provincia de Puntarenas, Monteverde, 1400–1465 m (KU 142063, 142066–8, 143315, 143398; UMMZ 115425, 116904–8, 117102–4; USNM 566458); Monteverde, Cerro Amigos, 1760 m (KU 142064–5); Monteverde, Reserva Bosque Nuboso, La Ventaña (USNM 559054); Vera Cruz, 1320 m (KU 143502). Provincia de San José, El Copey de Dota, 6000 ft (UMMZ 64039–40, 65071); Los Higuerones, Escazú (AMNH 137291, 138020–6, 138076–9); Cerro de Buena Vista, 10,342 ft (AMNH 9567/7909); Cerro de la Muerte, summit (on Pan Am Hwy), 10,200 ft (UMMZ 112280); Cerro de la Muerte, 5.5 mi S (via Pan Am Hwy) summit, La Georgina (UMMZ 112281–2); Cerro de la Muerta, Villa Mills (UMMZ 115426); 9 mi N (via Pan Am Hwy) San Isidro del General, 4800 ft (UMMZ 111970); 11 mi N (via Pan Am Hwy) San Isidro de General, 5200 ft (UMMZ 111971–5, 112279); San Joaquín de Dota, 3800 and 4000 ft (UMMZ 62882–3, 62887–8).

Panama: Provincia Bocas de Toro, northeast of Boquete, near Río Cylindro, 2380 m (USNM 516745); 3 km NE Escopeta, Quebrada de los Gatos, 1375 m (USNM 541172); 3.5 km E Escopeta, Cerro Bollo, 1800–1856 m (USNM 541186–8); 20 mi SSW Changuinola, upper Río Changena, Rancho Mojica, 4800, 5000, and 5400–5600 ft (USNM 319316–26); Fish Camp, 4900 ft, 08°58′N/82°40′W (USNM 520730–5); Upper Camp 1975, 08°56′N/82°42′W (USNM 520736); 17.5 km NNW El Hato del Volcán, NE Cerro Pando, 2180 m (USNM 516758–9); 25 km NNE San Félix, 1425–1500 m (USNM 541184–5). Provincia de Chiriquí, Bambito, 5800 and 5900 ft (USNM 314355, 314777); Boquete, 4000, 4500, and 4800 ft (AMNH 18825–8, 18834–6; FMNH 14298, 14302, 14304–6, 18518–9; MCZ 10297–8, 10300–4, 10308–10; USNM 242339); head of Río Candela, 17 km NNW El Hato del Volcán, 2000 m (USNM 516764); Casita Alta, 7000 ft (ANSP 18546–7, 18624); Río Chebo (ANSP 18514, 18516–7, 18522); Río Chiriquí Viejo, 3800 ft (ANSP 18523–5, 18945), 1600–1850 m (UMMZ 116911–8, 117100); Cotito Hot Springs (USNM 396546); Cylindro (ANSP 20956); Río Gariche, 5350 ft (ANSP 18409, 18618–23); Hortigal (ANSP 20825, 20830, 20968, 21024); Finca Lerida (ANSP 20761, 20768, 20803, 20871, 20921, 20923); Osta Clara Camp (ANSP 18334); Cerro Pando, 4100 ft (AMNH 147790; ANSP 17853–9); Peña Blanca (ANSP 20852, 21039); Cerro Punta, 1825 m (ANSP 18744, 18746–54, 18756–7; UMMZ

116921); 0.5 mi W Cerro Punta, 1825 and 1880 m (UMMZ 116919–20); 0.5 mi SE Cerro Punta, Volcán de Chiriquí, 2000 m (UMMZ 116922–5); Cerro Punta, Boquete Trail, 7000, 7700, 7750, and 7800 ft (USNM 323883–97); Cerro Punta, Casa Tilley, 5300 ft (USNM 314344, 318429–30); Cerro Punta, Finca Martinz, 6800 ft (USNM 314345–54); Finca Santa Clara, 14.5 km NW El Hato de Volcán, 1200–1500 m (USNM 395547, 516742, 516757, 516761, 516763, 516767, 516774, 537618); Río Santa Clara, 4150 ft (ANSP 18628, 18634, 18637–8); Siola, 4100–4300 ft (ANSP 17852, 18389–91, 18532, 18543, 18550–611, 18944, 18956–8, 18960, 18964–5, 18969, 18971, 18978, 18981–3, 18989, 18991, 18994, 18998–9, 19081–2, 19088–9); locality unknown (AMNH 173903; ANSP 17825, 21046).

Oligoryzomys fulvescens (Saussure)

H. [*esperomys*] *fulvescens* Saussure, 1860: 102 (type locality—Mexico, Veracruz, vicinity of Orizaba—as subsequently restricted by Merriam, 1901:295).

Oryzomys costaricensis Allen, 1893:239 (type locality—Costa Rica, Puntarenas, El General, 2150 ft; holotype—AMNH 9581/7922).

Oryzomys delicatus Allen and Chapman, 1897:19 (type locality—Trinidad, Caparo; holotype—AMNH 7317/5925).

Oryzomys navus Bangs, 1899:9 (type locality—Colombia, Magdalena, Sierra Nevada de Santa Marta, Pueblo Viejo, 8000 ft; holotype—MCZ 8107).

Oryzomys navus messorius Thomas, 1901: 151 (type locality—British Guiana [Guyana], Kanuku Mountains; holotype—BMNH 1901.6.4.97).

Oryzomys tenuipes Allen, 1904b:328 (type locality—Venezuela, Merída, Merída, 1630 m; holotype—AMNH 21330).

Oryzomys (*Oligoryzomys*) *nicaraguae* Allen, 1910:100 (type locality—Nicaragua, Matagalpa, Vijagua; holotype—AMNH 29543).

Oryzomys (*Oligoryzomys*) *munchiquensis* Allen, 1912:85 (type locality—Colombia, Cauca, La Florida, 7700 ft; holotype—AMNH 32603).

Oryzomys fulvescens lenis Goldman, 1915: 130 (type locality—Mexico, Michoacán, Los Reyes; holotype—USNM 125941).

Oryzomys fulvescens mayensis Goldman, 1918:92 (type locality—Mexico, Campeche, near Yohaltún, Apazote, 200 ft; holotype—USNM 107979).

Oryzomys fulvescens engraciae Osgood, 1945:300 (type locality—Mexico, Tamaulipas, northwest of Ciudad Victoria, Hacienda Santa Engracia, 240 m; holotype—FMNH 54164).

Oryzomys fulvescens pacificus Hooper, 1952: 23 (type locality—Mexico, Chiapas, Mapastepec, 150 ft; holotype—UMMZ 96764).

Remarks.—While we defend our sample sizes and the coarse density of geographic sampling as adequate to clarify the status of *O. vegetus,* they are insufficient to evaluate geographic differentiation within *O. fulvescens* and to address attendant nomenclatural questions to their proper depth. Nevertheless, the several subspecies examined and the morphological divergence encountered warrant some comment on intraspecific variation.

The extensive dispersion of specimens along the second canonical variate principally involves the four subspecific taxa of *O. fulvescens* and suggests a north–south trend of increase in average size, with individuals of *f. fulvescens* and *f. pacificus* smaller, *f. nicaraguae* intermediate, and those of *f. costaricensis* larger (Fig. 7). Although a broad trend may exist (verification with more samples is desirable), individual scores within the conventional subspecies vary greatly and group polygons overlap extensively. Dimensions that load heavily on CV II include IOB, BPL, LM1-3, and WM1, all of which reach their most robust expression in certain samples of *costaricensis* (for example CR2–3, PA7—Appendix). If one ignores his inclusion of *vegetus* and the later additions of new geographic races, these results provide some corroboration of Goldman's (1918) general remarks on craniodental variation within *fulvescens.*

Cohesiveness of certain subspecific boundaries, however, is eroded in phenograms generated from clustering of sample means. Whether using a distance or correlation measure of phenetic similarity, OTUs of *f. costaricensis* fail to group exclusively of others representing *fulvescens* proper, *f. pacificus,* and some *f. nicaraguae* (Fig. 8). Certain samples of *f. costaricensis* from central Panama (PA1–3) actually link with northern subspecies instead of geographically proximate OTUs from western Panama (PA7) and eastern Costa Rica (CR2–3). Pygmy rice rats from northern and central Nicaragua (NI1 = *f. nicaraguae*) consistently formed a pair-group with *fulvescens* from Veracruz, a resemblance in accord with the opinion of Jones and Engstrom (1986), who suggested that *nicaraguae* may prove inseparable from the nominate race.

The most divergent OTU (NI2) among our samples of *O. fulvescens* is that drawn from scattered localities along the Pacific coastal region of Nicaragua. Jones & Engstrom (1986) noted the smaller cranial size and pale buff venter of *fulvescens* from this region as compared to those from the central and northern highlands; they assigned, with reservation, the former to *f. costaricensis* and the latter to *f. nicaraguae.* We do not attach much significance to the apparent size divergence of this one OTU in view of its small sample size ($n = 7$), the skewed age representation (mostly young-, some full-, and no old-adults), and the coarse lumping of localities within Nicaragua necessarily employed by us and by Jones & Engstrom (1986). In particular, the reputedly smaller cranial size can be attributed to youthful age representation in this one sample; it is significant that the length of the molar rows, which once erupted do not increase with age, of the two Nicaraguan OTUs are essentially identical ($\bar{X}$ LM1–3 = 2.86 and 2.87 mm in NI1 and NI2, respectively). Chromatic distinctions of the coastal specimens (paler dorsum and a white to light buff venter) do set them apart from north-central populations (darker dorsal tone and gray venter), and instead resemble examples of *costaricensis* from Costa Rica. As noted by Jones & Engstrom (1986), the geographic extent of this Pacific lowlands morphotype, its possible intergradation with Hooper's (1952) *pacificus* to the north and with Allen's (1893) *costaricensis* to the south, deserves amplification.

Two chromosomal morphologies have been reported, both as *Oryzomys fulvescens,* for populations of *Oligoryzomys* from Central America. Gardner & Patton (1976) described a diploid complement consisting of one large and four small pairs of metacentrics, three pairs of large subtelocentrics, and 18 pairs of small acrocentrics (2N = 54; FN = 68) for a single individual from near Santa Ana, San José, Costa Rica. In contrast, Haiduk et al. (1979) discovered a higher diploid count (three additional acrocentric pairs; 2N = 60; FN = 74) for three individuals collected northeast of Catemaco, Veracruz, Mexico; they did not attach any taxonomic import to the difference. We have examined the former specimen (LSU 13169) and found it to be a typical example of *O. fulvescens costaricensis.* In view of their origin from Veracruz, and having encountered no other form of *Oligoryzomys* in the region, we presume the latter to represent *O. f. fulvescens.* Taxonomic implication of the reported chromosomal differences, their degree of conservatism, and the existence of still other karyotypic variants within populations now classified as *O. fulvescens* are all topics for future study.

Central American populations and infraspecific taxa of *O. fulvescens,* now divorced of Bangs's (1902) *vegetus* and Goodwin's (1945) *creper* and *reventazoni,* appear conspecific to us. Yet questions remain—such as the divergence and relationship of populations in western Nicaragua and the significance of the disparate karyotypes reported—and underscore the need for further investigation. The specific limits and systematic standing of forms of *Oligoryzomys* named from South America are far more tentative. Future research should amplify the specimen-based distribution of *fulvescens* south of the Isthmus of Panama and confirm or reject the relationship and synonymy of South American species-group taxa that we have provisionally associated with it (Carleton & Musser 1989, Musser & Carleton 1993). Pending completion of such studies, we below list the Central American specimens examined according to recently published viewpoints on subspecies and their ranges (that is, Hall 1981, Jones & Engstrom 1986).

Oligoryzomys fulvescens costaricensis (Allen)

Specimens examined.—311, as follows.

Costa Rica: Provincia de Alajuela, Lajas Villa Quesada (AMNH 139735); 5 mi SW San Ramón (KU 71300); Upala, Colonia Puntarenas, Route 4—KM 93, Río Chimurria, 80 m (KU 142726–8); Upala, San José, 45 m (KU 142729); Upala, Aguas Claras, Colonia Libertad, Finca La Anita (KU 142730). Provincia de Cartago, Agua Caliente (KU 16581–2, 16584–6, 27015–6); Cartago, 4800 ft (KU 16535, 16583; UMMZ 66469, 66472, 66476); 3 km S Cartago, 1400 m (KU 27004); Cervantes (AMNH 123501; FMNH 35196–7; MCZ 27805; USNM 250374–5, 256479); La Carpintera (AMNH 9565/7907); Girara (KU 16580); El Guarco (KU 165789, 16588); El Muñeco, 10 mi S Cartago, Río Navarro, 3700 and 3800 ft (UMMZ 67311, 67314); near Paraiso (UMMZ 105658); 1 mi W Paraiso, 1415 m (UMMZ 112286); Santa Teresa, Peralta (AMNH 140364–5, 141890, 141892); 3 mi SE Turrialba, Instituto Interamericano, 602 m (UMMZ 111976–81, 112285); 5 km SE Turrialba (KU 27005–14). Provincia de Guanacaste, 2 km SE (via rd to Caño Negro) Arenal (UMMZ 115513); Finca Jiménez, 0.5 mi E headquarters, 30 m (UMMZ 115291); Cerros de San Juan, 8 mi S Santa Cruz, 1200 ft (UMMZ 65048); Hacienda Santa María, 3200 ft (UMMZ 65218–9); Palo Verde, 2 km S and 12 km E Bolsón, 50 m (KU 143733); Rincón de La Vieja National Park, near headquarters, 780 m (KU 143748). Provincia de Puntarenas, Boruca (AMNH 9572, 9573/7914, 9574/7915, 9575/7916, 9577/7918, 9580/7921; FMNH 5369); Buenos Aires (AMNH 9578/7919, 9579/7920); Cañas Gordas (AMNH 142440–58, 142490–5, 142500); Osa Peninsula, Corcovado National Park, Sirena Station (USNM 565820–1); El General, 2000 and 2150 ft (AMNH 9568/7910, 9581–2/7922–3; UMMZ 66470–1, 66475); Finca Helechales, 910 m (USNM 547947–9); Palmar Sur, 15 m (KU 88240–4); 4 km S San Vito de Java, Finca Las Cruces, 1250 m (UMMZ 116909–10); Monteverde, Pension Quetzal, 1400 m (FMNH 128494). Provincia de San José, Escazú, 3000 ft (AMNH 131738); Monterrey, 22 km S San José, 1000 m (KU 60485), 1100 m (KU 39253, 60486); San Gerónimo de Pirrís (AMNH 123538–9, 123541; FMNH 35198–9; MCZ 27801, 27803–4, 28864–5; USNM 250377, 250380–93, 256480–1); 9.3 mi W (via rd to Dominical) San Isidro del General (UMMZ 105656); 2 km NW Santa Ana (LSUMZ 13169); Sabanilla de Pirrís (USNM 256449). Costa Rica, locality unknown (AMNH 10101, 10103, 19230).

Nicaragua: Carazo, 3 mi NNW Diriamba (KU 71294–9); 3 km N and 4 km W Diriamba, 600 m (KU 110465, 115438). Chinandega, 1 km N Cosiguina, El Paraiso, 20 m (KU 115432). Granada, 10 km SE Guanacaste, Finca El Progreso, 1000 m (KU 106551–2).

Panama: Canal Zone, Albrook Field (USNM 302684); Barro Colorado Island (UMMZ 59935–6; USNM 256183–5); Curundu (USNM 297943, 301594); Fort Clayton (USNM 297942); Fort Kobbe (USNM 300351); Buena Vista Peninsula, 1.75 km NNW Frijoles (USNM 503718); Rodman Naval Station (USNM 457327–9, 457917). Provincia de Chiriquí, Boquete, 3800, 4000, and 4800 ft (MCZ 10293–4, 10296, 10299, 10307); Río Chebo (ANSP 18386–7, 18511–3, 18515, 18518–20, 18941–2, 19077–8); Colorado Camp, 24 km NNE San Felix, 1275–1325 m (USNM 541162–71, 541173–83); Río Gariche, 5350 ft (ANSP 18408); 7 km NE El Hato de Volcán, 1820 m (UMMZ 117099); Finca Lerida (ANSP 20762, 20769, 20924–5); Finca Santa Clara, 14.5 km NW El Hato del Volcán, 1200–1500 m (USNM 396541–5, 396548–50, 516741, 516743–4, 516746–51, 516754–6, 516760, 516762, 516765, 516768–73, 537619); Río Santa Clara, 4150 ft (ANSP 18383–4, 18627, 18629–33, 18635). Provincia de Coclé, El Valle (USNM 303417–20, 304766). Provincia de Panamá, Cerro Azul, 930 m (USNM 303262, 305676–94, 305697–8, 306951); Cerro Campana (USNM 303416); La Chorrera (AMNH 31431); 6 mi E El Valle (USNM 304767–92); 4 mi E and 1 mi S Pacora (USNM 305675); Panama City, Río Chilibrillo (AMNH 36722–3).

Oligoryzomys fulvescens fulvescens (Saussure)

Specimens examined.—103, as follows.

Mexico: Estado de Veracruz, Achotal (FMNH 14105–8, 15882); Cerro Azul, 350 ft (KU 30559); Boca del Río, 10 ft (KU 30570); 3 km W Boca del Río, 10 ft (KU 24124–6); Cautlapan, 4000 ft (KU 30573–5); Coscomatepec, 5000 ft (KU 30571–2); Jalapa, 4400 ft (AMNH 12536/10846–12541/10851, 12543/10853–12549/10859, 12583–5; FMNH 5370; USNM 93369–73, 93394); 5 km N Jalapa, 4500 ft (KU 19394); Jico, 6000 ft (FMNH 13112; USNM 55032–3); 2 km W Jico, 4200 ft (KU 19722–3); 20 km E Jesus Carranza, 300 ft (KU 24133–4); 25 km ESE Jesus Carranza, 200 ft (KU 32156); 0.5–3 mi NE Las Minas, 1200–1400 m (USNM 329805–8); Mirador, 3500 ft (KU 24122; USNM 10107/12174); Monte Blanco, 1300 m (KU 29495–6); 2 km N Motzorongo, 1500 ft (KU 19400); Orizaba, 4000 ft (USNM 58243–4, 58246–8, 58254–6, 58259–62, 58288), 4200 ft (USNM 63685–8); 3 km SE Orizaba, 5500 ft (KU 19721, 19723); Ozulama, 500 ft (KU 30558); 4 km W Paso de San Juan, 250 ft (KU 24123); Planton Sánchez, 800 ft (KU 88700–2); Potrero Viejo, 1700 ft (KU 24127–9, 24170, 30576–9, 32155); San Andreas Tuxtla (USNM 65540); 3 km E San Andreas Tuxtla, 1000 ft (KU 24130–2); 2 km SSW Tenochtitlán, 60 m (UMMZ 116316–8); Teocelo, 4500 ft (KU 30564–9); 12.5 mi N Tihuatlan, 300 ft (KU 88704); 5 km S Tihuatlan, 700 ft (KU 24119); Tlacolula, 60 km WNW Tuxpan (KU 83067); 15 km ENE Tlacotepec, 1500 ft (KU 24120); 4 km W Tlacotepec, 1700 ft (KU 24121).

Oligoryzomys fulvescens nicaraguae (Allen)

Specimens examined.—28, as follows.

Nicaragua: Boaco, 17 km N and 15 km E Santa Rosa, 300 m (KU 110461). Chontales, 1 km N and 2.5 km W Villa Somoza, 330 m (KU 110464). Jinotega, Yali, 860 m (KU 106546, 106549). Matagalpa, 1 km N and 5 km E Esquipulas, La Danta, 760 and 780 m (KU 115433–4); Santa María de Ostuma, 1250 m (KU 106550); Vijagua (AMNH 29543). Nueva Segovia, 1.5 km N and 1 km E Jalapa, 660 m (KU 110455–7); 4.5 km N and 2 km E Jalapa, 680 m (KU 110453–4); 3.5 km S and 2 km W Jalapa, 660 m (KU 110458–9). Rivas, Isla de Ometepe, 4 km S and 1.5 km E Alta Gracia, 40 m (KU 115439). Zelaya, Cara de Mono, 50 m (KU 115435–6); El Recreo, southern side of Río Mico, 25 m (KU 106553–8, 110462–3, 115437; USNM 337770).

Oligoryzomys fulvescens pacificus (Hooper)

Specimens examined.—22, as follows.

Mexico: Estado de Chiapas, Maspastepec, 45 m (UMMZ 96750–66); Pijijiapan, 10 m (UMMZ 96767–9, 96798); Ariaga, 100 m (UMMZ 96770).

Acknowledgments

We thank the following museum staff for timely loan of specimens and-or the hospitality extended during the use of collections under their charge: Edward B. Daeschler, ANSP; Bruce Patterson, FMNH; Robert M. Timm and Thorvald Holmes, KU; Leanna Good and Mark Hafner, LSUMZ; Maria Rutzmoser, MCZ; Philip Myers, UMMZ. Patricia Wynne prepared the line drawing in Fig. 2, and Dave Schmidt, with his usual competence and concern for detail, undertook the cranial photography, distribution maps, and other figures. The final manuscript benefitted from the careful reviews and comments of Robert D. Fisher, Dave Schmidt, and Neal Woodman.

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Appendix.—Descriptive statistics for selected cranial and external variables and OTUs of *Oligoryzomys.*

Species and OTU	*n*	Mean	Range	*SD*
		Total length		
O. fulvescens fulvescens				
FUL	55	178	157–205	11.6
O. fulvescens costaricensis				
PA3	19	197	184–217	8.0
PA7	24	174	149–198	12.2
CR2	21	177	160–196	10.2
CR4	23	173	150–193	10.4
CR5	21	177	154–197	11.2
O. vegetus				
PA4	12	207	185–235	15.1
PA5	28	192	170–213	10.7
PA6	63	211	191–238	12.6
CR1	4	196	179–216	15.3
CR7	15	193	158–214	14.1
		Tail length		
O. fulvescens fulvescens				
FUL	55	101	82–116	7.3
O. fulvescens costaricensis				
PA3	19	112	102–125	6.5
PA7	24	99	85–118	7.3
CR2	21	102	92–115	5.7
CR4	23	102	88–112	6.1
CR5	22	99	90–115	5.7
O. vegetus				
PA4	12	119	110–130	6.6
PA5	28	113	97–126	6.3
PA6	63	126	113–142	8.3
CR1	4	113	107–125	8.3
CR7	15	114	94–129	8.5
		Hindfoot length		
O. fulvescens fulvescens				
FUL	57	21.4	19–24	1.1
O. fulvescens costaricensis				
PA3	20	22.1	21–23	0.8
PA7	24	20.2	18–23	1.4
CR2	22	20.1	18–21	1.1
CR4	23	19.9	18–21	0.8
CR5	23	20.8	17–23	1.4
O. vegetus				
PA4	13	23.7	20–25	1.3
PA5	30	22.9	21–26	1.0
PA6	62	24.5	23–27	1.0
CR1	11	22.4	21–24	1.1
CR7	16	23.0	20–25	1.4
		Occipitonasal length		
O. fulvescens fulvescens				
FUL	50	21.2	19.6–23.7	0.8
O. fulvescens costaricensis				
PA3	20	22.0	21.5–23.0	0.4
PA7	24	21.7	20.2–23.2	0.7
CR2	14	22.0	20.8–23.9	0.9
CR4	16	21.3	19.2–23.0	1.1
CR5	15	21.5	20.1–22.5	0.7
O. vegetus				
PA4	8	23.3	22.3–24.4	0.7
PA5	33	22.5	20.9–24.0	0.7
PA6	49	23.2	21.0–25.6	1.0
CR1	13	22.8	21.1–24.1	0.8
CR7	15	22.4	21.4–23.6	0.7
		Zygomatic breadth		
O. fulvescens fulvescens				
FUL	50	11.0	10.3–12.2	0.4
O. fulvescens costaricensis				
PA3	20	11.3	10.8–11.9	0.4
PA7	24	11.0	10.1–11.9	0.4
CR2	14	11.3	10.6–12.4	0.5
CR4	16	11.1	10.0–11.8	0.5
CR5	16	11.2	10.4–11.8	0.4
O. vegetus				
PA4	8	12.3	11.8–12.9	0.4
PA5	33	11.9	10.8–12.9	0.5

Appendix.—Continued.

Appendix.—Continued.

Species and OTU	*n*	Mean	Range	*SD*
PA6	49	12.0	11.1–13.5	0.5
CR1	13	11.9	11.1–12.5	0.5
CR7	16	11.7	10.8–12.5	0.4
Breadth of braincase				
O. fulvescens fulvescens				
FUL	50	10.0	9.4–10.5	0.3
O. fulvescens costaricensis				
PA3	20	10.0	9.7–10.4	0.2
PA7	24	9.9	9.4–10.4	0.2
CR2	14	10.3	9.9–10.7	0.2
CR4	16	10.1	9.6–10.5	0.3
CR5	16	10.1	9.7–10.4	0.2
O. vegetus				
PA4	8	10.9	10.6–11.2	0.2
PA5	33	10.7	10.1–11.2	0.3
PA6	49	10.7	10.3–11.3	0.2
CR1	13	10.7	10.1–11.0	0.2
CR7	16	10.6	10.3–10.8	0.2
Interorbital breadth				
O. fulvescens fulvescens				
FUL	50	3.4	3.1–3.7	0.1
O. fulvescens costaricensis				
PA3	20	3.7	3.5–3.9	0.1
PA7	24	3.7	3.5–4.2	0.1
CR2	14	3.7	3.4–4.1	0.1
CR4	16	3.7	3.3–3.9	0.1
CR5	16	3.6	3.3–3.9	0.1
O. vegetus				
PA4	8	3.7	3.5–4.0	0.1
PA5	33	3.6	3.1–4.0	0.1
PA6	49	3.6	3.3–3.9	0.1
CR1	13	3.7	3.5–4.0	0.1
CR7	16	3.7	3.4–3.9	0.1
Length of rostrum				
O. fulvescens fulvescens				
FUL	50	6.3	5.5–7.0	0.4
O. fulvescens costaricensis				
PA3	20	6.5	6.0–7.1	0.2
PA7	24	6.4	5.8–7.1	0.3
CR2	14	6.7	6.1–7.6	0.4
CR4	16	6.4	5.3–7.2	0.5
CR5	15	6.4	6.0–7.1	0.3
O. vegetus				
PA4	8	6.9	6.4–7.5	0.3
PA5	33	6.7	5.7–7.4	0.4

Appendix.—Continued.

Species and OTU	*n*	Mean	Range	*SD*
CR1	13	7.0	6.4–7.6	0.3
CR7	15	6.6	6.1–7.1	0.3
Postpalatal length				
O. fulvescens fulvescens				
FUL	50	7.0	6.1–7.9	0.6
O. fulvescens costaricensis				
PA3	20	7.5	7.1–7.9	0.2
PA7	24	7.1	6.5–7.7	0.3
CR2	14	7.2	6.7–8.5	0.5
CR4	13	7.0	6.2–7.9	0.6
CR5	16	7.0	6.4–7.8	0.4
O. vegetus				
PA4	7	7.9	7.5–8.9	0.5
PA5	33	7.4	6.7–8.2	0.4
PA6	49	7.7	6.7–8.5	0.5
CR1	11	7.4	6.8–8.0	0.4
CR7	16	7.3	6.9–7.7	0.2
Length of diastema				
O. fulvescens fulvescens				
FUL	50	5.1	4.2–5.8	0.3
O. fulvescens costaricensis				
PA3	20	5.4	5.1–5.7	0.2
PA7	24	5.1	4.7–5.8	0.3
CR2	14	5.3	4.9–6.3	0.4
CR4	17	5.1	4.3–5.8	0.4
CR5	16	5.2	4.9–5.8	0.3
O. vegetus				
PA4	8	5.7	5.4–6.2	0.3
PA5	33	5.5	4.9–6.2	0.3
PA6	49	5.7	4.9–6.6	0.4
CR1	13	5.7	5.2–6.4	0.4
CR7	16	5.5	5.1–5.9	0.2
Length of incisive foramen				
O. fulvescens fulvescens				
FUL	50	3.7	3.3–4.1	0.3
O. fulvescens costaricensis				
PA3	20	4.0	3.7–4.5	0.2
PA7	24	3.9	3.6–4.3	0.2
CR2	14	4.0	3.7–4.3	0.2
CR4	17	3.7	3.1–4.0	0.2
CR5	16	3.8	3.5–4.2	0.2
O. vegetus				
PA4	8	3.8	3.7–4.1	0.1
PA5	33	3.7	3.1–4.0	0.2

Appendix.—Continued.

Species and OTU	*n*	Mean	Range	*SD*
PA6	49	3.7	3.3–4.3	0.2
CR1	13	3.7	3.4–4.0	0.2
CR7	16	3.7	3.3–4.0	0.2
		Breadth of bony palate		
O. fulvescens fulvescens				
FUL	50	3.9	3.7–4.2	0.1
O. fulvescens costaricensis				
PA3	20	4.0	3.7–4.2	0.1
PA7	24	3.9	3.6–4.3	0.1
CR2	14	4.0	3.8–4.4	0.1
CR4	17	4.0	3.8–4.2	0.1
CR5	16	4.1	3.8–4.4	0.1
O. vegetus				
PA4	8	4.3	4.2–4.5	0.1
PA5	33	4.2	3.9–4.4	0.1
PA6	49	4.3	4.0–4.8	0.2
CR1	13	4.2	3.9–4.5	0.2
CR7	16	4.0	3.8–4.2	0.1
		Breadth of zygomatic plate		
O. fulvescens fulvescens				
FUL	50	1.8	1.4–2.1	0.1
O. fulvescens costaricensis				
PA3	20	2.1	1.9–2.3	0.1
PA7	24	2.0	1.7–2.2	0.1
CR2	14	2.0	1.8–2.2	0.1
CR4	17	1.8	1.5–2.1	0.2
CR5	16	1.9	1.5–2.1	0.1

Appendix.—Continued.

Species and OTU	*n*	Mean	Range	*SD*
O. vegetus				
PA4	8	1.9	1.8–2.0	0.1
PA5	33	1.8	1.4–2.2	0.2
PA6	49	1.9	1.5–2.1	0.1
CR1	13	1.9	1.6–2.2	0.1
CR7	16	1.8	1.6–2.0	0.1
		Length of maxillary toothrow		
O. fulvescens fulvescens				
FUL	50	2.8	2.5–3.0	0.10
O. fulvescens costaricensis				
PA3	20	3.0	2.8–3.2	0.10
PA7	24	3.1	2.9–3.2	0.09
CR2	19	3.1	2.8–3.3	0.11
CR4	22	2.9	2.8–3.1	0.08
CR5	24	3.0	2.8–3.1	0.08
O. vegetus				
PA4	12	3.0	2.8–3.1	0.08
PA5	34	2.9	2.8–3.1	0.06
PA6	58	2.9	2.7–3.1	0.08
CR1	13	2.9	2.8–3.1	0.08
CR7	16	2.8	2.6–3.0	0.10

OTU Codes.—FUL: Mexico, Veracruz, various localities; CR1: Costa Rica, Limón, Valle El Silencio; CR2: Costa Rica, Puntarenas, Cañas Gordas; CR4: Costa Rica, San José, San Gerónimo Pirrís; CR5: Costa Rica, Cartago, valley of Río Reventazón; CR7: Costa Rica, Puntarenas, Monteverde; PA3: Panama, Chiriquí, Colorado Camp; PA4: Panama, Chiriquí, Boquete; PA5: Panama, Chiriquí, Cerro Punta & vicinity; PA6: Panama, Chiriquí, Siola; PA7: Panama, Chiriquí, Finca Santa Clara.

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108(2):370. 1995.

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108(2):371–372. 1995.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Applications published in the *Bulletin of Zoological Nomenclature*

The following Applications were published on 30 March 1995 in Vol. 52, Part 1 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.

2901 *Stictostroma* Parks, 1936 (Porifera, Stromatoporoidea): proposed conservation, and designation of *S. gorriense* Stearn, 1995 as the type species.

2949 *Aplysia juliana* Quoy & Gaimard, 1832 (Mollusca, Gastropoda): proposed conservation of the specific name.

2922 *Octopus vulgaris* Cuvier, [1797] and *Loligo vulgaris* Lamarck, 1798 (Mollusca, Cephalopoda): proposed conservation of the specific names.

2899 *Dodecaceria concharum* Örsted, 1843 and *Heterocirrus fimbriatus* Verrill, 1879 (currently *D. fimbriata*) (Annelida, Polychaeta): proposed conservation of the specific names by the designation of a neotype for *D. concharum.*

2944 *Eophacops* Delo, 1935 and *Acernaspis* Campbell, 1967 (Trilobita): proposed conservation.

2914 *Diplocentrus mexicanus* Peters, 1861 (Arachnida, Scorpiones): proposed confirmation of the rediscovered holotype as the name-bearing type.

2941 *Nepa rustica* Fabricius, 1781 and *Zaitha stollii* Amyot & Serville, 1843 (currently *Diplonychus rusticus* and *Belostoma stollii*; Insecta, Heteroptera): proposed conservation of the specific names.

2918 *Aspidiphorus* Ziegler in Dejean, 1821 (Insecta, Coleoptera): proposed conservation as the correct original spelling, and ASPIDIPHORIDAE Kiesenwetter, 1877 (1859): proposed placement on the Official List.

2872 XANTHOLININI Erichson, 1839 and QUEDIINI Kraatz, 1857 (Insecta, Coleoptera): proposed precedence over senior synonyms, and *Quedius* Stephens, 1829: proposed designation of *Staphylinus levicollis* Brullé, 1832 as the type species.

2916 *Metablastothrix* Sugonjaev, 1964 (Insecta, Hymenoptera): proposed designation of *Blastothrix* (*Metablastothrix*) *isomorpha* Sugonjaev, 1964 as the type species.

2897 *Agonus* Bloch & Schneider, 1801 (Osteichthyes, Scorpaeniformes): proposed conservation; AGONIDAE Kirby, 1837 (Insecta, Coleoptera) and AGONIDAE Swainson, 1839 (Osteichthyes, Scorpaeniformes): proposed removal of homonymy.

2931 Proposed conservation of nine specific names of southern Afrotropical birds which are junior synonyms.

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 30 March 1995 in Vol. 52, Part 1 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.

1792. *Pleurotoma meneghinii* Mayer, 1868 (currently *Asthenotoma meneghinii*; Mollusca, Gastropoda): neotype replaced by rediscovered lectotype.
1793. *Chtenopteryx* Appellöf, 1890 (Mollusca, Cephalopoda): confirmed as the correct original spelling.
1794. *Sigara coleoptrata* Fabricius, [1777] (Insecta, Heteroptera): specific name conserved, and *Notonecta obliqua* Thunberg, 1787: specific name placed on the Official List.
1795. *Corisa sexlineata* Reuter, 1882 (currently *Sigara* (*Tropocorixa*) *sexlineata*; Insecta, Heteroptera): specific name not conserved, and that of *C. confluens* Fieber, 1851 placed on Official List.
1796. *Platynectes* Régimbart, 1879 (Insecta, Coleoptera): conserved.
1797. *Oecothea* Haliday in Curtis, 1837 (Insecta, Diptera): conserved, and *Helomyza fenestralis* Fallén, 1820 designated as the type species.
1798. *Rivulus marmoratus* Poey, 1880 (Osteichthyes, Cyprinodontiformes): given precedence over *R. ocellatus* Hensel, 1868, and a neotype designated for *R. marmoratus.*
1799. *Naucrates* Rafinesque, 1810 and *Xyrichtys* Cuvier, 1814 (Osteichthyes, Perciformes): conserved.
1800. *Emys* Duméril, 1806 (Reptilia, Testudines): conserved.
1801. *Cetiosauriscus* Huene, 1927 (Reptilia, Sauropodomorpha): *Cetiosauriscus stewarti* Charig, 1980 designated as the type species.
1802. *Dinodontosaurus* Romer, 1943 (Reptilia, Synapsida): conserved.

INFORMATION FOR CONTRIBUTORS

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PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY
OF
WASHINGTON

VOLUME 108 NUMBER 3
19 SEPTEMBER 1995
ISSN 0006-324X

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Known office of publication: National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Printed for the Society by Allen Press, Inc., Lawrence, Kansas 66044

Second class postage paid at Washington, D.C., and additional mailing office.

POSTMASTER: Send address changes to PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON, P.O. Box 1897, Lawrence, Kansas 66044.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(3):373–387. 1995.

Nomenclature of the Hawaiian Akialoas and Nukupuus (Aves: Drepanidini)

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Abstract.—The generic names *Hemignathus* Lichtenstein, 1839, and *Heterorhynchus* Lafresnaye, 1839, often used for the akialoas and the nukupuus, respectively, have the same type species (*Hemignathus lucidus*) so if the akialoas are given the status of a separate genus or subgenus, there is no generic-level name available for them. From a review of evidence concerning dates of publication we conclude that for nomenclatural purposes *Hemignathus* and *Heterorhynchus* were published simultaneously and *Hemignathus* has precedence according to the first reviser principle. The correct citation for the Oahu Akialoa is shown to be *Drepanis ellisiana* G. R. Gray (1859) rather than *Hemignathus lichtensteini* Wilson (1889). The name *Hemignathus stejnegeri* Wilson (1889) has priority over *H. procerus* Cabanis (1890) and is restored for the Kauai Akialoa. As no other name is available for akialoas, the new generic name *Akialoa* is proposed here (type species *Certhia obscura* Gmelin). The new names resulting from these nomenclatural changes are listed.

In the spectacular Hawaiian radiation of cardueline finches of the tribe Drepanidini, there are few more distinctive birds than the akialoas and nukupuus, which constitute the genus *Hemignathus* in the sense of Amadon (1950) and other authors, before and after him. The akialoas comprise five named taxa (one fossil) of medium-sized to large drepanidines with very long, decurved bills, the upper and lower parts of which are of nearly equal length (Fig. 1). Similar probing bills have evolved in various other groups of arboreal birds such as the babblers (*Xiphirhynchus*: Timaliidae), sunbirds (*Arachnothera*: Nectariniidae), woodcreepers (*Campyloramphus*: Dendrocolaptidae), and the woodhoopoes (Phoeniculidae). In the nukupuus (four named taxa, including the akiapolaau of Hawaii—*Heterorhynchus wilsoni* Rothschild), the upper jaw is likewise prolonged into a long, decurved probe, but the lower is much shorter (Fig. 1) and is used for pounding, prying, and pecking. The bill morphology of nukupuus is unique and has no parallel among other birds.

Unfortunately, upon these birds are heaped some of the most convoluted nomenclatural problems, at both the generic and specific levels, to be found in any group of Hawaiian birds. Numerous authors, particularly in the earlier literature, maintained *Hemignathus* and *Heterorhynchus* as distinct genera (e.g., Rothschild 1893d, Bryan 1901). Since the revision of Amadon (1950), however, *Heterorhynchus* has usually been treated as a subgenus of *Hemignathus* (e.g., Greenway 1968, American Ornithologists' Union 1983). As we shall see, this is nomenclaturally incorrect, as both generic names have the same type species.

Pratt (1979) greatly expanded the genus *Hemignathus* by including in it the amakihis (*Loxops virens, L. parva,* and *L. sagittirostris* sensu Amadon 1950), which he placed in the subgenus *Viridonia* Rothschild 1892). At the same time he continued to

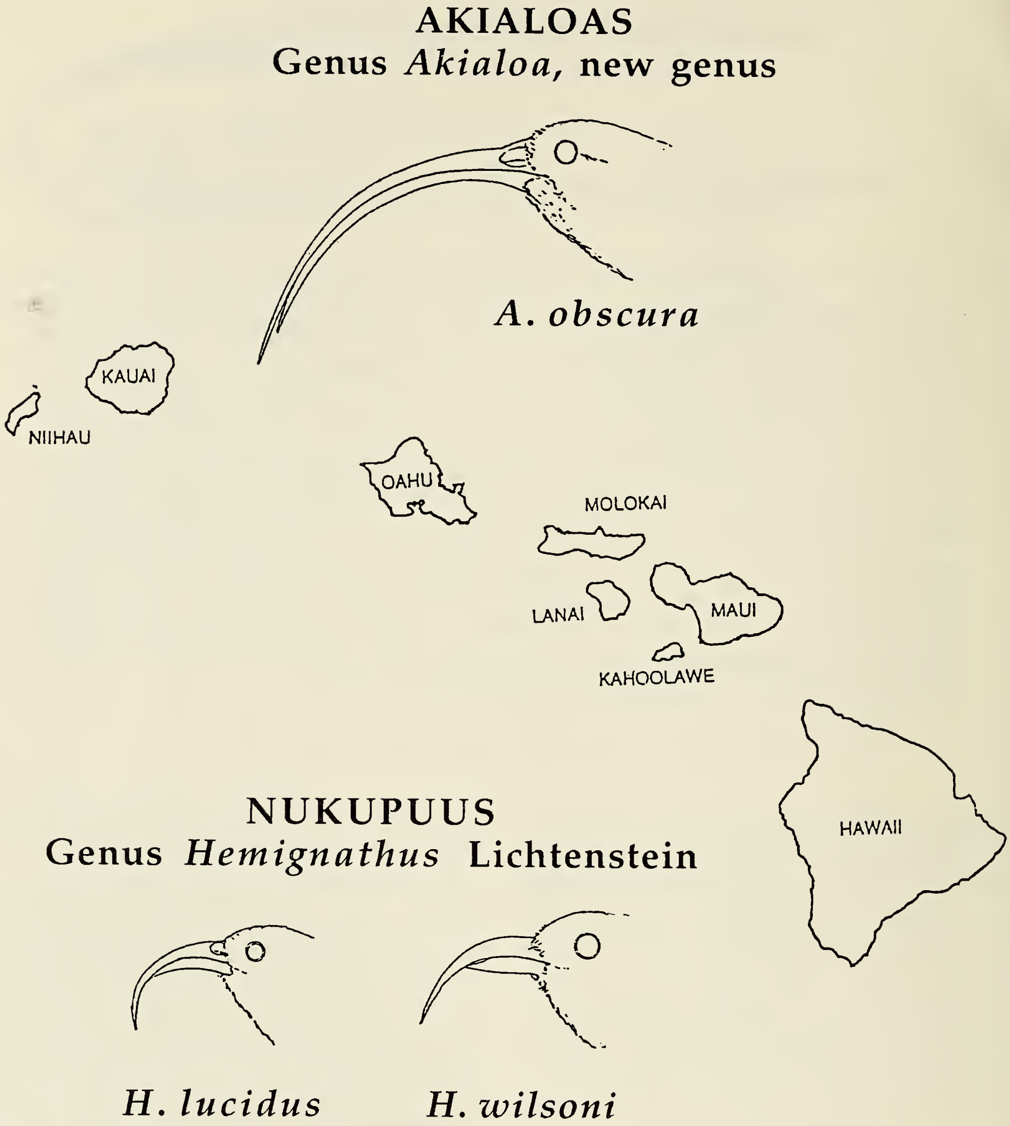

Fig. 1. Map of the Hawaiian Islands with outlines of head and bill (from Bryan 1901) of a representative akialoa (*Akialoa obscura* = *Hemignathus obscurus* auct.) and of the nukupuus *Hemignathus lucidus* and *H. wilsoni.*

recognize *Hemignathus* and *Heterorhynchus* as separate subgenera.

Although the portion of Pratt's dissertation pertaining to this problem remains unpublished, his nomenclature was adopted first by Berger (1981) and then by the American Ornithologists' Union (1983) in their Check-list, whereupon Pratt's treatment became entrenched among non-taxonomists without any consideration having been given to its merits. This lumping created a many new combinations that had never appeared in the entire history of Hawaiian ornithology, including two homonyms of well-known species that had to be re-named (Pratt 1979a, 1979b, 1989; Olson & James 1988). Based on myology and osteology (Olson & James 1988), we would maintain the amakihis, akialoas, and nukupuus as at least three genera, with the amakihis being referred to the genus *Loxops* Cabanis. This is supported by recent genetic studies, with the proviso that the the akialoas have not yet been analyzed and that the amakihis may need to be further split (R. Fleischer, pers. comm.) It is not our intention to deal with systematic problems here, but rather to clear up some long-festering points concerning the nomenclature that should be used for these birds by those who would place them in separate generic-level taxa.

The Type Species of *Hemignathus*

The genus *Hemignathus* as first proposed by Lichtenstein (1839) included both an akialoa and a nukupuu. The specimens available to him were all from Oahu, collected by Ferdinand Deppe (Olson & James 1994a). The akialoa he considered to be the same as that of Hawaii (*Certhia obscura* Gmelin), whereas the nukupuu was obviously a new species and was given the name *Hemignathus lucidus.*

Stejneger (1887:93, footnote) and Rothschild (1893d:87) each tried to argue that Lichtenstein's wording made *H. obscurus* the type of the genus *Hemignathus.* Mathews (1930) merely followed Rothschild, as apparently did Amadon (1950:168), who stated that the type was *Certhia obscura* by "original designation." The following is what Lichtenstein wrote (translation from Rothschild 1893d:87) that bears on the matter:

> Latham describes in the genus *Certhia* a species from the Sandwich Islands, which struck him particularly in so far that the lower mandible was a quarter of an inch shorter than the upper. This species was included in the system under the name of *Certhia obscura*; but it is so distinct from all the different subgenera into which this group has rightly been divided, that one is forced to make a new genus for it, for which I propose the name [*Hemignathus*].

All this says is that of the previously recognized species assigned to *Certhia,* Lichtenstein considered *C. obscura* to differ to the extent that it must be put in another genus. He did not say that *C. obscura* was the only species to be included in this genus, as indeed he also placed his new species *H. lucidus* in it, and he did not specifically indicate either species as the type. "Mention of a species as an example of a genus or subgenus" does not constitute a type designation (ICZN 1985:Article 67a). Shortly after Lichtenstein's publication, G. R. Gray (1841) clearly designated *H. lucidus* as the type of the genus *Hemignathus.* Except for the authors mentioned above, all other authorities appear to have accepted this designation (e.g., Sharpe 1885, Bryan & Greenway 1944, Greenway 1968, American Ornithologists' Union 1983).

In the meantime, another generic name pertinent to these birds appeared nearly simultaneously with Lichtenstein's when Lafresnaye (1839) described the Oahu Nukupuu from specimens brought back by the voyage of the *Venus* as *Mellithreptus* (s.g. [subgenus] *Heterorhynchus*) *olivaceus.* Although several subsequent authors were confused as to the identity of Lafresnaye's species *olivaceus,* and even used this name for the Akiapolaau (*Heterorhynchus wilsoni* Rothschild) of Hawaii, it was the same taxon as Lichtenstein's *lucidus* (Newton 1887, Bangs 1930).

The species question aside, the name *Heterorhynchus* was seized upon and used by most subsequent authors, either as a genus or a subgenus, to distinguish the nukupuus from the akialoas. Stejneger (1887:93) appears to be the first to have articulated this sentiment:

> Generally this bird [the Kauai Akialoa] is referred to the same genus as *Hemignathus lucidus,* but with doubtful propriety I think. The bills in this group of birds have served as the chief character for the establishment of genera, and if we recognize more than one genus of Drepanine birds, the two species of *Heterorhynchus* with their unique bills should certainly stand alone.

Virtually all authors since have maintained the akialoas and nukupuus as distinct genera or subgenera, under the names

Hemignathus and *Heterorhynchus,* respectively, while ignoring the fact that these generic-level taxa have the same type species.

A half-century ago, Bryan & Greenway (1944:128), who merged the two groups, succinctly summarized the nomenclatural consequences for those who would separate them:

> In our opinion, the group with long lower mandibles and those with short lower mandibles may well be considered as congeneric. If it is desired to separate them generically then the former will require a new generic name and the latter (heretofore known as Heterorhynchus[)] will have to be called Hemignathus, since the two groups, as named heretofore, have the same type as designated by Gray and Lafresnaye. Rothschild's arguments [1893d:79] have no force under the rules of zoological nomenclature (Art. 30, II, g).

The message apparently never sank in. In the influential Check-list of Birds of the World, Greenway (1968), who must have forgotten what he had written previously, maintained *Hemignathus* and *Heterorhynchus* as separate subgenera within the genus *Hemignathus,* and then dutifully listed *H. lucidus* as the type for each! The equally influential Check-list of North American Birds (American Ornithologists Union 1983) is a later reference that acknowledges that these two generic-level taxa have the same type species.

So the fact remains that if one wishes to separate the akialoas nomenclaturally, a new generic-level name will be required. After an exhaustive search of the literature of Hawaiian birds, we found that there is no previously existing supraspecific name available that would be desirable to use. One very obscure name that still seems to be in limbo needs to be disposed of, however. This is the genus *Falcator* Temminck, 1821: 108, proposed in a footnote to an article otherwise totally unconnected to Hawaii: "Ce nouveau genre se compose des *Certhia pacifica, obscura, coccinea,* et *falcata* de Linn. Gmel."

G. R. Gray (1869), Giebel (1875), and Dubois (1901) all listed *Falcator* as a synonym of *Drepanis* Temminck, 1820 (type *Certhia pacifica* Gmelin by designation of Gray, 1840), doubtless because it comprised the very same species that were included in that genus as proposed by Temminck himself (1820) the preceding year. The diligent Richmond (1908) uncovered the name *Falcator,* but merely listed the species included by Temminck without mentioning a type designation. Dubois (1901), by assigning all the other species originally included in *Falcator* to other genera, would have made *Certhia pacifica* the type of the genus by elimination, but this does not constitute type fixation (ICZN 1985: Article 69b). If *Falcator* were restricted to the Hawaii Akialoa, which is one of the included species, this could have very undesirable consequences if the akialoas were combined with practically any other taxon because the virtually unknown name *Falcator* would have priority over all genera of Drepanidini except *Drepanis* Temminck, 1820, and *Psittirostra* Temminck, 1820. To eliminate any potential problems that the name might thus cause, we formally designate *Certhia pacifica* Gmelin as the type species of *Falcator* Temminck, 1821, so that *Falcator* then becomes a pure objective synonym of *Drepanis* Temminck, 1820.

Dates of Publication of *Hemignathus* and *Heterorhynchus*

The competing generic and specific names *Hemignathus lucidus* Lichtenstein versus *Heterorhynchus olivaceus* Lafresnaye are each now usually cited with the date of 1839 (e.g. Greenway 1968). In attempting to resolve the nomenclature of this group it thus becomes important to try to determine why Lichtenstein's names have traditionally been given precedence and whether they actually have priority over those of Lafresnaye.

Lichtenstein's paper is in the Abhandlungen of the Berlin Academy of Science for 1838, a serial that was traditionally published later than the year indicated. The announcement at the beginning of Lichtenstein's paper, which is mainly about California birds, states that it was read before the Academy on 27 June 1837. Hanna (1931) has pointed out that there was no meeting on that date and that the reading must have taken place on 25 May 1837. But Lichtenstein cannot have communicated anything about Hawaiian birds at that time because the collector Deppe, from whom he obtained them, did not return to his homeland until 1838, as stated elsewhere in the Lichtenstein paper (p. 448). Some early authors, however, have cited Lichtenstein's names as dating from 1838 or even 1837, both of which are shown here to be erroneous.

The introductory material at the front of the Abhandlungen for 1838 has a title page that is dated 1839 and contains an annual report that carries through to the end of 1838. The volume was issued in three separate sections: Physikalische (in which Lichtenstein's paper appeared); Mathematische, and Philologische und Historische Abhandlungen. Each of these parts has a separate title page, each of which is dated 1840. Thus the ostensible date of publication of Lichtenstein's paper is 1840, which Hanna (1931) thought to be correct. We have found no unequivocal evidence, such as library stamps, correspondence, or other archival sources that mention the receipt or appearance of this publication. We examined copies in the Vetenskaps Akademiens Bibliotek in Stockholm, the Linnean Society of London, the Smithsonian Institution, and the British Museum (Natural History) but none is stamped with a contemporary date of receipt. There is a pencilled annotation in the British Museum copy, however, to the effect that the paper by Lichtenstein (and three others mentioned) was published in 1839 and that the proper citation should be "1838 (1840) [1839]," meaning, we presume, that the volume is for 1838, with the ostensible date of 1840, but the actual publication date of 1839.

Enquiries made on our behalf at the Berlin Botanical Museum brought the response from the librarian there "Artikel ersch. 1840!" but with no further documentation (received in litt. from Harald Pieper, Kiel), so that this may have been based on the title page from the Physikalische Abhandlungen. What seems to be the most definitive source we have uncovered is an extensive review of the publication and contents of the Abhandlungen der Berliner Academie in the Isis von Oken (1844, Heft XI: columns 842–854) in which the years of appearance of the volumes is as follows: 1832=1834, 1833=1835, 1834=1836, 1835=1837, 1837=1839, 1838=1839, 1839=1841, 1840=1842, 1841=1843. Thus the volumes consistently ran two years behind except 1838, which supposedly appeared in 1839, with no volume being published in 1840. One wonders whether even this seemingly definitive indication of an 1839 publication date for the 1838 volume may be due to a misprint, as it seems unusual to have two volumes of this normally tardy serial appearing in the same year. One would assume that if the 1838 volume were indeed issued in 1839, it would have been late in the year.

We provisionally accept the 1839 date from the evidence of the review in Isis von Oken and the annotation in the British Museum copy, each of which could be equivocated. There is certainly no available evidence by which a more specific date can be refined, so that according to the rules of nomenclature (ICZN 1985: Article 21c) the date of Lichtenstein's paper must be fixed as the last day of the year—31 December 1839. Otherwise we must resort to the ostensible year of publication of 1840, likewise with the date of 31 December.

The Magasin de Zoologie, in which Lafresnaye's name *Heterorhynchus olivaceus* appeared, was issued in two series ("sections") of livraisons—the first for vertebrates and the second for invertebrates. The original wrappers for the first section that are bound with the volumes in the Smithsonian Institution Libraries have " Livraison.—Année 18 " set in type, with the number of the livraison and the year being written in ink by hand. The numbers of the plates in each livraison were also indicated by hand beside the appropriate printed categories of mammals, birds, reptiles, and fishes. According to the wrappers, the text and plate (10) for *Heterorhynchus olivaceus* appeared in the sixth and final livraison for 1839, along with plates 7–9 of birds (all of Lafresnaye), and 11–19 of mammals. Lafresnaye's plates and the recto pages of text bear the date 1839. Each of Lafresnaye's contributions in the sixth livraison bears the date October 1839 on the verso, after his signature, but this is obviously the date the manuscripts were completed, because the seventh livraison, with the wrapper dated 1840, contains one plate (11) and text by Lafresnaye which still has October 1839 on the verso, but 1840 on the recto and the plate.

The only contemporary source that we have found that might bear on the date of issue of one of the livraisons for 1839 is a notice in the Edinburgh Journal of Natural History for February 1840, which states: "The 7th Number, for the year 1839, of this elegant work has just appeared, and is occupied with a description" by Geoffroy Saint-Hilaire of three new genera of birds from Madagascar. This is puzzling, because according to the wrappers in the copy we examined, that article was in the fifth livraison, not the seventh, the latter having the date 1840. An additional consideration is that the livraisons may not have been issued in sequence. In a card file concerning dates of publication that was assembled by C. W. Richmond in the Division of Birds, Smithsonian Institution, there is an otherwise undocumented note saying "Mag. de Zool. Livr. 1–15 1840—Livr. 17–18 1841." Thus we have two extremely equivocal sources that suggest that the date of publication of *Heterorhynchus* may in fact be 1840.

Nevertheless, all references that we have seen give the date of publication of *Heterorhynchus olivaceus* as 1839. The original description of *Ampelis* (=*Xipholena*) *lamellipennis* Lafresnaye, which immediately preceded that of *H. olivaceus* and was issued in the same livraison, is also always cited with the date 1839 (e.g., Sclater 1883; Hellmayr 1929). Therefore, in the absence of concrete evidence to the contrary, we consider that the year of publication of *Heterorhynchus olivaceus* must be taken as 1839, but in the absence of further evidence, its date of publication must also be fixed as 31 December of that year. Thus, for purposes of nomenclature, the names *Hemignathus* and *Heterorhynchus* are here regarded as having been proposed simultaneously so that their relative precedence must be determined according to the first reviser principle (ICZN 1985: Article 24).

Hemignathus has traditionally been given precedence over *Heterorhynchus* throughout the literature of Hawaiian birds. This doubtless arose largely through various authors incorrectly taking the date of publication of *Hemignathus* as being 1838 (e.g., Sharpe 1885). Gray (1841) appears to be the first author to have formally synonymized *Heterorhynchus* with *Hemignathus,* but he cannot be considered to be the first reviser because he gave the latter the publication date of 1838 and therefore did not regard the names as having been published simultaneously.

There are other historical reasons why *Hemignathus* was given precedence over *Heterorhynchus.* When Lafresnaye published his description of *Heterorhynchus olivaceus,* it apparently created bad blood between him and the naturalists of the voyage of the *Venus,* who had collected the species and had deposited specimens at the Paris museum in August 1839 (Neboux 1840). Lafresnaye (1840) protested that he had purchased his specimen from a dealer named Dupont (who we imagine had probably received material originating in the voyage of the *Venus* as well) and had been ignorant of the fact that the museum had received the same species. He still maintained that the date of publication was October 1839, but went on to say that the ornithologist Natterer, when visiting Lafresnaye the previous month (October 1840), had informed him that the bird had already been described in Germany or Russia under a different generic name, which must be an allusion to the Lichtenstein publication. What Natterer's reasons were for thinking that Lichtenstein's publication had priority are no longer clear, there being now no copy of that volume of the Abhandlungen in the library in Vienna where Natterer worked (Ernst Bauernfeind, Naturhistorisches Museum Wien, in litt. 28 Dec 1994). It should be recalled that Lafresnaye was used to having his names pre-empted because, as Bangs (1930:152) has remarked:

> Lafresnaye lived in the country, in those days a real journey away from Paris, and, therefore, was often just a little later than some one else in securing some new bird. Also, I fancy, published descriptions were slow in reaching him. Several times I have read a complaint to that effect written by him on a label.

This may explain why Lafresnaye himself may have been willing to relinquish further claim to the priority of his name.

Some years later, in the official report on the zoology of the voyage of the *Venus,* the old rivalry with Lafresnaye resurfaced when Prévost and des Murs (1849) obviously set out to administer the 'coup de grâce' to *Heterorhynchus.* They titled a separate section of their account of the birds of the voyage "Notice sur le Genre Hemignathe (*Hemignathus,* Lichtenstein), (1837). *Heterorhynchus* (La Fresnaye) 1839." Here (p. 183) they advance the 1837 date that part of Lichtenstein's publication was read before the Academy, but then take Lafresnaye to task for having "forgotten" that *Hemignathus* had already been published in 1838 (pp. 185–186). And yet a bit further on they repeatedly give the publication date as 1839 (pp. 191–192), including in their account of the "Hémignathe brillant," where they list Lafresnaye's citation after Lichtenstein's. This order of precedence has been followed ever since. Although it is not at all certain in which year Prevost and Des Murs (1849) actually believed *Hemignathus* to have been published, they are the first authors to associate it with the year 1839 and simultaneously to give it precedence over *Heterorhynchus,* so perhaps they can be considered first revisers.

Should our activity in this connection make us the first revisers, we follow tradition and accord precedence to *Hemignathus.* This has the unfortunate consequence of having this name, long associated with the akialoas when those birds were separated generically, attach to the nukupuus. But it has the advantage of conserving the well-known name *lucidus* Lichtenstein over the long unused name *olivaceus* Lafresnaye. Furthermore, the scanty and inconclusive evidence as yet available suggests that if further information regarding dates of publication should surface, *Hemignathus* is the name more likely to have actual priority.

The Name for the Akialoa of Oahu

G. R. Gray (1859:9), who long believed the Hawaii Akialoa to be the female of the Iiwi, *Drepanis* (*Vestiaria*) *coccinea,* named a new species of drepanidine as *Drepanis* (*Hemignathus*) *ellisiana* based on four references, including Lichtenstein (1839), who had included a specimen from Oahu under the name of the Hawaiian bird, *H. obscurus* (Gmelin). As was later established, Gray's species was clearly a composite, as the other three references pertained to the bird from Hawaii (=*H. obscurus*). Nevertheless, Gray's intention should have been clear, as he gave the "habitat" of his new species as Oahu, and Lichtenstein's reference was the only one unequivocally linked to that island.

Wilson (1889), in his review of *Hemignathus,* described the Oahu species as *H. lichtensteini,* based on the same specimen in Berlin that was figured by Lichtenstein

(1839), but without reference to Gray's *H. ellisiana.* The following interchange between the two rival camps engaged in describing new Hawaiian birds at the end of the 19th century provided as much sound as light on the matter, but summarizes the opinions that have been expressed.

> G. R. Gray, who in more than one case erroneously considered the green birds to be the females of the red, referred *H. obscurus* partly to the female of *Vestiaria coccinea,* partly to his *Drepanis ellisiana,* which, therefore, must rank as a synonym. Wilson & Evans (1892:68).

> Mr. Wilson places Gray's *Drepanis ellisiana* as a synonym under *Hemignathus obscurus* (Gmel.), and gives as his reason that Gray partly referred *H. obscura* to the female of *Vestiaria coccinea* and partly to his *Drepanis ellisiana.* . . . This is entirely erroneous, and proves that Mr. Wilson misquoted Gray, for the latter states [1859:9] that *Certhia obscura,* Gm., is the female of *Vestiaria coccinea,* while *Certhia* (*Hemignathus*) *obscura* Licht. nec Gm., is his *Drepanis ellisiana*; therefore I regret to have to reduce Mr. Wilson's name, *Hemignathus lichtensteini,* to synonymic rank and to reinstate Gray's *ellisiana.* Rothschild 1893d:88.

> Mr. Rothschild [ibid.] has referred this species to the "*Drepanis* (*Hemignathus*) *ellisiana*" of Gray [1859: 9], which I have already correctly quoted as a synonym of *H. obscurus.* It is pretty clear that Mr. Gray never saw a specimen of either, and it is absolutely certain that three out of the four authorities cited by him refer to *H. obscurus.* Vieillot, the first of them, as I have already shown, figured [Audebert & Vieillot 1802: pl. 53] the very specimen, now at Liverpool, which was formerly in the Leverian Museum, and actually the type of Latham's description, on which was founded the *Certhia obscura* of Gmelin, and hence the *H. obscurus* of modern ornithologists. Similarly the bird figured in Ellis's unpublished drawings (no. 28), which from the name used by Gray is doubtless to be regarded as the type of his supposed species, is most unquestionably *H. obscurus,* as anyone who examines the drawing in the British Museum may satisfy himself. The last of the authorities cited by Mr. Gray is Cassin, and he quotes Peale as saying that the species he speaks of was obtained in "Hawaii only," and that according to his observations it did "not inhabit Oahu; it was accordingly also *H. obscurus*; and the mere fact of Mr. Gray's mistakenly referring Lichtenstein's figure, and assigning Lichtenstein's locality, to the so-called "*Drepanis* (*Hemignathus*) *ellisiana*" cannot remove the incontestable objection that his other references show it to be but a synonym of *H. obscurus.* Wilson & Evans (1894: 65–66).

Both *ellisiana* and *lichtensteini* have continued to be used for the Oahu Akialoa, with the former generally being favored, but without any clear resolution of the matter. Because Gray's name *ellisiana* is a composite, its disposition must be determined by designation of a lectotype, which none of the authors quoted above really do. The fact has been overlooked that Gray himself appears to have resolved the matter long before, as in his Hand-list (Gray 1869:114) under *Drepanis ellisiana* he gave only the Lichtenstein reference, with "*obscura,* V. O. D. t. 53?" as a dubious synonym, the latter being a reference to Audebert & Vieillot (1802), which, as seen above, was shown by Wilson & Evans to refer to the Hawaii Akialoa. Incidentally, this reference (Gray 1869) shows that Bryan (1901:306, footnote) erred in considering Gray's original query (1859) by the Vieillot work to refer to the plate number rather than the identity of the species, which was Bryan's reason for favoring *lichtensteini.* Thus, we consider that Gray's (1869:114) subsequent action restricted his species *ellisiana* to Lichtenstein's (1839) description of a bird from Oahu, which his original designation of Oahu as the type locality also supports. In the event that others might consider that this still does not constitute proper selection of a lectotype, we specifically designate that of the four references originally given by Gray (1859), the lectotype is the bird from Oahu figured and described by Lichtenstein (1839). Therefore we use Gray's name *ellisiana,* with *H. lichtensteini* Wilson as a synonym, for the Oahu Akialoa.

The Name for the Akialoa of Kauai

The Kauai Akialoa has been widely but unjustly known under the name *Hemignathus procerus* Cabanis. The first specimens to be studied scientifically were collected by Valdemar Knudsen and sent to the Smithsonian Institution. They were described by Stejneger (1887), who, in the absence of comparative material, referred them to *Hemignathus obscurus.* On the basis of specimens he collected himself, Wilson (1889) differentiated the bird from Kauai and honored Stejneger's contribution by naming it *Hemignathus stejnegeri* in a publication issued 1 November 1889. In a postscript (p. 402), Wilson added: "Prof. Möbius [Director of the Royal Zoological Collection at Berlin] has also had the goodness to transmit two specimens of '*Hemignathus procerus,* Cab[anis]. n. spec.' I am not aware of any published description of this species; but the specimens sent seem to be immature males of that which I have above called *H. Stejnegeri.*"

At the Berlin Museum, Jean Cabanis was not idle and proceeded to name the same taxon himself, based on the forementioned specimens from Kauai purchased from a dealer, J. Wentscher, on 2 June 1887, that were doubtless also collected by Valdemar Knudsen (Olson & James 1994a). Cabanis's description of *Hemignathus procerus* was published in the October 1889 issue of *Journal für Ornithologie,* a periodical that Cabanis initiated and edited for forty years. During that time the *Journal* was notorious for appearing considerably later than the stated date of publication, which gave rise to numerous complaints in a day when new taxa were being described at a rapid pace and the law of priority was respected. By 1876 (Anon. Nature 14:309) Cabanis was a "well-known sinner" at the "evil practice" of antedating his Journal, and he must have put this practice in effect at least as early as 1856 (Peters 1932). It continued for the rest of his tenure, despite continual protestations from his colleagues. In the present instance, the original wrappers (copy in Smithsonian Institution Libraries) show that the issue in which the name *Hemignathus procerus* was proposed could not have appeared before January 1890. In a review in which the problem of antedating the Journal für Ornithologie is addressed at length (Anon. 1891, Ibis, ser. 6, 3:616), it was shown that the number in question was not received by the Zoological Society of London until 11 July 1890, long after Wilson's name had been published. In this connection, it is worth recording that Stejneger (1890), in a report that was issued 8 March 1890, referred two new specimens of Kauai Akialoa to Wilson's species *H. stejnegeri,* with no mention of *H. procerus,* so that Wilson's paper was obviously already at hand, whereas Cabanis's was not. Likewise, Wilson (1890:191) in the Ibis for April 1890 (received at the Smithsonian on 21 April) again states that he had not seen a description of *H. procerus,* which he regarded as "identical with *H. stejnegeri.*"

Doubtless realizing at the time that his name stood to be forestalled, Cabanis (1890: 331) added a footnote to his description to the effect that the name *H. procerus* had first been published in the newspaper Vossische Zeitung for 14 September 1889. We can only speculate that he may have been comforted by the likelihood that few taxonomists would be able to check this obscure reference, for, as we shall see, the contents thereof would not have been regarded as enhancing either Cabanis's reputation or the validity of his name.

It is certain that Wilson had not seen the Vossische Zeitung when he wrote that "the species *is said* to have been described" therein (Wilson & Evans 1892:61, footnote—emphasis added). Furthermore, the carefully chosen wording employed in Wilson & Evans (1892:61) in relating the events surrounding the description of this bird make it clear that Cabanis had exercised himself considerably to attach his own name to the Kauai Akialoa:

> As the result of inquiry regarding the various species of the genus in the Berlin Museum, information was received through Professor Möbius that Professor Cabanis had come to a similar conclusion [that the Kauai birds were distinct from *H. obscurus*] on inspection of the specimens there, and had forestalled

> my proposed title by a few weeks; so that I must at once acknowledge his activity in securing priority for his name *H. procerus.*

This concession of priority to *H. procerus* can only have been on the strength of Cabanis's citation of the Vossische Zeitung article, because it must have been well known at the time that the description in Journal für Ornithologie was published after Wilson's name had appeared. Yet if any subsequent researcher availed himself of the newspaper article, he kept his knowledge to himself. We were able to obtain a photocopy of the page containing the first use of the name *Hemignathus procerus,* which appeared in No. 429 of Vossische Zeitung, dated 14 September 1889, in a notice entitled "Allgemeine deutsche ornithologische Gesellschaft," being the minutes of the meeting of that society held 9 September 1889. The pages are unnumbered, but the notice occupies about two-thirds of the middle column of the page on which it occurs and is initialled "P. M.", for Paul Matschie, who was secretary of the D.O.G. from 1894 to 1907 (Prestwich 1958). The text of the portions of this notice in the original German and in English translation that pertain to Cabanis's discussion of Hawaiian birds follows in it's entirety.

> Herr Prof. Dr. J. Cabanis beschrieb eine neue Abart eines merkwürdigen Vogels von den Sandwich inseln. 1837 hatte der bekannte Botaniker Doppe [sic], der lange in Mexiko gesammelthatte, einige merkwürdige kleine, sehr krummschnäblige Vögel mitgebracht, deren feuerrothe Federn den Eingeborenen zur Anfertigung von Mänteln dienen. Die Thierchen haken von unten mit den fast halbkreisförmigen Schnabel in den Kelch der Blüthen, um so zu den Dem Blüthensaft nachgehenden Insekten zu gelangen. Die Sandwichinseln scheinen, ähnlich wie Neu-Zeeland, Madagaskar und Australian, einen eigenen Schopfungsheerd zu bilden und weisen ganz wudersame Vogelformen auf. Herr Cabanis nannte die vorliegende Art *Hemignathus procerus.*

> Herr Prof. Dr. J. Cabanis described a new variety of a remarkable bird from the Sandwich Islands. The well-known botanist Doppe [sic = Deppe], who was collecting for a long time in Mexico, brought along, in 1837, a few remarkable small birds with a strongly curved beak, which provide the aboriginals with bright red feathers that are used for making cloaks. The creatures peck the calyx of blossoms from below with their almost semicircular beak to reach the nectar-seeking insects. The Sandwich Islands, like New Zealand, Madagascar and Australia, appear to constitute a separate center of creation and show wonderful forms of birds. Herr Cabanis called the species in question *Hemignathus procerus.*

Cabanis's claim to priority for *H. procerus* based on the above notice thus falls to the ground. Probably through Matschie, Cabanis's message had become at best garbled, with some of his introductory remarks about drepanidines being combined with the mention of his new name. The only bird described here possessed a "strongly curved beak" and bright red feathers, which can only apply to the Iiwi, *Vestiaria coccinea* (Forster). Furthermore, the mention of Deppe is irrelevant to the description of a bird from Kauai, because Deppe collected only on Oahu (Olson & James 1994a). By strict application of the rules of nomenclature, *Hemignathus procerus* Cabanis (in Matschie 1889) could be considered a junior synonym of *Certhia coccinea* Forster, 1781. Nevertheless, because this was clearly not Cabanis's intent, a more charitable assessment would be to regard the first use of *Hemignathus procerus* as a nomen nudum. It is also a nomen nudum as published by Schalow on or after 7 November 1889, in another account of the meeting of the Gesellschaft (Schalow 1889). As we have seen, it was also published twice as a synonym by Wilson (1889, 1890), and only months later was the name *H. procerus* ever associated with a legitimate description. Wilson's name *Hemignathus stejnegeri* clearly has priority over *H. procerus* Cabanis and we have reverted to it.

The Resulting Nomenclature of Akialoas and Nukupuus

The nukupuus consist of two very distinct species (Olson & James, 1994b), the Nukupuu proper (*Hemignathus lucidus*), and the Akiapolaau (*Hemignathus wilsoni*). There are three named taxa of the former that are now considered to be subspecies of a single species, a treatment for which we can as yet offer no contrary evidence, as the only stated differences are minor plumage variations in adult males, and there is some doubt that a specimen of adult male even exists for the Oahu bird (there may be size differences between the forms, however—Thane Pratt, in litt.). Pending more detailed revisionary work we continue to rank these taxa as subspecies.

Hemignathus Lichtenstein

Hemignathus Lichtenstein, 1839 (31 December). Type, by subsequent designation (Gray 1841), *Hemignathus lucidus* Lichtenstein. The name has precedence over *Heterorhynchus* Lafresnaye according to the first reviser principle.

Heterorhynchus Lafresnaye, 1839 (31 December). Type, by monotypy, *Heterorhynchus olivaceus* Lafresnaye 1839 = *Hemignathus lucidus* Lichtenstein.

Hemignathus lucidus lucidus Lichtenstein

Oahu Nukupuu

Hemignathus lucidus Lichtenstein, 1839 (31 December) :451. The name has precedence over *Heterorhynchus olivaceus* Lafresnaye according to the first reviser principle.

Heterorhynchus olivaceus Lafresnaye, 1839 (31 December):text accompanying plate 10.

Distribution and status.—Island of Oahu, extinct, evidently fairly abundant in 1837 but not collected thereafter.

Hemignathus lucidus hanapepe Wilson

Kauai Nukupuu

Hemignathus hanapepe Wilson, 1889:401.

Distribution and status.—Kauai, where now presumed extinct, there having been no sightings since the 1970's.

Hemignathus lucidus affinis Rothschild

Maui Nukupuu

Hemignathus affinis Rothschild 1893a:112.

Distribution and status.—Known historically only from the upland forests of Maui, where it may still exist in extremely low numbers.

Hemignathus lucidus subspp. indet.

A historic specimen of this species, of indeterminate race, was collected on the island of Hawaii by the U.S. Exploring Expedition in 1840 or 1841 (Olson & James 1994b), but the species was never again taken on that island. A fossil almost certainly of this species was also recovered from sand dune deposits on Molokai (Olson & James 1994b).

Hemignathus wilsoni (Rothschild)

Akiapolaau

Hemignathus olivaceus.—Wilson, 1889 (nec *Heterorhynchus olivaceus* Lafresnaye—Wilson was the first to recognize this species but erred in thinking that Lafresnaye's name applied to it).

Heterorhynchus wilsoni Rothschild, 1893d: 95 (key), 97.

Hemignathus munroi Pratt, 1979b:1581 (new name for *Heterorhynchus wilsoni* Rothschild, 1893d, preoccupied by *Himatione wilsoni* Rothschild, 1893c, if these taxa are regarded as congeneric).

Distribution and status.—Known only from the island of Hawaii, where it is considered endangered but is locally distributed in fair numbers.

As we have detailed above, a new generic name is needed for the akialoas. Because there has already been so much nomenclatural confusion generated with regard to these birds, we propose to use the Hawaiian name, *akialoa,* which is the only name now in use for these birds that conveys an unequivocal meaning, as a formal generic name. The four historically known taxa of akialoas were treated as full species in the early literature, but have also been listed as subspecies of a single species (e.g., Bryan & Greenway 1944). Amadon (1950) divided them into two species, keeping the Kauai birds separate because of their large size and treating the birds of Oahu and Lanai (known from a total of 5 specimens) as subspecies of *obscurus* of Hawaii. We find that the birds of Oahu and Lanai are closer in size to those of Kauai, whereas *obscurus* of Hawaii is distinctly smaller than any of the others. The amount of variation between the four populations seems too great to be encompassed by a single species, but it is not yet clear how many species should be admitted, nor what the contents of each should be. Furthermore, we now know that the historically known akialoas were sympatric with another fossil species at least on Kauai and Oahu (James & Olson, 1991), two fossil species of akialoa appear to have been sympatric on Maui (James & Olson, unpublished data.), and yet another unnamed large species was sympatric with *obscurus* on Hawaii (unpublished data). Until these systematic questions can be resolved, for nomenclatural purposes, we provisionally treat each taxon of akialoa as though specifically distinct.

Akialoa, new genus

Type species.—*Certhia obscura* Gmelin, 1789.

Etymology.—The Hawaiian name for these birds. Hawaiian words do not have gender but as the present name ends in "a" we arbitrarily treat it as feminine. Of the trivial epithets now in use, this effects the spelling only of the type species, whose original name, *Certhia obscura,* is feminine in any case.

Included species.—The following are the new combinations resulting from the introduction of the new generic name, with their principal synonyms:

Akialoa obscura (Gmelin), new combination

Hawaii Akialoa

Certhia obscura Gmelin, 1789:470.

Distribution and status.—First collected on the third voyage of Captain James Cook in 1779 near Kealakekua Bay, island of Hawaii (Medway 1981). It was collected rather frequently on that island in the 19th century but became extinct about 1900 (Scott et al. 1986).

Akialoa lanaiensis (Rothschild), new combination

Maui Nui Akialoa

Hemignathus lanaiensis Rothschild, 1893b: 24.

Distribution and status.—Known from three skin specimens taken in 1892 on the island of Lanai; never taken again. Extinct. Fossils of akialoas, most likely of this taxon, have been collected on Molokai and Maui (Olson & James 1982, James & Olson 1991 and unpublished data).

Akialoa ellisiana (Gray), new combination

Oahu Akialoa

Drepanis (*Hemignathus*) *ellisiana* Gray, 1859:9.

Hemignathus lichtensteini Wilson, 1889: 401.

Distribution and status.—This taxon was long believed to be known only from the holotype in the Berlin Museum collected in the Nuuanu Valley, Oahu, in January 1837 by Ferdinand Deppe (Olson & James 1994a). We have identified a second specimen in the collections of the Philadelphia Academy taken at the same time and place by J. K. Townsend. The species was not encountered on Oahu after 1837 and is now extinct.

Akialoa stejnegeri (Wilson), new combination

Kauai Akialoa

Hemignathus stejnegeri Wilson, 1889:400.
Hemignathus procerus Cabanis, 1890:331.

Distribution and status.—Known from many specimens taken on Kauai in the 19th century. The last specimen was obtained in July 1960 (Richardson & Bowles 1964), the last observation was in 1965, and the species is now considered to be extinct (Scott et al. 1986).

Akialoa upupirostris (James & Olson), new combination

Hoopoe-billed Akialoa

Hemignathus upupirostris James & Olson, 1991:60.

Distribution and status.—Not known historically. The species was described from Holocene fossils from Makawehi dunes, Kauai, and from Barbers Point, Oahu.

Acknowledgments

For bibliographic assistance of various sorts we are most grateful to Harald Pieper (Zoologisches Museum, Kiel—especially for his providing a photocopy of a crucial page from Vossische Zeitung), Leslie Overstreet (Smithsonian Institution Libraries, Washington), Ernst Bauernfeind (Naturhistorisches Museum, Vienna), Gina Douglas (Linnean Society, London), William Lindsay (Natural History Museum, London), and Per Ericson (Swedish Museum of Natural History, Stockholm). We also thank Andrzej Elzanowski for translating the passage from Vossische Zeitung, M. Ralph Browning for supplying numerous references to the problems of dating the Journal für Ornithologie, and Richard C. Banks for commenting on several versions of the manuscript.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(3):388–391. 1995.

A new lizard of the genus *Sphenomorphus* (Reptilia: Scincidae) from Mt. Kitanglad, Mindanao, Philippine Islands

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Abstract.—A new lizard, *Sphenomorphus kitangladensis,* is described from Mindanao, Philippine Islands. It is in Group 3, the *Sphenomorphus laterimaculatus* Group. It differs from other species of this group in the separation of the anterior loreal from the labials and, except for *Sphenomorphus acutus,* the smaller eye relative to snout-length. In color pattern and general appearance, this species is most similar to *Sphenomorphus leucospilos* and *S. laterimaculatus* from Luzon Island; but differs from the former in the greater number of scale rows between parietals and base of the tail, and from the latter in the lower number of midbody rows.

Brown & Alcala (1980) recognized six species Groups (assemblages) of the scincid genus *Sphenomorphus* in the Philippines. Group 1 included two Philippine species characterized by very high counts for dorsal scale rows. Group 2 included six species characterized by small size and low lamellar and midbody scale-counts. Group 3 included four species characterized as relatively slender, intermediate in size (rarely exceeding 60 mm in snout-vent length), with 30–36 (rarely 38–40) midbody scale rows and four supraoculars. *Sphenomorphus acutus,* a fifth species tentatively included in this group at the time, has six supraoculars and 26–30 midbody scale rows. Group 4 included five species characterized by a shorter, blunter snout, relatively longer limbs, usually five or six supraoculars, and usually 36–50 plus midbody scale rows. Group 5 included four species characterized by their relatively large size (usually greater than 55 mm snout–vent length) and a more slender, tapered snout than group 4. Group 6 included one species (*S. fasciatus*) characterized by the very distinctive, banded color pattern, and the high number of dorsal scale rows (78–90).

A recent sample from the mountain area northeast of Lake Lanao in north-central Mindanao Island differs in several characters from all previously described species of *Sphenomorphus.* This sample represents a taxon which belongs in Group-3 as defined above.

Materials and Methods

Material examined included all species of Group 3: *leucospilos* (2), *laterimaculatus* (1), *victoria* (2), *acutus* (16), *mindanensis* (20 plus), and *kitangladensis* (4).

Measurements on preserved specimens were determined to the nearest 0.1 mm, using a Helios dial caliper. Head length (HL) was measured from posterior edge of ear opening to tip of snout; head breadth (HB) at the widest point near the angle of the jaws; snout length (SnL) from anterior edge of eye socket to tip of snout; eye diameter (ED) from anterior to posterior edge of socket; tympanum diameter (TD) from anterior to posterior edge; snout-vent length (SVL) from tip of snout to posterior edge of preanals; axilla-groin distance (Ax-Gr) from base of fore limb to base of hind limb; hind limb length from base of hind limb to tip of longest toe.

Scale counts were standardized as follows: lamellae beneath the digits were counted down to the base or to the point where subdigital scales became less than two times the breadth of the solar scales; (2) midbody scale rows (MBSR) were counted at a point midway between fore and hind limbs, and (3) dorsal scale rows (DSR) were counted between the parietals and the row on the base of the tail at the level opposite the vent. Standard nomenclature for the headshields of the Scincidae is followed (Boulenger 1890, Smith 1935, and Brown & Alcala 1980).

Sphenomorphus kitangladensis, new species
Fig. 1

Holotype.—FMNH 250644, an adult male collected 9 May 1992 on Mt. Kitanglad, Bukidnon Province, north-central Mindanao Island by L. R. Heaney. MBSR 38; DSR 76; fourth toe lamellae 15; SVL 56.4 mm; HL 12.5 mm; HB 8.0 mm; SnL 3.7 mm; ED 2.6 mm; Ax-Gr 31.5 mm.

Paratypes (3).—FMNH 250641, 250643, CAS 191084 (same locality as the holotype).

Diagnosis.—This species is differentiated from other species of *Sphenomorphus* by the following combination of characters: (1) MBSR 34–38; (2) DSR 73–76; (3) fourth toe lamellae 15–17; (4) anterior loreal small, triangular, not in contact with upper labials; (5) prefrontals in moderate to broad contact; (6) frontoparietals fused; (7) interparietal large; (8) SVL at maturity about 50–60 mm.

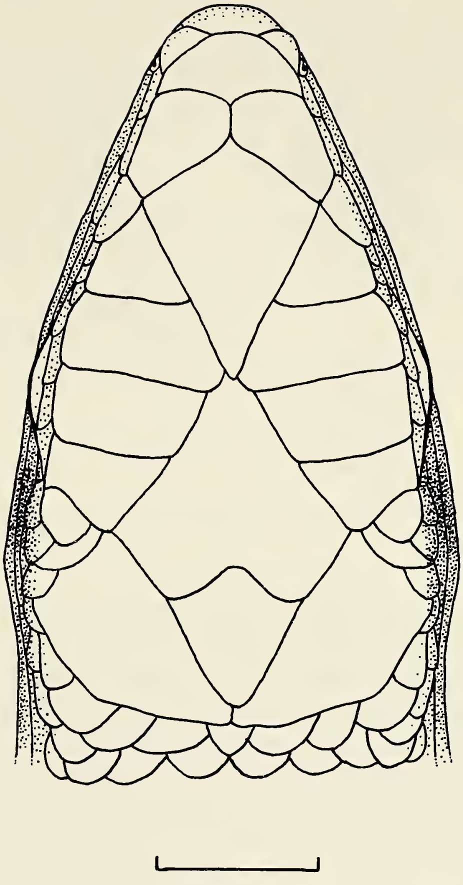

Fig. 1. *Sphenomorphus kitangladensis.* Dorsal headshield pattern, CAS 191084, paratype.

Description (based on four specimens).—SVL at maturity 55.8–56.4 mm for two males and 51.9 mm for one female; snout tapered, bluntly rounded, SnL 28–30% of HL and 43–50% of HB; HB 13–14% of SVL; ED 59–70% of SnL and 30–33% of HB; rostral broader than high, in broad contact with frontonasal; prefrontals in moderate to broad contact; frontal long, in contact with two or three supraoculars; four large supraoculars; frontoparietals fused; interparietal large; parietals in narrow contact posteriorly; no nuchals (Fig. 1); anterior loreal small, triangular, not in contact with upper labials; posterior loreal large, in contact with first and second or second upper labials (posterior loreal forming two superimposed scales in one specimen); seven upper labials, fifth enlarged and beneath eye; six or seven lower labials; tympanum shallow, TD 42–57% of ED; dorsal scales smooth, 73–76 transverse rows along vertebral line between parietals and base of tail; 34–38 midbody scale rows; two enlarged preanals; limbs well developed; length of extended

Table 1.—Standard scale counts and other pertinent characters for Philippine species referred to Group 3 of the genus *Sphenomorphus*.

Part A

Species	Adult SVL (mm)	Midbody scale rows	Dorsal scale rows	Fourth toe lamellae
S. mindanensis	42–56	30–32	66–78	17–20
S. laterimaculatus	52±	40	72	18
S. leucospilos	52–55	32	63–68	16–18
S. kitangladensis	50–57	34–38	73–76	15–17
S. victoria	45	30	64–65	18–20

Part B

	Fronto-parietals		Anterior loreal contacts labials		Prefrontals in contact	
Species	Fused	Not fused	Yes	No	Yes	No
S. mindanensis		X	X			X
S. laterimaculatus	X		X		X	
S. leucospilos	X		X		X	
S. kitangladensis	X			X	X	
S. victoria		X	X			X

hind limb 77–82% Ax-Gr distance (probably conservative since limbs were stiff); 15–17 lamellae beneath fourth toe; 6–7 lamellae beneath first toe; tail much longer than body.

Color (in preservative).—Dorsum grayish tan, variously marked with small blackish spots, especially along vertebral line; dorsolateral area marked by a narrow, wavy, blackish band with some vague to prominent, pale blotches along dorsal margin; lips usually with some dark bars; lateral surfaces of body dusky; venter grayish ivory, relatively uniform for one specimen, mottled with black anterior to fore limbs for three specimens.

Etymology.—Based on the name of the mountain which is the type locality.

Range.—Known only from the type locality, Mt. Kitanglad, Bukidnan Province, Mindanao Island.

Comparisons

Comparisons are made with the four species that might be easily confused with *Sphenomorphus kitangladensis. Sphenomorphus kitangladensis* is most similar to *S. laterimaculatus,* but differs in the somewhat lower number of midbody scale rows (34–38), 40 for *laterimaculatus*; the small anterior loreal which is not in contact with the upper labials (Table 1); and the shorter snout relative to the head breadth. *Sphenomorphus leucospilos* and *S. victoria* exhibit lower counts for both midbody and dorsal scale rows and have the anterior loreal in contact with the upper labials (Table 1). *Sphenomorphus mindanensis* and *S. victoria* differ in the smaller prefrontals which are not in contact with each other and the fronto-parietals are not fused. *Sphenomorphus mindanensis* further differs from this species in the lower number of midbody scale rows (Table 1).

Some examples of *Sphenomorphus decipiens* (a Group 4 species) resemble *S. kitangladensis* in exhibiting a small anterior loreal which is not in contact from the upper labials. However, *S. decipiens* differs in the blunter, shorter snout, evidenced in the SnL/HB ratio (35–39% for *decipiens* and 43–50% for *kitangladensis*) and the HB/HL ratio (65–81% for *decipiens* and 58–64% for *kitangladensis*); the smaller size (SVL 31–45 mm for 20 adult *decipiens* and 52–56 mm for 3 adult *kitangladensis*); and the lower number of dorsal scale rows (57–66 for *decipiens* and 73–76 for *kitangladensis*).

Acknowledgments

I wish to thank L. R. Heaney and R. F. Inger, Field Museum of Natural History, Chicago, for the opportunity to describe this species and anonymous reviewers for many helpful suggestions. The illustration was prepared by Colleen Sudekum of the California Academy of Sciences.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(3):392–394. 1995.

A new species of *Brachymeles* (Reptilia: Scincidae) from Catanduanes Island, Philippines

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Abstract.—A new scincid lizard, *Brachymeles minimus,* is described from Catanduanes Island, Philippines. It differs from known species, other than *Brachymeles vermis* and *B. apus,* in the absence of external limbs. *Brachymeles minimus* differs from *B. vermis* and *B. apus* in its smaller size, lower dorsal scale row count, and pattern of head shields.

Catanduanes, an island of low mountain terrain and about 1450 sq. km in area, lies slightly less than 10 km off the southeast coast of Luzon Island. Until recently, published information on its herpetofauna was limited to three species, one crocodile, one lizard, and one snake. Ross & Gonzales (1992), following a survey of the island in 1990, reported a total of 58 species; 13 amphibians, 27 lizards, 17 snakes, and one crocodile. They described one amphibian, *Kaloula kokacii* as new, and list two lizards *Brachymeles* sp., *Gonocephalus* sp., and one snake, *Oxyrhabdium* sp., as being based on specimens not readily assignable to any known species.

Recently, while identifying some *Brachymeles* from other Philippine islands, we also examined the specimens of the unidentified Catanduanes' *Brachymeles.* A sample of four specimens are now available. These, indeed, represent a previously undescribed taxon, the description of which is the subject of this paper.

Materials and Methods

Materials examined include examples of all 14 previously described species of the genus *Brachymeles* as well as the four known examples of the new species.

Measurements were determined to the nearest 0.1 mm, using a Helios dial caliper. In addition to snout–vent length (SVL), other measurements include head breadth (HB), made at the widest point; snout length (SnL) from anterior corner of eye to tip of snout; and eye diameter (ED) from anterior to posterior corner of the eye. Midbody scale counts (MBSR) were made about halfway between the tip of the snout and the vent, and the dorsal scale count (DSR) from the parietals to the transverse row opposite the vent. Standard nomenclature for headshields in the Scincidae is followed (Boulenger 1890, Smith 1935, Brown & Alcala 1980).

Brachymeles minimus, new species
Fig. 1

Holotype.—FMNH 247990, a male (apparently mature based on hemipenes), collected in original forest at 600 m on Mt. Tungaw-tungaw (13°40′N, 124°21′E), about four km west of Gigmoto, Catanduanes Prov., Catanduanes Island, by the junior author on 18 June 1991. MBSR 22; DSR 94; ED 1.2 mm; SvL 64.0 mm; SnL 2.4 mm; HB 4.1 mm.

Paratypes (3): FMNH 247991, 250817, CAS 182569 (same locality as holotype)

Diagnosis.—A small *Brachymeles,* 56.3 and 64.0 mm for two (apparently mature) males; MBSR 22; DSR 94–102; no external vestige of limbs; no ear opening; frontoparietals in moderate to broad contact; eye relatively large, ED 43–50% of SnL.

Description (based on four specimens).—A small slender *Brachymeles,* SVL 56.3 and 64.0 mm for two males and 38.4 and 48.5 mm for two apparent juveniles; HB 6.4–8.2% of SVL; SnL 53.5–58.5% of HB; eye large, ED 43–50% of SnL and 23.3–29.3% of HB; rostral broader than high, having narrow contact with prefrontal; supranasals large, narrowly separated at midline; frontonasal broader than long; prefrontals narrow, narrowly separated at midline; frontal about as broad as long, in contact with two anterior supraoculars; five supraoculars, separated from eye by five or six superciliaries; frontoparietals in relatively broad contact; interparietal large; parietals in contact; one pair of narrow nuchals (Fig. 1); no postnasal; anterior loreal larger than posterior, in contact with first and second upper labials; six upper labials, anterior largest and fourth beneath center of eye; six lower labials; pair of contacting shields behind postmental; no vestige of ear opening; 22 MBSR; 94–102 DSR between parietals and base of tail; no external vestiges of fore or hind limbs (Table 1).

Color (in preservative).—Dorsum light brown to chocolate brown, (holotype lightest in color); ventral surface almost same color as dorsum for the holotype, but somewhat more grayish brown in paratypes. This color pattern results from the pale margins of the ventral scales.

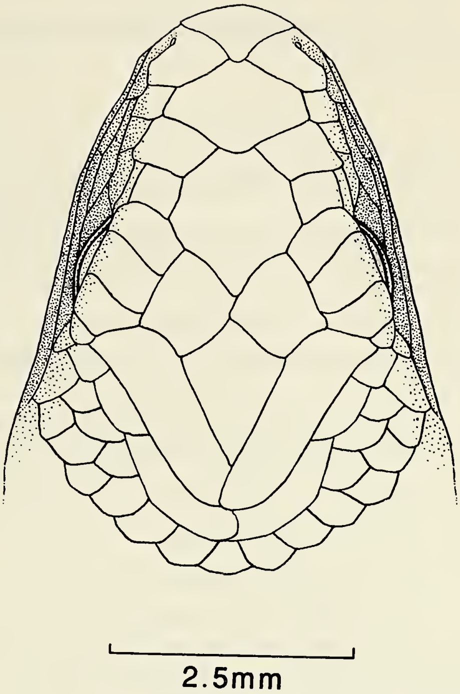

Fig. 1. *Brachymeles minimus.* Pattern of dorsal head shields, FMNH 247991, paratype.

Habitat note.—Specimens were found beneath decaying logs and rocks lying in the duff of original forest at 600 m elevation.

Range.—Known only from the type locality on Catanduanes Island.

Table 1.—Scale counts and other pertinent characters for *Brachymeles minimus, vermis, apus,* and *samarensis.*

Species	SVL (mm) adults	DSR	MBSR	Number of super-ciliaries	Fronto-parietals Contact	Fronto-parietals Separate	*ED* SnL	*HB* SVL	External limbs
B. minimus	56.3–64.0 (2)	94–102 (4)	22 (4)	6	X		43–50%	8.3%	None
B. vermis	61.0–76.0 (4)	104–109 (6)	22–23 (6)	2		X	35–44%	2.2–3.3%	None
B. apus	119–131 (2)	108–113 (6)	22–24 (6)	2		X	35%	5.7%	None
B. samarensis	55.6–65.2 (14)	87–96 (19)	22–24 (19)	6	X		25–33%	6.5–8.3%	Short Stubs

Etymology.—From the Latin *minimus,* meaning small.

Discussion

Skinks of the genus *Brachymeles,* popularly referred to as burrowing lizards, are rarely if ever seen except when one looks beneath the duff, rotting logs, or in top soil. In association with adaptation to these subterranean habitats, the species of this genus exhibit a remarkable series of limb reduction stages (from relatively short, pentadactyl limbs to complete absence of external limb structures), and correlated body elongation and attenuation stages. For a discussion of limb loss in lizards, see Greer (1989) and Greer & Cogger (1985).

Of the 15 known species of *Brakhymeles,* 14 are from the Philippines (Brown & Alcala 1980) and one from Borneo (Hikada 1982). Five of the 15 species (*bicolor, boulengeri, gracilis, schadenbergi,* and *talinis*) are pentadactyl, but the limbs and digits are short. Seven of the species (*bonitae, cebuensis, elerae, pathfinderi, samarensis, tridactylus,* and *wrighti*) exhibit further reduction of the limbs and loss of digits ranging from one on either the fore or hind limbs to four or all five on both fore and hind limbs. The remaining three species (*apus, vermis,* and *minimus*) have lost all vestiges of external limbs.

Brachymeles minimus differs from the other limbless species (*apus* and *vermis*) in the smaller size and lower count for DSR (Table 1). It also differs from these two species in the pattern of the head shields: (1) frontoparietals large, in contact (separated for *apus* and *vermis*) and (2) five or six superciliaries (two beneath anterior supraoculars for *apus* and *vermis*), Table 1 and Fig. 1. *Brachymeles minimus* is most similar to *B. samarensis* in the pattern of the head-shield arrangement. Both species have: (1) the fronto-parietals in contact, (2) five supraoculars, (3) a pair of narrow nuchals, and (4) lack a postnasal. *Brachymeles minimus* differs from *B. samarensis* in the complete absence of external limb structures, the number of dorsal scale rows, and the slightly larger eye relative to snout length (Table 1).

The evidence from scale counts and patterns of head-shield development suggests that *apus* and *vermis* may be the end products of a different evolutionary branch than that from which *minimus* is derived. A phylogenetic study, using additional lines of evidence to those presently available, is very much needed to clarify relationships within this genus.

Acknowledgments

We wish to thank L. Heaney and C. Ross for suggesting that we undertake this study. We also thank R. F. Inger, A. Leviton, R. Drewes, and anonymous reviewers for helpful suggestions during the preparation of the manuscript. Illustrations of the head shield patterns were made by Colleen Sudakum, California Academy of Sciences.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(3):395–400. 1995.

A new skink (*Emoia:* Lacertilia: Reptilia) from the forest of Fiji

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Abstract.—A moderate-sized turquoise-colored skink from the montane forest of Vanua Levu, Fiji differs from all other central Pacific skinks in a combination of mensural and scalation characters. This skink, *Emoia mokosariniveikau* n. sp., is a member of the *Emoia samoensis* species group and *concolor* subgroup, and its coloration and color pattern are unique among skinks of the genus *Emoia.*

Vanua Levu is the second largest island of the Fijian group. In spite of its size and accessibility, no one has surveyed methodically the diversity and distribution of its amphibians and reptiles. Forest lizards, such as *Lepidodactylus manni* and *Emoia parkeri,* should occur there, but no records exist of such occurrences (Zug 1991). We have begun such a survey, but as yet our efforts are small. Our first survey in 1992 provided new distributional records for a number of lizard species (e.g., *Emoia parkeri*) and yielded a single specimen of a new *Emoia.* Because this species is a forest lizard and the native forest of Vanua Levu continues to disappear, we wish to alert Fijians and biologists of this, presumably, Vanualevuan endemic by describing the lizard promptly. Forests, where they still persist, are threatened throughout Oceania, and the continual discovery of new species of forest plants and animals re-enforces the urgency of forest conservation and the establishment of forest reserves.

Methods

Mensural and meristic characters follow the definitions and protocols of Zug (1991).

Family Scincidae

Genus *Emoia*

Emoia mokosariniveikau, new species

Figs. 1–2

Holotype.—USNM 322473, adult female from near Saivou, ca. 23 km (road) NW of Savusavu, Vanua Levu, Fiji, collected 23 October 1992 by I. Ineich and G. R. Zug.

Diagnosis.—*Emoia mokosariniveikau* is a member of the *samoensis* group (sensu Brown 1991) and the *concolor* subgroup. It differs from other Fijian *Emoia* by: size of adult females (55 mm SVL), larger than *caeruleocauda* (42–50 mm), *cyanura* (39–53 mm), *impar* (40–47 mm) and *parkeri* (43–52 mm) and smaller than *campbelli* (57–64 mm), *concolor* (59–77 mm), *nigra* (88–108 mm) and *trossula* (75–100 mm); adult coloration (coppery brown dorsal ground color overlain by turquoise on neck and trunk and dark transverse bars on sides of trunk onto back), *caeruleocauda, cyanura, impar* and *parkeri* (light stripes on black or dark brown background), *campbelli* and *trossula* (small dark transverse bars scattered over beige to brassy background), *concolor* (uniform or nearly so green to olive-beige ground-color), and *nigra* (uniform black ground-color); number of lamellae beneath the fourth toe

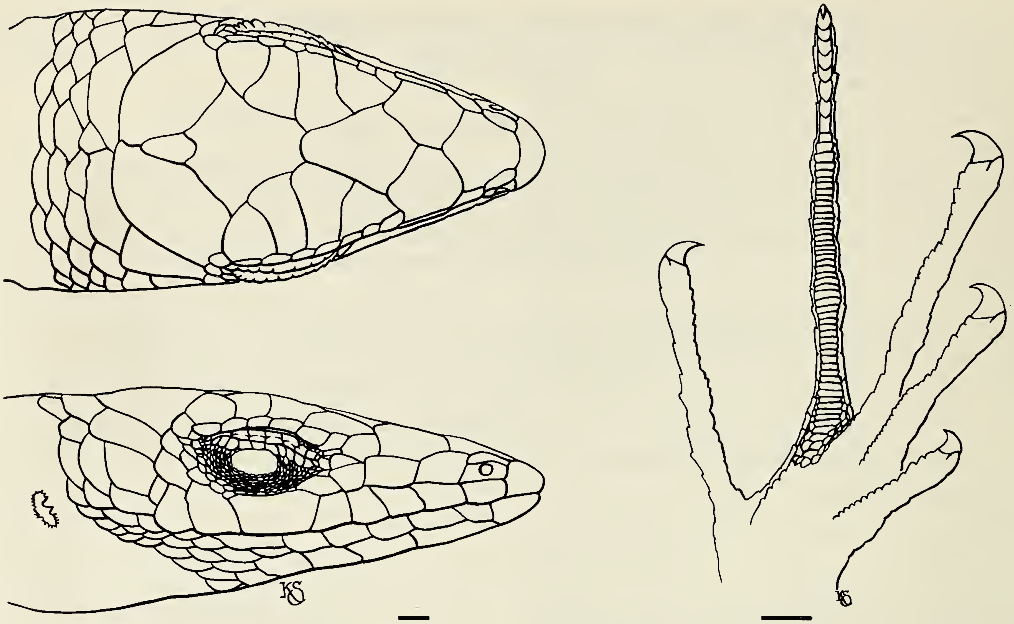

Fig. 1. Scalation of the holotype of *Emoia mokosariniveikau* (USNM 322473). Dorsal and lateral views of the head (left); ventral surface of the right fourth toe (right); scale bars equal 1 mm.

(48–49), *caeruleocauda* (33–41) and *parkeri* (31–41), *cyanura* and *impar* (57–80), and *nigra* (31–39). From members of the *samoensis* group of *Emoia, E. mokosariniveikau* differs by: size of adult females (55 mm SVL), smaller than *aneityumensis* (≥75 mm), *campbelli* (≥68 mm), *concolor* (≥59 mm), *flavigularis* (≥59 mm), *loyaltiensis* (≥60 mm), *nigra* (≥88 mm), *samoensis* (≥79 mm), *sanfordi* (≥68 mm) and *trossula* (≥75 mm); scale rows around midbody (30), *aneityumensis* (≥39), *flavigularis* (≥34) and *nigra* (≥32); number of lamellae beneath fourth toe (48–49), *aneityumensis* (≤38), *campbelli* (≤42), *flavigularis* (≤48), *murphyi* (≥65), *nigra* (≤39), *nigromarginata* (≤48), *parkeri* (≤41) and *sanfordi* (≥61); see Tables 1 & 2 for summary of measurements and scalation.

Description of holotype.—An adult female (55.1 mm SVL), slender-bodied with long tail (91 mm, regenerated, round in cross-section, tapering gradually to point) and well-developed limbs; hindlimb length 45% SVL, fourth toe tip extending nearly to axilla when adpressed to side of body; body length 48% SVL. Digits of fore- and hindfeet long and strongly clawed; hindtoes length pattern 4>5≃3>2>1 (Fig. 1). Head long and slender, slightly depressed, snout pointed; head length (HL) 22% SVL; neck length (ear to axilla) 14% SVL; head width 60% HL; snout length (anterior corner of eye to tip of snout) 48% HL; and preocular length (eye to naris) 32% HL.

Shiny, imbricate scales on body; dorsal scales grossly smooth but with shallow, longitudinal striations visible microscopically; 61 scales from parietals to base of tail, anteriormost pair enlarged as nuchals; middorsal scales subequal in size to more lateral ones; 30 scales around midbody. Narrow lamellae on underside of all digits; 42/39 (left/right) beneath 4th finger; 48/49 beneath 4th toe (Fig. 1). Head scales smooth (Fig. 1); rostral broad, touching frontonasal across broad suture; supranasals small, narrowly rectangular; prefrontals broadly in

Table 1.—Summary of mensural characteristics of the *Emoia samoensis* group (sensu Brown 1991). All measurements are for sexually mature individuals; only ranges are provided and all measurements are in millimeters.

Species of *Emoia*	Sex	Snout–vent length	Hindlimb length	Head length	*n*
aneityumensis[a]	F	74.9–85.4	34.8–36.9	17.2–18.2	2
campbelli	F	92.9	37.2	18.5	1
	M	68.0–89.8	31.6–42.0	15.7–20.3	4
concolor[b]	F	58.7–77.3	26.2–38.0	12.9–19.8	15
	M	56.8–85.5	27.6–40.6	13.6–20.0	27
flavigularis[c]	F&M	58.9–75.5	—	—	22
loyaltiensis[c]	F&M	60.0–83.2	—	—	5
mokosariniveikau	F	55.1	25.0	12.4	1
murphyi[d]	F	59.4–65.4	25.1–30.3	13.5–14.4	3
	M	65.7	33.9	15.5	1
nigra[b]	F	87.7–107.5	42.3–53.3	18.9–23.9	8
	M	88.0–112.1	44.8–53.4	20.0–25.5	10
nigromarginata[c]	F&M	51.8–77.4	—	—	26
parkeri[b]	F	42.9–52.0	18.9–23.7	9.9–11.7	8
	M	46.9–50.0	20.4–23.0	10.6–12.4	5
samoensis[c]	F&M	78.0–118	—	—	24
sanfordi[c]	F&M	68.3–115.0	—	—	36
trossula[b]	F	75.4–100.1	34.7–46.4	16.9–21.1	30
	M	74.1–106.5	35.6–53.0	17.3–24.2	51

[a] *Emoia aneityumensis* includes all concolor-like specimens from Aneityum, Futuna, and Tanna.
[b] Data from Fijian specimens only (Zug 1991).
[c] Data from Brown (1991).
[d] Data from Samoan specimens only.

contact medially; frontoparietal single; interparietal small with a parietal eye; parietal large and in contact behind interparietal; 4/4 supraoculars on each side bordered laterally by 8/8 supraciliaries; anterior loreal longer than high and equal in area to posterior loreal; posterior loreal longer than high; upper eyelid immoveable with 9/9

Table 2.—Summary of scale characteristics of the *Emoia samoensis* group. Sexual dimorphism has not been identified in scale characters; the following ranges derive from juveniles and adults. Footnote legend as in Table 1.

Species of *Emoia*	Number of scales		Subdigital lamellae		*n*
	Dorsal	Midbody	4th finger	4th toe	
aneityumensis[a]	74–80	39–41	23–30	33–38	5
campbelli	57–64	30–34	31–38	42–51	10
concolor[b]	54–62	27–33	30–48	43–65	78
flavigularis[c]	53–64	34–40	—	36–48	22
loyaltiensis[c]	62–71	30–34	—	51–60	5
mokosariniveikau	61	30	39–42	48–49	1
murphyi[d]	54–58	28–31	45–51	65–74	8
nigra[b]	60–69	32–40	20–24	31–39	33
nigromarginata[c]	56–64	28–32	—	38–48	26
parkeri[b]	54–60	28–33	22–30	31–41	24
samoensis[c]	58–68	30–34	—	45–54	24
sanfordi[c]	56–64	28–34	—	61–76	36
trossula[b]	58–77	30–40	27–42	42–65	117

Fig. 2. Dorsolateral view of the holotype of *Emoia mokosariniveikau* (USNM 322473) in life. The dorsolateral "stripe" is a reflection from the photographic flash.

scales along upper edge; lower eyelid moveable with large transparent disc surrounded by small opaque scales; 8/8 supralabial scales, enlarged 6th beneath eye; 8/8 infralabial scales. Ear opening vertically elliptical, top tilted posteriorly, with 2/2 distinctly enlarged scales on anterior edge.

In life (Fig. 2), dorsal ground-color shiny coppery brown, head uniform bright coppery; broad turquoise bands on side of neck and trunk, bands extend upward toward midline, continuous on neck and anterior trunk, and staggered and discontinuous on posterior half of trunk; at abdominal level, small, irregular bars of dark brown or black appear on side and extend onto dorsum, bars usually edged with blue; on tail, dark bars alternate at midline and interspaced with brown then beige. Venter from mid throat onto base of tail light orangish yellow, bordered on chin and ventrolaterally by light turquoise from lateral bands. Limbs coppery beige dorsally with dark spots, uniform yellow ventrally; distinct dark stripe on posterior surface of thigh.

In alcohol, dorsal ground-color bluish gray anteriorly and coppery beige posteriorly, lateral bars black; ventrally, chin and anterior throat bluish ivory, throat to base of tail pale yellow, bluish tinted laterally on trunk.

Etymology.—Fijians, Polynesians as well (Crombie & Steadman 1986), largely ignore their native lizards. **Moko** is the widely used colloquial name for lizard, whether it is a skink or gecko, big or small. A few other names do exist. **Vokai** refers exclusively to the Fijian iguana (*Brachylophus*) and is used and recognized by all Fijians. **Sari** and **boliti** refer also to lizards, although they are of uncommon usage. **Sari** refers to a small green lizard (Capell, 1973) when used in combination with the Fijian **moko** as a suffix, and to this Fijian word, we append the Fijian **ni veikau,** meaning of the forest. This combination produces **mokosari ni veikau** or small green lizard of the forest, and is a noun in apposition. [We have taken liberties with "green lizard" as turquoise is greenish blue rather than strictly green.]

Distribution.—*Emoia mokosariniveikau* is known only from the type locality on the northern slope of Vanua Levu's central mountain range. Since the type locality is not isolated ecologically or geographically, *E. mokosariniveikau* likely occurs throughout the length of island where original forest remains or has regenerated sufficiently. Dick Watling (in litt., Aug 1994) described an *Emoia* captured (Aug 1978) at Solevu, Vanua Levu. His description closely matches *E. mokosariniveikau* but cannot be confirmed because the specimen has not been located. One (Calif. Acad. Sci./CAS 155973; Joske's Thumb, Viti Levu) of the paratypes of the *Emoia campbelli* series does not match the other members of that type series and shares some similarities with *E. mokosariniveikau*; however, its discoloration and poor preservation prevent confirmation of its specific identity.

Comments on Relationships

Brown first recognized the *Emoia atrocostata* and the *E. samoensis* "complexes" in 1953 (Brown & Marshall 1953). He gave a set of characters defining the *atrocostata* complex and noted that the *samoensis* complex was closely related to the former and differed in the presence of more numerous and more highly modified digital lamellae. Later in a privately circulated key to *Emoia,* Brown (1970) recognized five "natural groups" of *Emoia*: *adspersa*; *atrocostata*; *baudini-cyanura*; *cyanogaster*; *physicae. Emoia concolor, murphyi,* and *samoensis* were listed as members of the *cyanogaster* group. Brown later reintroduced the *samoensis* group with the recognition of *E. campbelli* and *E. trossula* (Brown & Gibbons, 1986). The *samoensis* group was not characterized therein and remains defined largely by its species content. A characterization is possible, however, by listing the identifying features from Brown's (1991) species group key: 11 premaxillary teeth; alpha palate; unfused nasal bones; parietal eye present; anterior loreal as long or nearly as long as posterior loreal; dorsal scale rows ≤87; midbody scale rows ≤44; rounded to moderately thin subdigital lamellae. The included species are listed in Tables 1 and 2.

Assuming the *samoensis* group to be a natural assemblage, we here recognize two species subgroups within the central Pacific (Fiji-Samoa-Tonga area) members of the *samoensis* group. The *samoensis* subgroup contains *samoensis* and *trossula.* These *Emoia* are moderately large (74–118 mm adult SVL), heavy-bodied skinks with 57–77 dorsal scale rows, 30–40 midbody scale rows, and 42–65 lamellae on the fourth toe. The *concolor* species subgroup contains *campbelli, concolor, mokosariniveikau* and *murphyi.* These *Emoia* are moderate-sized (56–90 mm adult SVL), slender-bodied with 54–67 dorsal scale rows, 27–34 midbody scale rows, and 42–74 lamellae on the fourth toe. These subgroups are tentative groupings and serve only for our initial analysis of relationships within the *samoensis* group. This division of species agrees with Brown's (1991) *concolor* and *samoensis* subgroups, except for exclusion of *E. nigra* and *E. parkeri.* We question the status of these two species as members of the *samoensis* group. In addition to its distinctive coloration (black or dark brown ground color in contrast to coppery beige to green), *E. nigra* is behaviorally unlike the other semiarboreal to strongly arboreal *samoensis* group members. For example, *E. trossula* forages on and above the ground and regularly escapes by climbing, in contrast *E. nigra* forages on the ground and, even if resting in a tree, regularly escapes downward and away from the tree (Zug 1991). *Emoia parkeri* has dorsolateral stripes unlike any other juvenile or adult *samoensis* group member. Its snout is more attentuate and its prefrontals are not, or slightly, in contact on the midline.

Our analysis of intragroup relationships is not yet sufficiently advanced to declare which character-states are synapomorphic or, for that matter, to have identified a useful set of characters for initiating a cladistic analysis. All scalation and mensural features of *E. mokosariniveikau* lie within the range of the *concolor* subgroup. Its dorsal and lateral coloration of neck and trunk is unique within both subgroups. Its lateral dark, light-bordered bars on the trunk are similar only to the bar-pattern of some populations of Fijian *E. trossula*; however, its dark thigh stripe occurs only in other *concolor* subgroup members. No trait currently suggests a closer affinity of *E. mokosariniveikau* to any one of the other three central Pacific *concolor* subgroup members.

Acknowledgments

We appreciate and thank the following individuals and agencies for their encouragment and assistance of our biological investigations of Fijian and other Pacific lizards. The Ministry of Primary Industries, Forestry & Co-operatives gave us permission to study lizards in Fiji and to retain vouchers in the Smithsonian (USNM). Field work was supported by the Smithsonian Scholarly Studies Program. Milika Naqasima and Michael Doyle of The University of the South Pacific provided the proper Fijian construction of the new specific epithet. Kate Spencer skillfully illustrated the head and hindfoot of *Emoia mokosariniveikau*. Ronald Crombie, Robert Fisher, and Dick Watling reviewed and improved our early drafts of this article.

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Appendix. 1. Specimens Examined

Emoia aneityumensis. Vanuatu: BMNH 1956.1.3.64, 1973.1534–35; FMNH 69151, 69638.

Emoia campbelli. Fiji: CAS 155967–70, 155972–73, 156257–58, 156710–12.

Emoia concolor. Fiji: mensural and meristic data from Appendix table B in Zug, 1991; MNHN 7084, 7084A.

Emoia flavigularis. Solomon Islands: mensural and meristic data from species descriptions in Brown, 1991.

Emoia loyaltiensis. Loyalty Islands: mensural and meristic data from species descriptions in Brown, 1991.

Emoia murphyi. Samoa: USNM 268363, 322743–49.

Emoia nigra. Fiji: mensural and meristic data from Appendix table B in Zug, 1991.

Emoia nigromarginata. Vanuatu: mensural and meristic data from species descriptions in Brown, 1991.

Emoia parkeri. Fiji: mensural and meristic data from Appendix table B in Zug, 1991.

Emoia samoensis. Samoa: mensural and meristic data from species descriptions in Brown, 1991.

Emoia sanfordi. Vanuatu: mensural and meristic data from species descriptions in Brown, 1991.

Emoia trossula. Fiji: mensural and meristic data from Appendix table B in Zug, 1991.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(3):401–435. 1995.

Lovén's law and adult ray homologies in echinoids, ophiuroids, edrioasteroids, and an ophiocistioid (Echinodermata: Eleutherozoa)

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Abstract.—Lovén's law, which is summarized by an AABAB rule, is found to apply to the structure of *Stromatocystites* and *Astrocystites* (edrioasteroids) and *Gillocystis* (an ophiocistioid) and was previously known in echinoids and in Paleozoic ophiuroids. Chance coincidence and convergent evolution are not likely explanations. Lovén's law is interpreted from edrioasteroids as a manifestation of 2-1-2 symmetry, and in echinoids, ophiuroids and ophiocistioids it is interpreted as a vestige of 2-1-2 symmetry. Thus, Lovén's law is a plesiomorphic character that indicates ray homologies. Roman numerals as used by Lovén for echinoids are applied to edrioasteroids, ophiuroids and ophiocistioids. The anterior ray in exocyclic echinoids is ray III, whereas it is ray II in edrioasteroids. This is reconciled by noting that ray II was anterior in the elongate tests of the Ordovician echinoids *Ectinechinus* and *Eothuria.* In echinoids the anterior-posterior axis of the bilateral larva lines up with ray II in the imago [von Übisch's axis of primordial symmetry]. This relation is used to deduce that the anterior-posterior axis of edrioasteroids coincided with the axis of their larvae. Studies by Fell, Strathmann, and Smith are used to speculate that the larval type of Ordovician ophiuroids was a bilateral planktotroph but not yet an ophiopluteus. Lovén's law is a distinctive and fundamental feature of the body plan that validates the Subphylum Eleutherozoa. There are at least two distinct constructions of 2-1-2 symmetry (Eleutherozoa and Blastozoa) and possibly a third (crinoids).

This paper investigates the value of Lovén's law in establishing ray homologies among echinoderms. Lovén's law of heterotropy describes an AABAB pattern of relative sizes of echinoid basicoronal plates. In an earlier paper (Hotchkiss 1978), my a priori hypothesis was that demonstration of the AABAB pattern of Lovén's law in the ambulacra of Paleozoic ophiuroids would establish either the madreporite or the anus as the landmark for homologous orientation of echinoderms. The unexpected finding was that possibly neither the madreporite nor the anus is reliable. Several a posteriori hypotheses came out of that work, including the possibility that Lovén's law may be fundamental to the echinoderm ground plan.

The program for this research was laid out in the earlier paper (Hotchkiss 1978). 1. Attempt to determine which, if any, of the conflicting propositions for designating ray homologies may be the correct proposition. 2. Investigate the location of the plane of hydrocoele closure and the orientation of the embryological or developmental axes as part of this analysis. 3. Attempt to decide whether Lovén's law independently evolved in echinoids and ophiuroids, or whether it is indicative of a recent common ancestry between echinoids and ophiuroids [review also the embryological evidence], or whether it is fundamental to the ground plan of the phylum. 4. Investigate whether Lovén's law is expressed in other echinoderm groups

Table 1.—Quick reference list of the numbered hypotheses (see text).

H0	The null hypothesis that the arrangement of ambulacrals in the different rays is a matter of chance
H1	The hypothesis of a selective advantage that led to convergent evolution of Lovén's law in separate classes of echinoderms
H2	The hypothesis that in edrioasteroids Lovén's law is a manifestation of 2-1-2 symmetry and that in descendent groups it is a vestige of this ancient symmetry [symplesiomorphy]
H3	The hypothesis that ray II was the original anterior ray
H4	The hypothesis that the relation of the anteroposterior axis of the larva to the rays of the imago has remained the same in echinoids, ophiuroids, edrioasteroids, and ophiocistioids
H5	The hypothesis that Lovén's law is fundamental to the ground plan of the clade Eleutherozoa
H6	The hypothesis that there are at least two distinct constructions of 2-1-2 symmetry, that seen in Blastozoa and that in Eleutherozoa

with alternating ambulacral plates (specific example: *Astrocystites*). 5. Attempt to determine the functional significance, if any, of Lovén's law [Jackson (1927) noted that Lovén's law itself is without obvious meaning]. 6. Investigate whether the fidelity of Lovén's law in Paleozoic ophiuroids varies between taxa (not studied). 7. Investigate whether the madreporite has a constant or statistically preferential position with respect to Lovén's law in ophiuroids.

The sequence and progress of the research depended on serendipity. From 1978 to 1992 I accumulated information on bilaterality in echinoderms [e.g., axes of symmetry, situs inversus, teratology, and behavior] but did not gain any new insight into ray homologies. In 1988 I worked out new methods for investigating the location of the madreporite in Paleozoic ophiuroids (point 7 supra). The chance discovery came in 1992 when I noticed an instance of Lovén's law in Smith's (1985) drawing of *Stromatocystites walcotti.* I proposed a new table of ray homologies for edrioasteroids, ophiuroids and echinoids at the second North American Friends of Echinoderms conference and workshop in July 1992 (no published proceedings). The results were confirmed and extended in 1994 when I noticed the instance of Lovén's law in Jell's (1983) drawing of the ophiocistioid *Gillocystis.* Building on previous studies (Hotchkiss & Seegers 1976, Hotchkiss 1979) the new results are used to suggest ray homologies for asteroids. This paper is the first publication of this research. To keep the presentation as direct as possible, complex supporting information is given in numbered notes. Table 1 lists the numbered hypotheses for quick reference.

In this paper, ray identifications that are based on Lovén's law are labeled with Roman numerals [see Note 1]. The labeling that results for edrioasteroids is different from that of Bather (1914a), Regnéll (1966) and Bell (1976a): the anterior unpaired ray is ray II in my labeling, whereas it is ray III in their ray labeling. In Appendix 1 the madreporite of Paleozoic ophiuroids is shown to be located adjacent to ray IV in interradius III/IV.

Lovén's Law in Echinoderms

An essential part of the program for this research was to investigate whether Lovén's law is expressed in other echinoderm groups with alternating ambulacral plates (point 4 supra). Lovén's law is an empirical statement of the unequal sizes of echinoid basicoronal plates (Fig. 1). The five plates that begin the ambulacral columns Ia, IIa, IIIb, IVa, Vb are larger than the basicoronal plates that begin columns Ib, IIb, IIIa, IVb, Va (Lovén 1874, Melville & Durham 1966:fig.

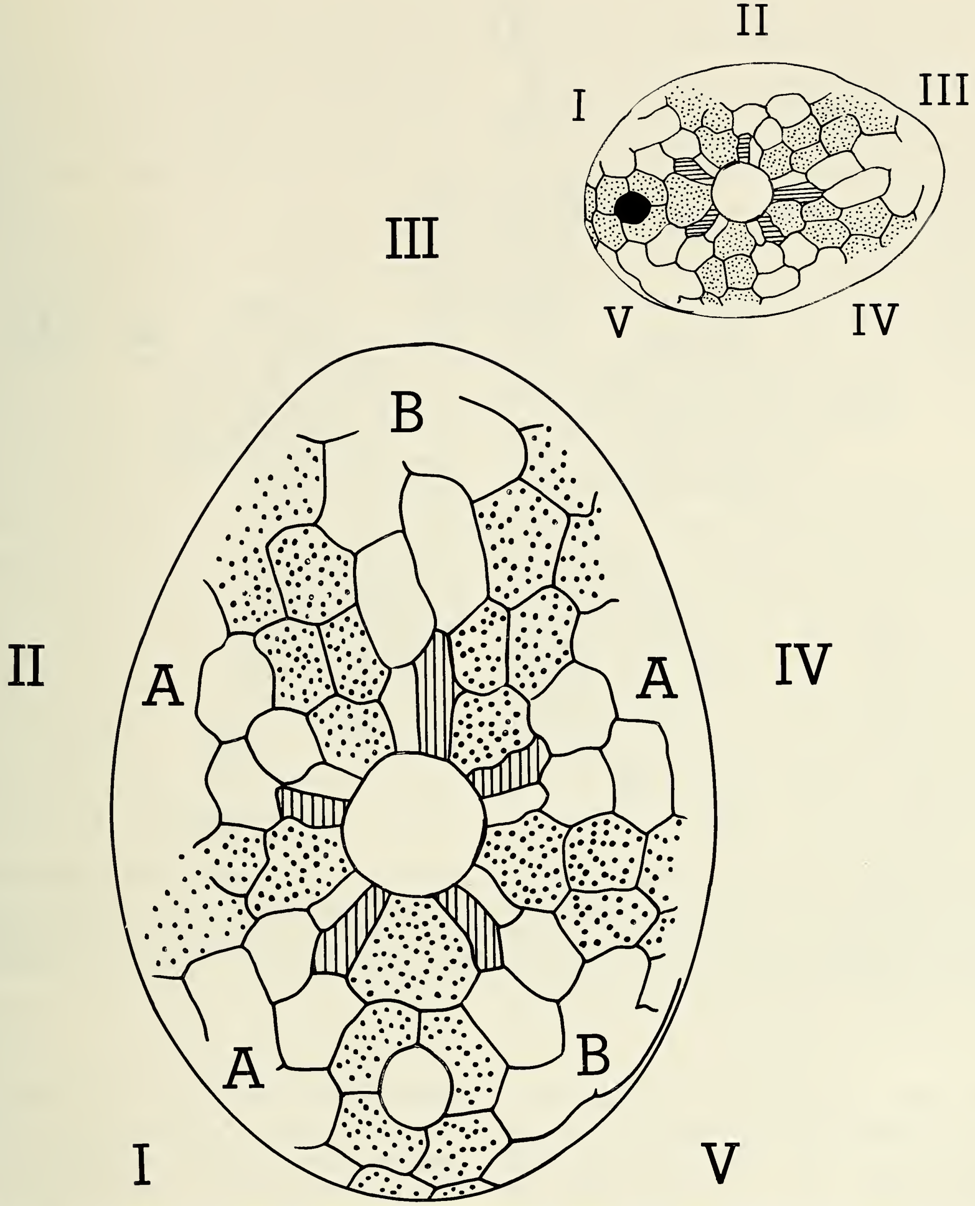

Fig. 1. Lovén's law in the Recent echinoid *Echinocyamus bisexus* (oral side). Basicoronal plates Ia, IIa, IIIb, IVa and Vb, shown vertically ruled, are larger than the unshaded partner basicoronal plates of the same ambulacral area. Interambulacral areas are stippled. Interambulacrum V/I contains the periproct (shown). The madrepore is on the apical surface (not shown); in regular echinoids the madreporic plate is formed by genital 2 in interambulacrum II/III. Although irregular echinoids such as *Echinocyamus* are elongate with ray III anterior, ray II is inferred to have been the original anterior ray in early Paleozoic echinoids and edrioasteroids. In the small insert the echinoid is rotated to have the same orientation as in Figs. 2-5. (Redrawn and annotated from Kier 1968.)

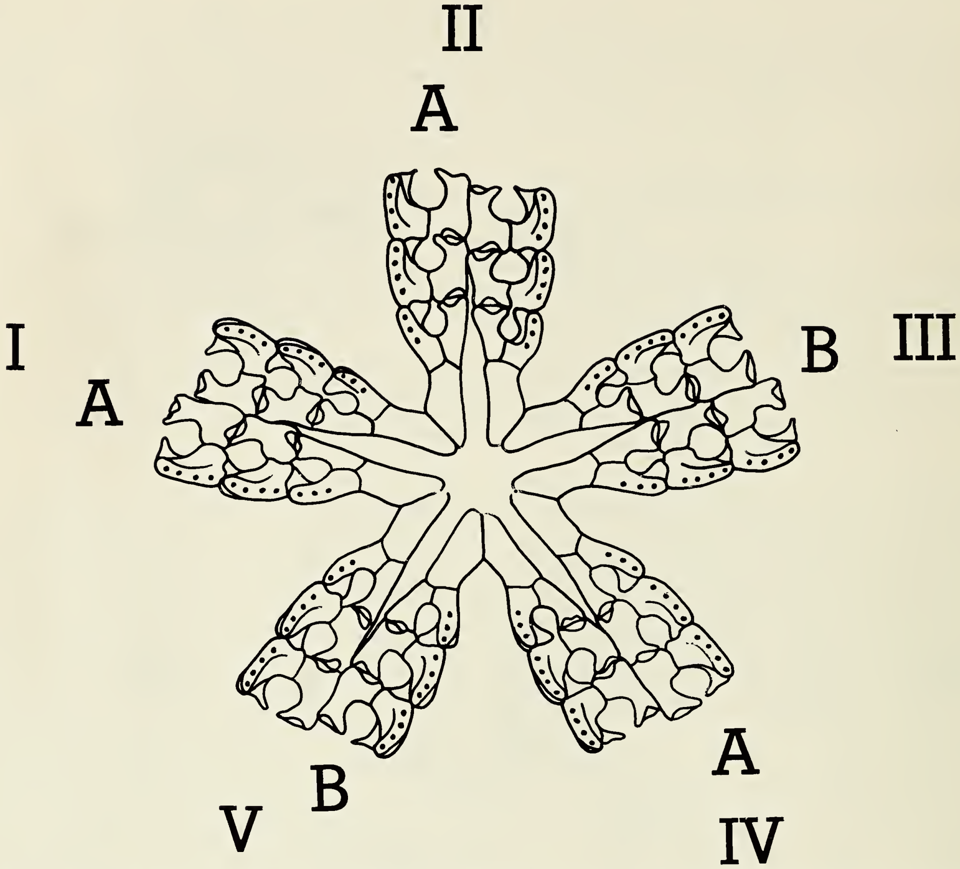

Fig. 2. Lovén's law in the Devonian ophiuroid *Eugasterella thorni* (oral side). The ambulacral half-series on the anticlockwise side of each arm is labeled as either in advance (A) or behind (B) the half-series on the clockwise side of the arm. The arrangement AABAB is Lovénian. From comparisons with edrioasteroids (Figs. 3, 4), ray II is anterior and interray IV/V is posterior. Right posterior interray III/IV contains the madreporite (not shown). (Modified from Hotchkiss 1978; after Kesling 1969.)

164). This arrangement is termed Lovén's law of heterotropy by Gordon (1929) and simply Lovén's law by Melville & Durham (1966:U222). The unequal size of the basicoronal plates initiates columns of echinoid ambulacral plates that alternate according to an AABAB rule (Appendix 1). Based on this rule I showed that Lovén's law applies to Paleozoic ophiuroids that have alternating ambulacral plates (Hotchkiss 1978). Here I report Lovén's law in two edrioasteroids and an ophiocistioid. It could affect the inclusion of somasteroids and asteroids in the clade Eleutherozoa if there was cause to think that they obeyed a law that was different from Lovén's law, or cause to think that they could not obey Lovén's law. I report that somasteroids and asteroids had alternating ambulacral plates (primitive character state) and that it is plausible that Lovén's law will eventually be found to apply to somasteroids and to asteroids.

Echinoids (Fig. 1). — Lovén's law has been so singularly associated with echinoids that it was used by Jackson (1929:508) as part of the evidence that *Bothriocidaris* is properly assigned to the Echinoidea. Lovén's law was found to apply to *Bothriocidaris ar-*

chaica by Jackson (1912:34, 241, plate 1 fig. 1; 1927:451) and to *B. pahleni* by Mortensen (1930) [see also Durham 1966:figs. 214–217]. MacBride & Spencer (1938:121, fig. 10) reported that Lovén's law appears to apply to the Upper Ordovician *Aulechinus grayae.*

Ophiuroids (Fig. 2).—Hotchkiss (1978) reported that Lovén's law applies to Paleozoic ophiuroids and suggested that the ophiuroid madreporite is located in interradius III/IV. Harper (1985) described new material of *Eugasterella logani* (Hall), reporting that it conformed with Lovén's law and that "the madreporite is situated on the disc in interray III/IV, adjacent to the distal portion of the first ambulacral of IV." The association of the madreporite with a ray (now identified as ray IV), as noted by its eccentric location in the interradius, has been documented in both the Zeugophiurina (Sollas & Sollas 1912:216) and the Lysophiurina (Spencer 1914:37, 1925:277, 1934: 459; Hotchkiss 1970:69, Kesling & LeVasseur 1971:329, Petr 1989:8, text-fig. 6). Petr (1989:8, 16) suggested that movement of the lateral plate functioned to uncover and to irrigate the madreporite.

Appendix 1 presents additional data on Lovén's law in Paleozoic Oegophiurida. Complete specimens that obey Lovén's law have the madreporite in interradius III/IV. Analysis of incomplete specimens demonstrates that each arm position relative to the madreporite has a preferred character state, that the preferred character states conform with Lovén's law, and that this pattern identifies the madreporic interradius as III/IV.

Somasteroids.—Lovén's law has not yet been documented in somasteroids. As part of his research on the ancestry of sea stars, Fell (1963a,b,c) studied the morphology of the early Paleozoic somasteroids collected by Thoral (1935) and described by Spencer (1951). He found that the ambulacral ossicles of *Chinianaster* and *Villebrunaster* form opposite pairs in the middle and base of the arm but form alternating series in young specimens and at the tip of the arm in older specimens (1963c:465, fig. 5).

The somasteroid *Archegonaster* has alternating ambulacrals (Spencer 1951:102, fig. 10; Smith & Jell 1990:753, fig. 40). The madreporite is typically preserved, including portions of the stone canal (Spencer 1951:105, Smith & Jell 1990:762). Thus, a careful study of the arrangement of the ambulacral plates at the mouth frame (such as Smith & Jell 1990:fig. 47D) recorded with reference to the location of the madreporite would permit an analytical search for Lovén's law in the same manner as done in this paper (see Appendix).

The statement of Spencer & Wright (1966: U39) that in somasteroids the ambulacrals are "generally in opposite pairs but apparently alternating in some forms" conveys the wrong emphasis. In addition to *Archegonaster, Chinianaster* and *Villebrunaster* which have been mentioned above, alternating ambulacrals are described for *Ampullaster* (Fell 1963c:fig. 6A,D) and all of the Archophiactinidae (Spencer 1927:361). The recently described *Ophioxenikos langenheimi* has "proximal ambulacrals slightly offset, distal ambulacrals clearly offset across arm axis" (Blake & Guensburg 1993: 109). It is plausible that *Archegonaster* and other Paleozoic somasteroids with alternating ambulacral ossicles will eventually be shown to have the ambulacrals arranged in accordance with Lovén's law.

Asteroids.—Lovén's law has not yet been documented in asteroids. Although Spencer & Wright (1966:U13) stated "In this subclass the ambulacrals are invariably opposite one another, never alternating, as in somasteroids and early ophiuroids," this is not truly invariable. The situation in the Paleozoic Asteroidea echoes that of the somasteroids. The ambulacrals in some of the older species are not exactly opposite, but neither are they definitely alternating except perhaps near the tip of the arm. Spencer (1914:19) used the phrase "irregularly alternating" and expressed the view that this

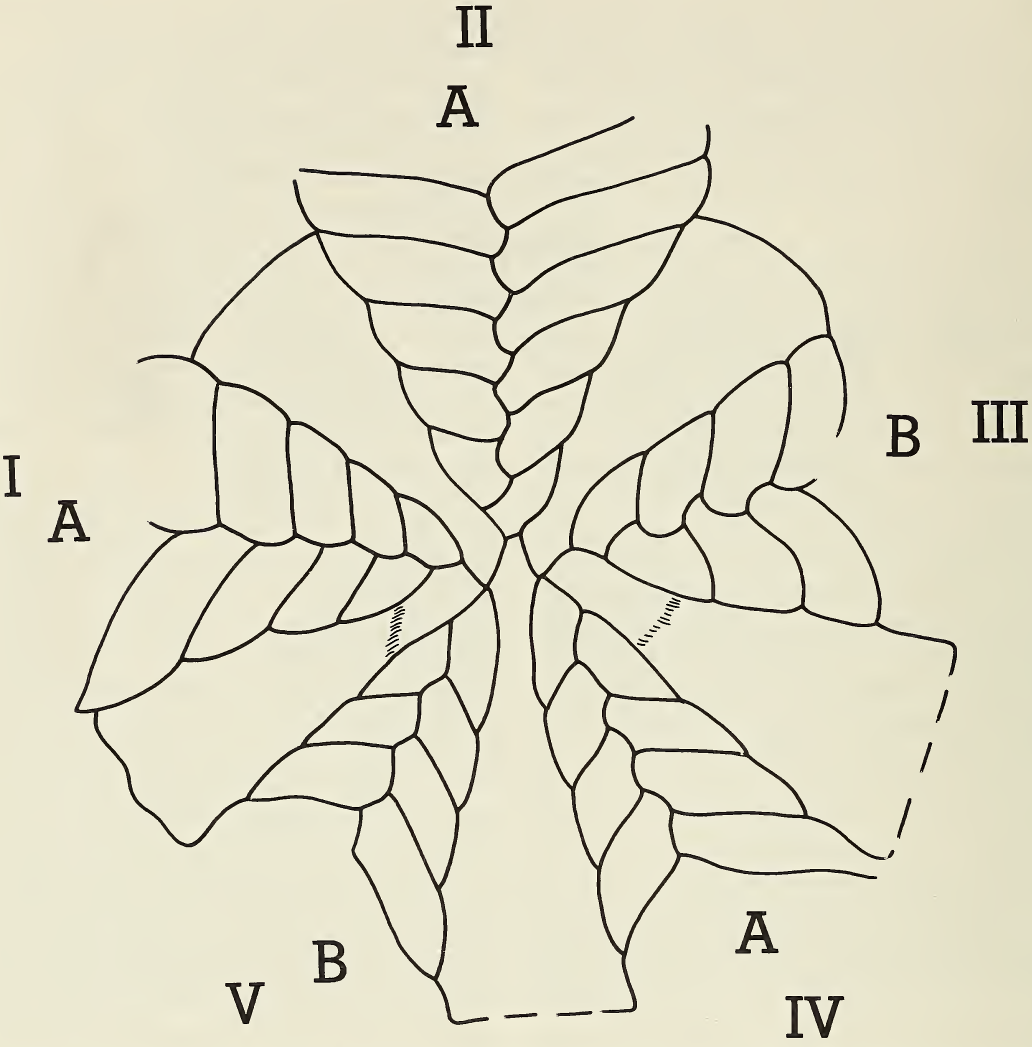

Fig. 3. Lovén's law in the Ordovician edrioasteroid *Astrocystites ottawaensis.* The cover plate half-series on the anticlockwise side of each ambulacrum is labeled as either in advance (A) or behind (B) the half-series on the clockwise side of the ambulacrum. The arrangement AABAB is Lovénian. Ray II is anterior; posterior interray IV/V contains the anus, hydropore and unpaired oro-tegminal plate. (Copied and annotated from Bather 1914b.)

was the primitive stock "from which two sets of forms arose, namely, those with opposite ambulacralia and those with definitely alternating ambulacralia."

Blake & Guensburg (1989:table 1, character no. 16) described the primitive character state of the "positions of ambulacral ossicles relative to one another across the furrow" as "weakly and locally alternate". They listed *Salteraster, Lacertasterias* and *Schondorfia* as having this primitive character state, and *Hudsonaster, Devonaster* and *Calliasterella* as having the derived character state of "opposite."

Other specific examples of early asteroids with "irregularly alternating" ambulacral plates are in the genera *Lanthanaster* and *Palasterina.* The holotype of *Lanthanaster cruciformis* [=*L. intermedius* (Schuchert, 1915); see Branstrator 1979] is very well preserved but has the region of the first few ambulacrals of each arm obscured from view by adambulacral spines. According to Branstrator (1972:68), "It is difficult to determine what the natural arrangement of ambulacral pairs across the ambulacral groove was when the animal was alive. The ambulacral ossicles of an arm appear (arm A, E) to have occurred in an alternate biseries, but the specimen is admittedly disturbed." Thus it is not possible to score the ambulacral plate arrangements of the arms as "A" or "B", but this will hopefully be possible in some future material. The madreporite is in an oral interradius. According to Spencer (1922:228) the holotype of *Palasterina bonneyi* Gregory [=*P. antiqua* (Hisinger); see Spencer 1922:228] has ambulacrals that "are opposite or slightly alternating in the proximal region, distinctly alternating distally"; a larger plate in one oral interradius "may represent the madreporite, but one cannot be certain of the madreporiform markings." It is plausible that *Lanthanaster, Palasterina* and other Paleozoic asteroids with "irregularly alternating" ambulacrals will eventually be shown to have the ambulacrals arranged in accordance with Lovén's law.

Edrioasteroids (Figs. 3, 4).—In Lower Cambrian *Camptostroma* and *Stromatocystites* the ambulacra are constructed of flooring plates arranged biserially and alternately (Paul & Smith 1984:470). This suggests searching for Lovén's law in edrioasteroids.

Order Edrioblastoida (see Smith & Jell 1990): Bather's illustration (1914b:201, fig. 6; Fay 1967:S289, fig. 172) of the exact sutures of the Middle Ordovician edrioblastoid *Astrocystites ottawaensis* Whiteaves, reproduced here as Fig. 3, shows that the arrangement of the cover plates conforms with Lovén's law (Hotchkiss 1978:543). It seems likely that the underlying ambulacrals are arranged in the same pattern as the cover plates. If the null hypothesis H0 is that the arrangement of ambulacrals in the different rays is a matter of chance and that the "A" arrangement is as probable as the "B" arrangement, then the probability of obtaining Lovén's law by chance alone in this specimen is 5/32 = 0.165. Thus the one specimen does not allow us to reject the null hypothesis; however, the edrioasteroid that is next described turns out to provide the additional evidence that is needed to reject the null hypothesis and to draw a conclusion regarding Lovén's law in edrioasteroids.

Order Stromatocystitoida: Smith's (1985: 724, fig. 7) camera lucida drawing of specimen USNM 376690 of *Stromatocystites walcotti* Schuchert accurately presents the precise arrangement of the proximal ambulacral flooring plates including the oral area. [A portion of this drawing was published by Paul & Smith (1984:454, fig. 7).] Photographs of this specimen (Smith 1985: plate 88, figs. 3–5) corroborate the drawing. Essential to my interpretation is the information that Smith's drawing shows the interior of the oral surface. The plate arrangement is thus the mirror image of the plate arrangement that would be seen looking at the exterior oral surface. Using overhead transparency sheets and a photocopy machine, the image was reversed to simulate an exterior view of the oral surface (Fig. 4). Analysis of this external view shows that Lovén's law applies to this specimen.

The probability that Lovén's law will occur in this specimen by chance alone under the null hypothesis is 5/32 = 0.165. Comparison shows that Lovén's law in this specimen of *Stromatocystites* has the same relation to the posterior interradius as in the specimen of *Astrocystites.* The probability that the same relation of Lovén's law to the posterior interradius will occur in this specimen of *Stromatocystites* as was observed in the specimen of *Astrocystites* by chance alone under the null hypothesis is (5/32)

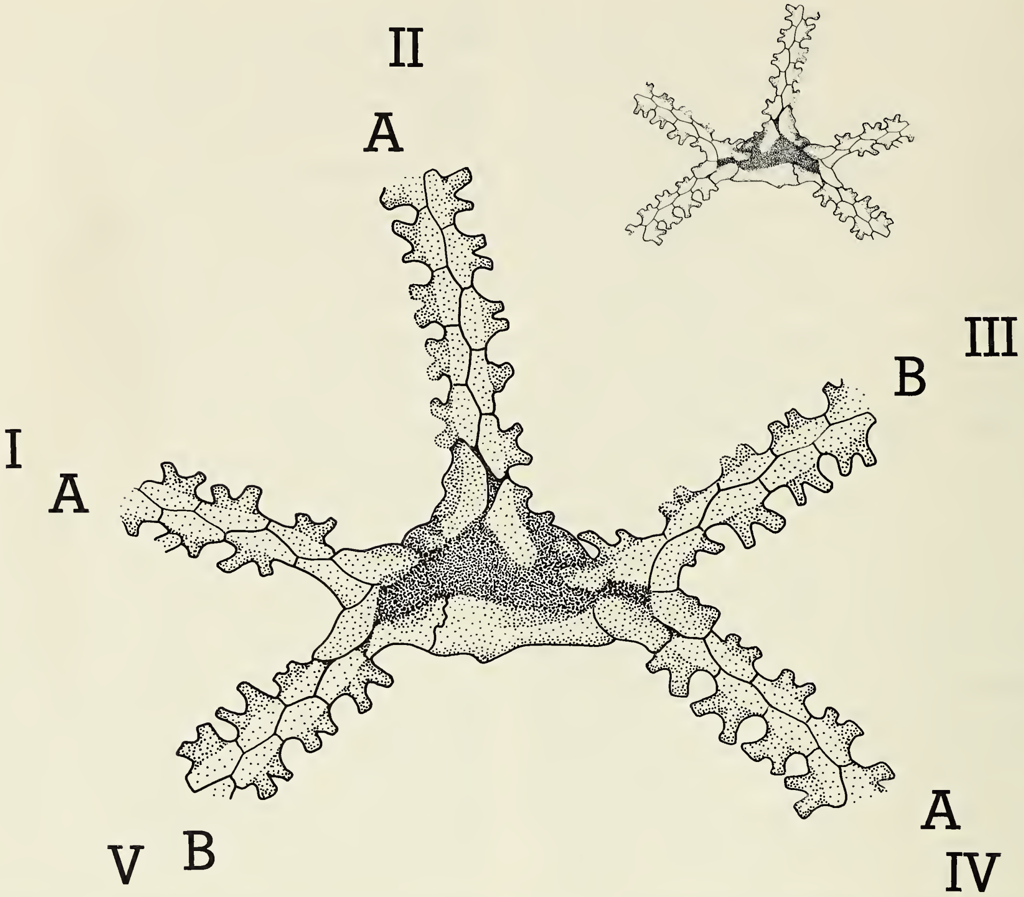

Fig. 4. Lovén's law in the Cambrian edrioasteroid *Stromatocystites walcotti.* Smith's drawing of the oral area and the proximal ambulacral flooring plates as seen from inside the test (small insert) has been reversed in the enlarged figure to simulate an external view. The flooring plate half-series on the anticlockwise side of each ambulacrum is labeled as either in advance (A) or behind (B) the half series on the clockwise side. The arrangement AABAB is Lovénian. Ray II is anterior; posterior interray IV/V contains the periproct and hydropore. The meaning of Lovén's law is interpreted from *Stromatocystites* to be a vestige of 2-1-2 pentaradiate organization, and to indicate a triradiate ancestry. (Copied and annotated from Paul & Smith 1984.)

(1/5) = 1/32 = 0.033. Thus, I reject the null hypothesis in favor of the belief that the observed arrangement of the ambulacrals is not due to chance alone. The new working hypothesis is that Lovén's law applies to *Stromatocystites walcotti* and to *Astrocystites ottawaensis* and that the posterior interradius is interradius IV/V in both species.

Ophiocistioids (Fig. 5).—Jell's (1983:230, fig. 14) camera lucida drawing of the oral surface of the well preserved holotype of the ophiocistioid *Gillocystis polypoda* shows the arrangement of the podial pores in the five ambulacral areas, together with the location of the madreporite and the periproct. Examination of Jell's drawing, reproduced here as Fig. 5, shows that Lovén's law applies to the arrangement of the podial pores, which alternate according to the AABAB pattern of Paleozoic ophiuroids. Based on Lovén's law, the madreporite of *Gillocystis* is in in-

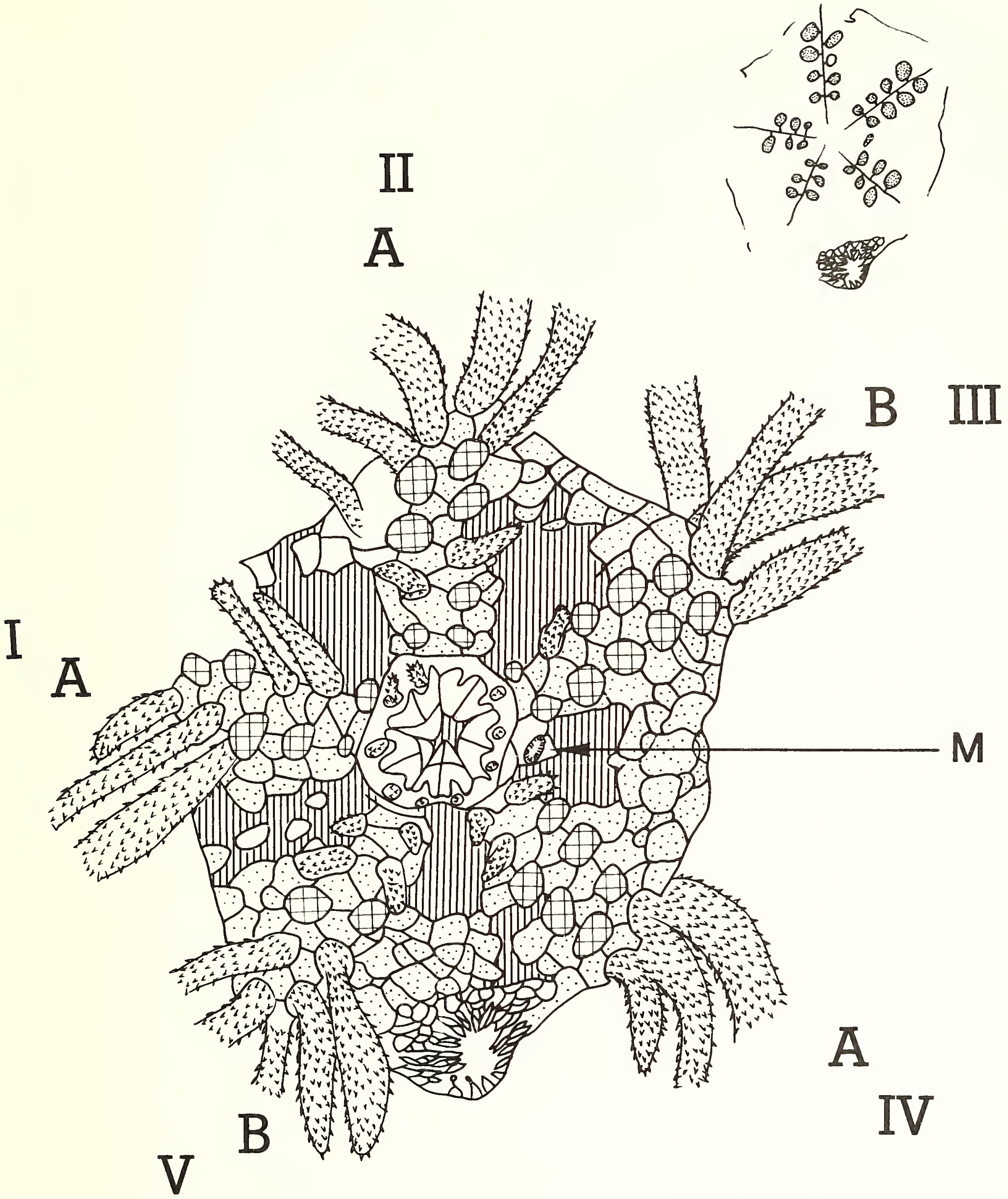

Fig. 5. Lovén's law in the Devonian ophiocistioid *Gillocystis polypoda* (oral side). Podial pores with no podia preserved are cross hatched. The small insert is a tracing of the podial pores and a reconstruction of the branches from the radial water vessel to the podia. The podial pores on the anticlockwise side of each ambulacrum are labeled as either in advance (A) or behind (B) the podial pores on the clockwise side. The arrangement AABAB is Lovénian. Ray II is anterior; posterior interray IV/V contains the periproct; right posterior interray III/IV contains the madreporite (M). (Copied and annotated from Jell 1983; areas where plates are not preserved are vertically lined or blank; positions of plates on the podia are stylized.)

terradius III/IV (as in ophiuroids), and the periproct is in the clockwise-adjacent interradius IV/V (as in edrioasteroids). The madreporite and periproct of *Sollasina woodwardi* also occupy clockwise-adjacent interradii (Haude & Langenstrassen 1976), but there are no observations concerning Lovén's law in this species.

In summary, Lovén's law is now known to apply to certain edrioasteroids, ophiuroids, echinoids, *Bothriocidaris* (considered a stem holothurian group by Smith 1984a) and an ophiocistioid. Thus, Lovén's law is not unique to ophiuroids and echinoids. As noted above, it is plausible that Lovén's law may eventually be found in the Asteroidea (such as *Lanthanaster*) and in the Somasteroidea (such as *Archegonaster*).

Symplesiomorphy of Lovén's Law

Is Lovén's law in ophiuroids, echinoids, edrioasteroids and ophiocistioids a similarity that is due to an ancestral character shared with a remote ancestor (symplesiomorphy)?

Because the relationships among echinoids, ophiuroids and edrioasteroids are distant, one must consider the likelihood (the probability under the null hypothesis H0) that these three lineages developed the same pattern of ambulacral plates merely by coincidence. [Ophiocistioids are not included because they cannot be treated as distantly related to echinoids: the jaw apparatus is so similar as to indicate that ophiocistioids were an offshoot from the echinoid lineage (Derstler 1985). Ophiocistioids may be grouped with echinoids or be substituted for echinoids, in this analysis.]

Of the 32 possible arrangements of alternating ambulacral plates around the peristome of a pentamerous animal, there are just 8 distinct patterns (Hotchkiss 1978): AAAAA, AAAAB, AAABB, AABAB, BBBBB, BBBBA, BBBAA, BBABA. Only the pattern AABAB conforms with Lovén's law. The patterns AAAAA and BBBBB can occur in an animal in only one arrangement, whereas five arrangements of each of the other six patterns can occur. Assuming that each of the arrangements confers equal fitness, the probability that three separate lineages of echinoderms would coincidentally develop the same pattern (not necessarily Lovén's law) of alternating ambulacral plates is given by $[2\times(1/32)(1/32)(1/32) + 6\times(5/32)(5/32)(5/32)] = 0.023$, which is an improbable coincidence. The probability that two lineages will coincidently develop Lovén's law given that the third lineage already conforms to Lovén's law is $(5/32)(5/32) = 0.024$, which again is an improbable coincidence. Therefore, I conclude that the presence of Lovén's law in echinoids, ophiuroids and edrioasteroids is not a chance coincidence. It is considered to be due either to a common inheritance (indicating ray homologies) or to convergent evolution (indicating a selective advantage to the pattern AABAB in each of its five arrangements but constituting a false guide to ray homologies because the five arrangements cannot be distinguished from one another). Lorenz (1974) has written a lucid account of how to distinguish convergent evolution (analogy) from common inheritance (false analogy), and here I follow the examples given in his paper very closely. In this method, if the improbable coincidental similarity has a very dissimilar function in the forms in which it occurs, then it is extremely improbable that the resemblance is due to parallel adaptation. The lifestyles of echinoids, ophiuroids and edrioasteroids are so obviously different that the functional morphology of their mouthframes and their proximal ambulacral plates must likewise be different. This makes the hypothesis H1 of a selective advantage that led to the convergent evolution of Lovén's law in these three classes very unlikely. On the other hand, the hypothesis H2 that in edrioasteroids Lovén's law is a manifestation of the 2-1-2 symmetry pattern and that in echinoids and in ophiuroids Lovén's law is a

Table 2.—Proposed ray homologies for echinoids, ophiuroids, ophiocistioids, edrioasteroids and asteroids. Roman numerals I, II, III, IV and V are used for homologous ray identifications based on recognizing Lovén's law. The numbering for edrioasteroids is different from that of previous authors (e.g., Bather 1914a, Regnéll 1966, Bell 1976a). The numbering for ophiocistioids is different from that of Jell (1983). Carpenter letters A, B, C, D and E for edrioasteroids are shown for reference (Moore & Fell 1966, Paul & Smith 1984). The ray homologies of asteroids are based on homologizing the location of closure of the ring canal in asteroids, ophiuroids and echinoids. Letters M, H, R and P mark the location of the madreporite (M) or hydropore (H), the location of closure of the hydrocoele crescent to form the ring canal (R), and the location of the anus/periproct (P).

Echinoids	II	M	III		IV	R	V	P	I
Ophiuroids	II		III	M	IV	R	V		I
Ophiocistioids	II		III	M	IV	R?/P	V		I
Edrioasteroids	II		III		IV	H/R/P	V		I
Edrioasteroids	A		B		C	H/R/P	D		E
Asteroids	A		B		C	R/P	D	M	E

vestige of this ancient symmetry, seems highly plausible. This result applies to the ophiocistioid as well. I exclude H1 and deduce from H2 that Lovén's law is a common inheritance that indicates ray homologies among ophiocistioids, echinoids, ophiuroids and edrioasteroids [see Note 2].

Ray Homologies Based on Lovén's Law

Ray homologies based on Lovén's law are proposed in Table 2. The location of the madreporite (M) or hydropore (H), the location of closure of the hydrocoele crescent to form the ring canal (R), and the location of the anus/periproct (P) are also shown in Table 2. Ray homologies for asteroids are included in Table 2 based on the proposal of homologizing the location of hydrocoele ring closure in asteroids with the IV/V interradius of ophiuroids and echinoids (Hotchkiss 1978). [The proposed ray homologies for asteroids are indicated by Carpenter letters in Table 2. Roman numerals are not used because asteroid ray identifications are not yet based on Lovén's law. Carpenter letters are assigned on the basis that the IV/V interradius of edrioasteroids is also the CD interradius.]

Location of hydrocoele ring closure.—With the ray homologies that are proposed in Table 2, the location of closure of the ring canal coincides in echinoids, ophiuroids and edrioasteroids and is postulated to coincide in asteroids. It is in interradius IV/V when the ray numbering is based on Lovén's law, and in the CD interradius of Carpenter's system. Data on the plane of hydrocoele closure for echinoids, asteroids and ophiuroids is taken from Bury (1889). Bather's opinion on the location of the plane of hydrocoele closure in edrioasteroids is accepted (1915:401): "in the primitive Pelmatozoön, so far as can be inferred from the embryology of *Antedon* and the anatomy of early forms, the closure of the hydrocoele was in what I [Bather] have termed the M plane [the plane containing the hydropore]." I have no data on the location of ring closure in ophiocistioids (but predict that it was in interradius IV/V).

Location of the madreporite.—With the ray homologies that are proposed in Table 2, the madreporite has a different location in four out of five groups. The one exception is that the madreporite is in interradius III/IV in both ophiuroids and ophiocistioids. Relocation of the hydropore/madreporite from interradius IV/V in edrioasteroids to interradius III/IV in ophiuroids and ophiocistioids may mean that the hydropore was duplicated on either side of ray IV in some ancestor. I accept the assumption of MacBride & Spencer (1938) that the madreporite in *Ectinechinus* and *Eothuria* (Upper Ordovician) lies in interradius II/III. Relocation of the madreporite in asteroids from its original position in edrioasteroids was already conceded by Bather (1915), with the explanation that the hydropore has only a secondary connection to the hydrocoele [see Note 3]. Evidence cited by Moore & Fell (1966) against the doctrine of a "firmly fixed location of the madreporite in all echinoderm groups" included a documented history of migrations of the madreporite to different portions of the echinoid apical system; the fact that some asteroids carry several madreporites scattered about the aboral side; and the fact that several euryalid ophiuroids have five madreporites, or else five hydropores, disposed one in each interradius.

Location of the periproct/anus.—With the ray homologies that are proposed in Table 2, the periproct/anus has the same location in edrioasteroids, asteroids and the ophiocistioid. It is in interradius IV/V when the ray numbering is based on Lovén's law, and in the CD interradius of Carpenter's system; this is the posterior interradius of edrioasteroids. Ophiuroids do not have an anus [see Note 4]. In echinoids the anus/periproct has migrated to a new location: in exocyclic echinoids it is in the posterior V/I interradius; in endocyclic Cidaroida and post-cidaroid groups the anus is incipiently displaced in the direction of the V/I interradius, as indicated by the tendency documented by Jackson (1912, 1927) for oculars V and I to be insert (Fell *in* Moore & Fell 1966). In the Saleniinae and some other Echinacea there has been a tertiary posterolateral movement of the anus within the apical system toward ocular I (Fell & Pawson 1966:U368); in *Temnopleurus reevesi* the anus is markedly excentric, midway between oculars I and II (Clark & Courtman-Stock 1976:fig. 251; Baranova 1982:115, fig. 1). I suspect that the position of the madreporite and the anus in the ophiocistioid *Gillocystis* represents the original condition for echinoids.

Bilateral symmetries.—When oriented according to Table 2, the 2-1-2 plane of bilateral symmetry of edrioasteroids and Lovén's plane of bilateral symmetry through the bivium and trivium of echinoids do not coincide. In exocyclic echinoids ray III is anterior, and in edrioasteroids ray II is anterior. It is clear that there have been multiple changes in symmetry during the evolution of echinoderms, such as from bilateral to radiate, and from radiate to bilateral (Bell 1976a:31, Caster 1967:S583, footnote) [see Note 5]. Vestiges of such changes may be retained in the morphology and ontogeny of the organism. The 2-1-2 plan developed from an original plan of triradiate symmetry (Bather 1900a, Fell 1966a, Sprinkle 1973). The hypothesis H2, established above, is that in edrioasteroids Lovén's law is a manifestation of the 2-1-2 symmetry pattern and that in ophiocistioids, echinoids and ophiuroids Lovén's law is a vestige of this ancient symmetry. In echinoids this result is particularly significant as it shows that Lovén's III-5 plane of bilateral symmetry, which Fell showed to be a fundamental feature of all orders of echinoids from the Cidaroida onward, is a new, secondary plane. The hypothesis H2 leads by deduction to the hypothesis H3 that ray II was the anterior ray in ancestral lines of the Echinoidea. The Ordovician *Ectinechinus* and *Eothuria* have elongated tests with anterior mouth and posterior anus; they are elongate not in Lovén's III-5 plane, but along von Übisch's II-4 axis of primordial symmetry, with ray II anterior (MacBride & Spencer 1938) [see Note 6]. These observations support the hypothesis H3 that ray II was the original anterior ray in both echinoids and edrioasteroids. Applied to the ophiocistioid *Gillocystis*, the hypothesis H3 that ray II was anterior leads to the deduction that the periproct was posterior.

Identification of the Axis of the Bilateral Larva in the Adult

Echinoderm larvae have a definite anterior-posterior axis and a marked bilateral symmetry. Proposals by von Übisch (1913, 1927), Lane & Webster (1967), Macurda (1980) and Smith & Arbizu (1987) as to which axis of an echinoderm postlarva corresponds with the axis of the bilateral larva are summarized in Table 3 [see Note 7].

As the working hypothesis H4 for the present study I assume that the relation of the axis of anterior-posterior organization of the larva to the axis of anterior-posterior organization of the imago has remained the same in echinoids, ophiuroids, edrioasteroids and ophiocistioids through inheritance from their common ancestor. Von Übisch (1913, 1927) showed that the anterior-posterior axis of the echinopluteus larva can be traced through metamorphosis by following the fate of the pieces of the larval skeleton. In this way he showed that the II-4 axis of the adult corresponds to the anterior-posterior axis of the bilateral larva, with ray II "anterior" in relation to the larva. His results were confirmed and expanded upon by Gordon (1929), Onoda (1931) and Emlet (1988, 1989) [see Note 8]. The ray homologies of Table 2 show that von Übisch's II-4 "axis of primordial symmetry" in echinoids coincides with the axis of the 2-1-2 pattern of bilateral symmetry of edrioasteroids. The 2-1-2 plan of symmetry in edrioasteroids expresses a left-right and an anterior-posterior symmetry, with ray II anterior and the anal interradius posterior. Using hypothesis H4 we therefore deduce that the anterior-posterior axis of the larva of edrioasteroids coincided with the anterior-posterior axis of the edrioasteroid, with ray II 'anterior' both in relation to the larva and in the imago. [Supporting indirect evidence is found in the many invertebrate groups that carry the anterior-posterior polarity of the larva through to the adult, including holothurians. Exceptions, when they occur, are probably due to secondary changes of symmetry, as shown here for postcidaroid exocyclic echinoids.]

Smith & Arbizu (1987) reported a situs inversus specimen of the edrioasteroid *Krama devonica* and proposed that the mirror plane for situs inversus in edrioasteroids coincides with the anterior/posterior plane of symmetry in the adult. Although their proposal may have seemed intuitively correct due to the 2-1-2 pattern of bilateral symmetry of edrioasteroids, it overlooked the fact stated by Swan (1966:414-416) that mirror images made using any axis across the animal will each produce identical situs inversus results. Thus, situs inversus by itself does not permit identification in the adult of the axis of symmetry of the larva. Nevertheless, it turns out that Smith's conjecture on the relation of the larval axis to the adult edrioasteriod is supported by the present study. [Conversely, the identifications of the larval axes proposed for crinoids by Lane & Webster (1967) and for blastoids by Macurda (1980) are not consistent with working hypothesis H4 and imply either an error in analysis, or a change in the axis relating the larva to the imago during the evolution of these groups.]

Table 3.—Synopsis of some proposals concerning the identification of an axis in the adult that corresponds with the anterior-posterior axis of the bilateral larva [see Note 7].

Echinoids	II-4	(Übisch 1913, 1927)
Crinoids	E-BC	(Lane & Webster 1967)
Blastoids	D-AB	(Macurda 1980)
Edrioasteroids	A-CD	(Smith & Arbizu 1987)

Larval Type of Ordovician Ophiuroids

It is interesting to see what can be inferred about the larvae of primitive Paleozoic ophiuroids. [Direct paleontological evidence on the larval forms of echinoderms is commented on in Note 9.] Smith (*in* Smith & Arbizu, 1987) inferred a bilateral larva for edrioasteroids based on a situs inversus specimen of *Krama devonica*. In the same paper Smith referred to mirror image forms of the carpoid *Peltocystis cornuta*. The occurrence of mirror image forms is clear evidence of the 'handedness' that comes from deriving the water vascular system from the left hydrocoele of a bilateral larva in normal larvae and from the right hydrocoele in cases of situs inversus. It seems highly likely that not only edrioasteroids but also the derived asterozoans had a bilateral larva.

The extended arms of the ophiopluteus depend on the skeletal rods for their support (Strathmann 1988:60). The acquisition of skeletal rods by echinoderm larvae was explained by Strathmann (1993:91) as an example of heterochrony (or adultation) as follows: "Echinoderms have a type of calcite skeleton unique to the phylum. Within the echinoderms, the calcite skeleton does not develop until metamorphosis in the asteroids, but in the echinoids and ophiuroids, deposition of calcite begins in the embryo and produces supporting skeletal rods in the larva. This distribution of traits suggests that the skeleton originated in postlarval stages and that the pluteus originated by accelerated skeletal development." In comparing the pluteus skeleton of echinoplutei and ophioplutei, Strathmann (1988:62) commented that "the formation and branching of the skeleton is so different between classes that homology can be questioned." He suggested (in litt.) that independent evolution of arm rods in ophioplutei and echinoplutei is the simplest and most plausible hypothesis at this time.

Smith (1984a:figure 9.4) listed the development of the pluteus type of larva and also Lovén's law of heterotropy as two of the synapomorphies [shared derived character states] between echinoids and ophiuroids [see Note 10]. This was reiterated by Paul & Smith (1984:469): "Echinoids share a number of advanced morphological innovations with Ordovician ophiuroids. These include . . . oral plating in obedience to Lovén's law and (judging from living animals) . . . the development of a pluteus larva with a skeletal framework." Ordovician ophiuroids belong to the prephrynophiurid orders Oegophiurida and Stenurida. I favor a different hypothesis based on the proposal by Fell (1966b:131) that the ophiopluteus is a postphrynophiurid development.

In a series of papers, Fell (1948, 1963b, 1963c, 1966a, 1967) expressed his view that the pluteus arose independently in ophiuroids and echinoids and that possession of the pluteus larval form is not evidence of a close phylogenetic relation between ophiuroids and echinoids. He supported his views with data from embryology and larval forms and from the fossil record and adult anatomy. Differences between the ophiopluteus and the echinopluteus were summarized by Smith (1984b:452–453) as follows: "Neither the processes nor the skeleton are identical in echinoids and ophiuroids. The ophiopluteus has no pre-oral processes and the main locomotory processes that develop early on are the posterolateral ones, whereas in the echinopluteus, elongate pre-oral processes are present, and the main locomotory processes are the post-oral ones. The posterolateral processes either appear much later in development and remain small or are absent altogether. The ophiopluteus has just two centers of calcification from which calcite rods grow, one on either side, whereas the echinopluteus has five, two on the left, two on the right, and an anterior V-shaped rod for the pre-oral processes." Fell (1948: 83) described the same principal differences in the ophiopluteus: "the preoral arms of the echinopluteus are not represented; the internal skeleton takes the form of a pair of calcareous rods in the body, each sending branches into the four arms on its corresponding side; the posterior transverse rod is not represented." These differences support the opinion already accepted by de Beer (1940:373) that this is a case of similarity through convergence (see also Mortensen 1921:227).

Fell described the development of "Kirk's ophiuroid" (Fell 1941a), made observations on development in *Ophiomyxa* (Fell 1941b), and described the development of *Amphi-*

pholis squamata (Fell 1946). Fell (1941a: 416, 1948:fig. 4) observed that there was no trace of larva in the development of Kirk's ophiuroid and initially placed this form of development as the end member of his series of the regression of metamorphosis (Fell 1945:90, fig. 20, 1948:98, fig. 6). Subsequently, he identified Kirk's ophiuroid as *Ophiomyxa* sp. (Fell 1963b:fig. 15 caption, 1966b:139, 1967:fig. 25 caption), and he identified *Ophiocanops fugiens* as a surviving oegophiurid (Fell 1962). Fell then reexamined the development of the primitive Phrynophiurida and wrote (Fell 1963c:481): "Although we still know nothing of the embryology of *Ophiocanops,* many features of its anatomy declare its affinity to the Ophiomyxidae, a group of ophiuroids in which absolutely direct development occurs, without any trace of a larva at all. On the other hand, those genera of Ophiuroidea which have vestigial larvae have now been shown to fall in families of relatively late derivation, from groups which have pelagic larvae. They are groups with numerous secondary features in the skeleton, far removed from the archaic forms with somasteroid-like features. Thus it is now extremely probable that there are two quite distinct types of direct development in ophiuroids, one ancient, with no vestige of larva, the other secondary and showing both by the vestigial larva and by the characters of the skeleton that it is of late origin. I now suspect that the pluteus larva will eventually be proved to be a feature evolved by ophiuroids after the separation of ophiuroids from the somasteroid line, and that the pluteus of echinoids is an entirely independent development of that group." Fell (1966a:237, 1966b: 131) proposed that the ophiopluteus evolved in the order Ophiurida and was not the original larval form of ophiuroids. The Ophiurida are shown on paleontological and morphological evidence to be a late grade of evolution (Fell 1963b:410, Table 2).

Fell's work was reviewed and extended by Dorothy Patent (1970) who described the early embryology of the basket star *Gorgonocephalus caryi.* The embryos reached a pentagon stage, without podia, before dying. Further development may occur in nature inside polyps of the alcyonarian *Gersemia.* She reported (1970:262): "At no time did cilia or other locomotory structures develop. The development of *G. caryi* does not resemble that of any other ophiuroid studied. There is no trace of a pluteus, and it is postulated that the pluteus evolved after the Phrynophiurida and the Ophiurida were differentiated."

Strathmann (1974:334-336, 1975, 1978) has persuasively argued that non-feeding larvae appear to be derived from feeding larvae, rather than the reverse. He noted that planktotrophic development appears to have been lost entirely from all lines of descent in the order Phrynophiurida [see Note 11]. He reasoned that because "members of the order Ophiurida with lecithotrophy probably do not include the ancestors of the Phrynophiurida," lecithotrophic development must have evolved independently in the Phrynophiurida or their ancestors. In other words, the Phrynophiurida must have had a planktotrophic ancestor.

Combining the proposals of Fell, Patent, Strathmann, and Smith, I speculate that the larval type of the stem phrynophiurid was a bilateral planktotroph, but not yet an ophiopluteus. This hypothetical sequence is illustrated in Fig. 6, which includes the notion (following Fell 1962) that *Ophiocanops* may be a surviving representative of the stem group of the Order Phrynophiurida.

Ray Homologies and 2-1-2 Symmetry

Concerning the 2-1-2 pattern of ambulacra in Cambrian echinoderms, Paul & Smith (1984:470) stated that "in all of these early pentaradiate echinoderms, the single unbranched ambulacrum lies opposite the interambulacrum that contains the periproct, hydropore and gonopore (when they can be recognized)." They make it obvious

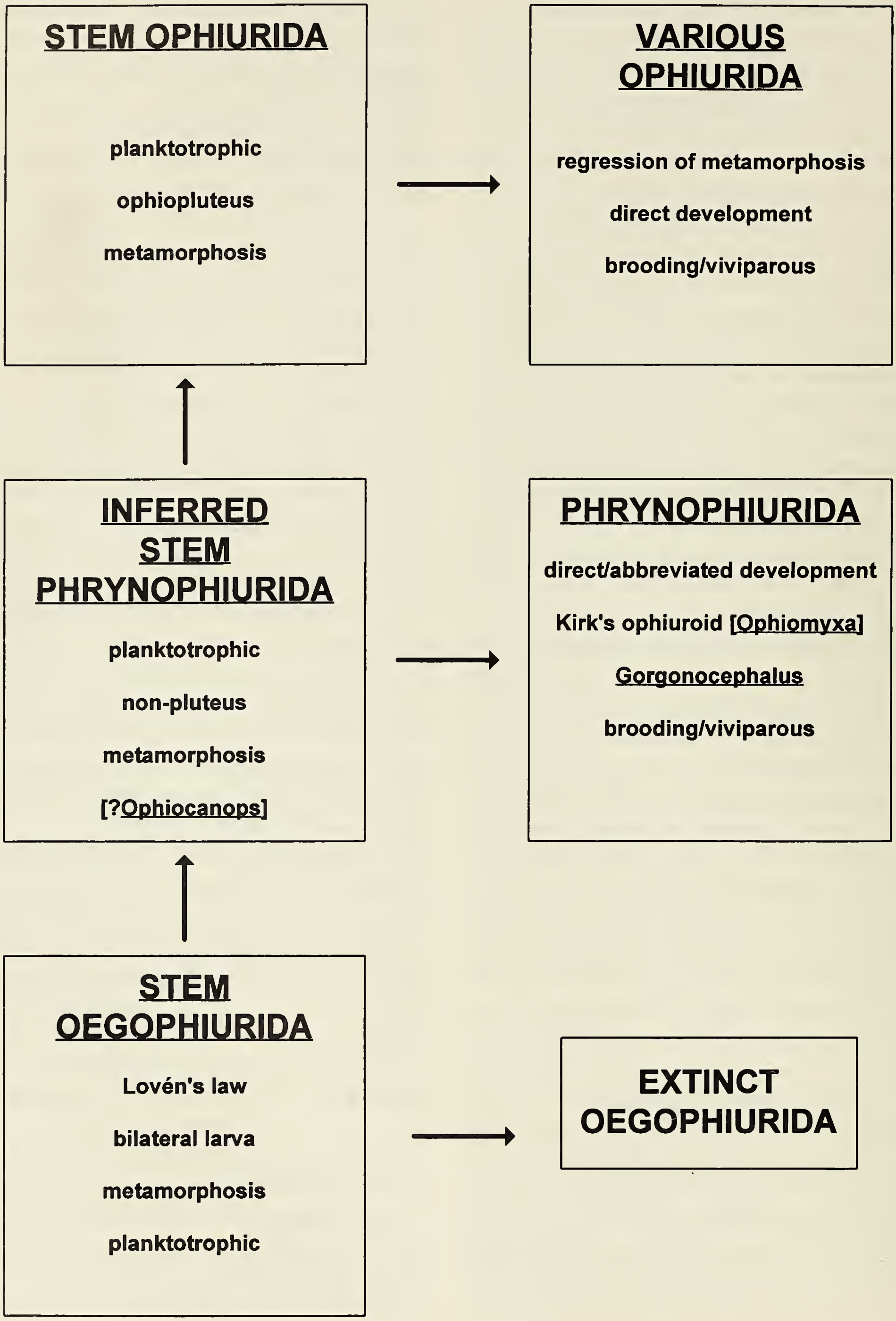

Fig. 6. Inferred evolution of ophiuroid larvae and ophiuroid development. The larval type of the stem phrynophiurid is inferred to have been a bilateral planktotroph, but not yet an ophiopluteus. The ophiopluteus is a postphrynophiurid development. Hence the similarity of the pluteus larvae of ophiuroids and echinoids is judged a homeomorphism.

that the solution to ray homologies is to identify the 2-1-2 pattern in the descendent groups. The present study shows that echinoids, ophiuroids, edrioasteroids and an ophiocistioid have retained the imprint of the 2-1-2 pattern of bilateral symmetry in the form of Lovén's law. Accordingly, ray homologies based on the 2-1-2 pattern of Lovén's law, as presented in Table 2, satisfy the requirements established by Paul & Smith.

Citing Lovén (1874), Fell (*in* Moore & Fell 1966) interpreted Lovén's law of heterotropy as a correlate of Lovén's plane of bilateral symmetry. Because the basicoronal plates of *Bothriocidaris* conform with Lovén's law of heterotropy, this (supposed) correlation enabled Fell to write (p. U124): "The archaic *Bothriocidaris* (Ord.) at least already exhibited the same anteroposterior plane of symmetry that is manifested in the Cidaroida and in post-cidaroid groups, as indicated by the potential, incipient, or consummated migration of the anus into interamb 5" [see Note 12]. It now turns out from the discovery of Lovén's law in the Cambrian edrioasteroid *Stromatocystites* that Lovén's law is more ancient than Lovén's plane of bilateral symmetry. Lovén's law appears to be a manifestation of the plane of symmetry of 2-1-2 pentaradiate echinoderms, and Lovén's plane is a superimposed secondary development in echinoids. In Lovénian symmetry, ray III is anterior; in 2-1-2 symmetry it is ray II that is anterior.

Adult Symmetry and Phylogeny

Bell (1976b:1017) studied the early growth stages of edrioasteroids and showed that "edrioasteroid ontogeny bespeaks a primitive triradiate symmetry that was later modified to a pentaradiate plan." He remarked that echinoids and Asterozoa, among others, show no apparent signs of triradial symmetry. He concluded (p. 1018) that "If some classes of echinoderms are primitively triradiates . . . and if, in contrast, others are indeed primitively pentaradiates, then a major phylogenetic dichotomy occurred early in the history of this phylum." The current research helps to remove this dichotomy and to unify the evolutionary history by showing that Lovén's law in echinoids, ophiuroids and ophiocistioids is a manifestation of the triradiate symmetry (2-1-2 pattern) of edrioasteroids.

The current research helps to answer questions posed in my first study: whether Lovén's law independently evolved in echinoids and ophiuroids, or whether it is indicative of a recent common ancestry between echinoids and ophiuroids, or whether Lovén's law is fundamental to the ground plan of the phylum (see Hotchkiss 1978). The probabilities calculated above show that the presence of Lovén's law in echinoids, ophiuroids, edrioasteroids and ophiocistioids is not a chance coincidence. Because edrioasteroids and ophiocistioids also obey Lovén's law, it is clear that Lovén's law is not evidence of a recent common ancestry between echinoids and ophiuroids [see Note 13]. My suggestion that Lovén's law might be fundamental to the ground plan of the phylum was based on the 'Treatise' classification (Fay 1967) of *Astrocystites* in the Class Edrioblastoidea, within the Subphylum Crinozoa, making it seem totally unrelated to either echinoids or ophiuroids. The situation is different now that Smith & Jell (1990) have shown that *Astrocystites* is an edrioasteroid. The result of this change is that all of the echinoderms in which Lovén's law is now known belong to classes that are placed by Smith (1984b) in the Subphylum Eleutherozoa. Therefore, I abandon my earlier suggestion and offer the more restricted hypothesis H5 that Lovén's law is fundamental to the ground plan of the clade Eleutherozoa (sensu Smith 1984b).

Mortensen's studies led him to regard *Bothriocidaris* "as a specialized offshoot from the Diploporite Cystids" (Mortensen 1928:93, 1930), and this caused him to search for Lovén's law in diploporite cystoids. He regretted that he did not have any definite proof of Lovén's law in diploporite cystoids, but he argued that "it is not so very wild a suggestion"; he also reasoned that if Lovén's law is due to mechanical reasons, then it might have arisen independently in *Bothriocidaris* (Mortensen 1928: 107, 1930:343). I have examined the illustrations in the 'Treatise' and other sources, hoping to detect Lovén's law in cystoids. I did not find Lovén's law but found an altogether different pattern. The 2-1-2 ambulacral areas of Blastozoa such as the cystoids *Cystoblastus, Bulbocystis, Protocrinites* and *Glyptosphaerites,* and the eocrinoids *Rhopalocystis, Mimocystites* and *Ascocystites* are all of the same "handedness", so that if one gives off a brachiole on the left side before any arise on the right, then it is that way in each of the ambulacral areas. This blastozoan pattern is so regular in its own way that it leads to the hypothesis H6 that there are at least two distinct constructions of 2-1-2 symmetry: that seen in the Blastozoa, and that seen in the Eleutherozoa. [Derstler (1985) maintained the crinoids as a 2-1-2 clade distinct from blastozoans and edrioasteroids, and so possibly there is a third construction of 2-1-2 symmetry (not studied here).] These observations support Derstler's working hypothesis that the transition from triradiate to 2-1-2 symmetry may have occurred independently in these groups.

[Epilogue: Thanks to Dr. David L. Pawson I received a copy of a new paper by Dr. Reimund Haude (1994) on fossil Holothuroidea (Eleutherozoa) just before returning this manuscript to the editor (February 1995). I wish to bring this paper to the attention of readers and to comment on its significance to the present results. Dr. Haude has observed in the pharyngial ring of a Devonian holothurian that the radial pieces have a left and a right anterior process, and that in each radial element one or the other of these processes is pierced by a pore. The pattern of these piercings is summarized by a RRLRL rule, where R stands for the right anterior process being pierced, and L for the left anterior process. Dr. Haude noted that this pattern might very well reflect Lovén's law in the ambulacral plates of the ancestor to the holothurians. Thus his observations support the hypothesis H5 that Lovén's law is fundamental to the clade Eleutherozoa. The relation of the RRLRL rule to the madreporite or to the bivium and trivium of holothurians is not yet known, but it seems likely that this information will be determined in the near future. At that time it will become possible to add holothurians to the table of ray homologies.]

Notes and Acknowledgements

Note 1.—When the solution to the question of ray homologies among the classes of echinoderms has been worked out, it will suffice to have a single system of ray identifications. At the present time there are several conflicting suggestions that purport to answer the question of the true ray homologies, including the one presented in this paper. In this circumstance it may be advantageous to have both Carpenter letters and Roman numerals available for the labeling of the rays. I recommend use of Roman numerals for ray identifications that are based on Lovén's law. Roman numerals were established for echinoids by Lovén (1874). Lovén (1874: pl. 53) numbered the rays of asteroids based on identifying the location of the madreporite with the II/III interradius of echinoids; Lovén (1874:88, figure) correctly observed the location of the asteroid anus, drawing it in interradius I/II adjacent to the madreporic interradius II/III. Gemmill (1914:276; see also Chadwick 1923:9) numbered the rays of asteroids based upon the location of the closure of the hydrocoele ring, beginning with I at the anterior (or dorsal) horn of the hydrocoele crescent, and proceeding clockwise in oral view. This placed the madreporite of asteroids in interradius I/II and the anus in V/I. Bather (1914a; see also Regnéll 1966, Bell 1976a:9) identified the ambulacra of edrioasteroids with Roman numerals: I is left posterior, II is left anterior, III is anterior, IV is right anterior, and V is right posterior; the anus and hydropore are in interradius V/I. Spencer used Roman numerals in his monograph of the Paleozoic Asterozoa. His text-figure 1 (Spencer 1914:5) of the "Pelmatozoan ancestor of the Asterozoa" shows the water pore in interradius IV/V and the numerals I through V in clockwise manner when looked at from the oral surface. His text-figure 59 (Spencer 1916:103) of *Mesopalaeaster*(?) *ketley* has the madreporite in interradius I/II and numerals I through V applied in clockwise manner when looked at from the aboral (apical) surface. I believe that he used the latter method to number the rays of *Protaster sedgwicki* (Spencer 1934:459–460). Hahn & Brauckmann (1981: 9) used the madreporite of the ophiuroid *Chattaster hueffneri* [as *C. dillensis*] to identify the right anterior interradius (by analogy with echinoids; see Haude 1982:25). Jell (1983) numbered the rays of the ophiocistioid *Gillocystis* with the periproct in interradius V/I (by analogy with echinoids).

Note 2.—A consequence of this finding is that Asterozoa with alternating ambulacrals must have been ancestral to those with opposite ambulacrals. In fact, this is exactly what Fell (1963c:476) had concluded from the arrangement of the ambulacrals in *Chinianaster* and *Villebrunaster:* "Since we have ascertained that the ambulacral ossicles alternate near the tip of the arm, and in the young stages of *Chinianaster,* it follows from Jackson's (1899, 1903) so-called "law of localized stages" that the opposite condition of ambulacral ossicles must have been derived from an original alternating condition. This alternating condition was retained in *Archegonaster,* in some Paleozoic asteroids, and in some of the Paleozoic ophiuroids."

Sollas & Sollas (1912:223) reported difficulty in deciding whether the free, partly alternating ambulacral ossicles of primitive Paleozoic ophiuroids represented alternation that was natural or that was due to displacement of free opposite ambulacral ossicles either during life or after death. The current research helps to resolve this difficulty by determining that the progression of evolution of the ambulacral ossicles in ophiuroids must have been from an alternating arrangement that obeyed Lovén's law, to a partly alternating condition, ultimately leading to ossicles that are paired. As noted by Sollas & Sollas, the paired ossicles were at first free, and later they connected and fused to form vertebrae.

Fell (1963b,c) removed the asterozoans from the Eleutherozoa when he proposed that somasteroids with metapinnular structure evolved from crinoids. The evidence presented here places the constraint of improbable chance coincidence or parallel evolution of Lovén's law onto that proposal. The cumulative evidence from the present study, from reanalysis of plate homologies (Hotchkiss 1993), and from the Middle Cambrian Burgess Shale crinoid *Echmatocrinus* (Sprinkle 1973) is that the crinoid arm and the somasteroid ray do not appear to be comparable structures. The conclusion that Lovén's law is a plesiomorphic character supports the working hypothesis of Bather (1900b) and Smith & Jell (1990) that the ancestry of sea stars is among edrioasteroids.

Note 3.—It seems that in asteroids the madreporite does not develop in the same position that it does in ophiuroids, because assigning the location of the closure of the ring canal to interradius IV/V places the asteroid madreporite in V/I. This puts an unexpected gulf between the ophiuroids and the asteroids. Bather (1915) tried to solve the problem of deriving the asteroids from edrioasteroids by invoking "a shifting of the whole hydrocoele [such] that each lobe of it becomes applied, not to the ray to which it would (especially on any homology with

Pelmatozoa) naturally belong, but to the neighboring ray." Bather also had to propose (p. 401) that "Such shifting need not involve the hydropore, with which the hydrocoele has only a secondary connection." Embryology is beyond the scope of this paper and beyond my own expertise. However, it seems to me that the best explanations concerning the relocating of the madreporite during the evolution of the echinoderm classes will most likely be associated with evolutionary changes that occurred in the larvae and in the process of metamorphosis. Perhaps the data are already available. [One of my own unsuccessful attempts at a solution may be worth noting. We know that loss or gain of rays can occur at the ends of the hydrocoele crescent during metamorphosis (Hotchkiss & Seegers 1976). It seemed to me that this offers the possibility of losing and gaining rays such that the ray count remains at five. This could change the relative positions of the madreporite and the anus in edrioasteroids, asteroids, echinoids and ophiocistioids. However, no reasonable solution came from my attempts and I am now convinced that this has not happened. Such an event is not consistent with retaining the imprint of 2-1-2 symmetry represented by Lovén's law in ophiuroids, echinoids and ophiocistioids.]

Note 4.—In discussing the Echinozoa and the Asterozoa, Fell wrote (1963b:426): "There is no anus in archaic asteroids, nor in any ophiuroid, nor is it known in any somasteroid. An aboral anus occurs as a late acquisition in post-luidiid asteroids. On the other hand, fossils show that an aboral anus is a fundamental character of echinoids, present in the earliest forms. All holothurians have an aboral anus." In the asteroid lineage the anus arose "after the initial differentiation of the Astropectinidae, so it is not an original feature of the family, and is lacking in some members" (Fell 1963b: Table 1). In Smith's (1988a:fig. 7.2, 7.3) cladograms, the anus was present in the edrioasteroids, became missing in the stem somasteroids, reappeared later in the asteroid line, did not reappear at all in the ophiuroid line, but reappeared in the echinoids, ophiocistioids and holothuroids as a post-stem ophiuroid development. In the experience of Smith (1988b:819): "The presence of an anus is difficult to detect in some fossils, but does genuinely appear to be absent in primitive asteroids and ophiuroids". Blake (1987: 499, 506–507, 522; 1988) suggested that loss of the anus occurs rather readily and that the absence of rectal caeca and of an anus in the Paxillosida is a derived character state. Kesling (1962) reported a probable anal pyramid in *Protopalaeaster narrawayi* [Middle Ordovician]; Kesling & Strimple (1966) observed in the central plate of *Calliasterella americana* [Missisippian, transferred to *Calyptactis* by Chesnut & Ettensohn 1988] a notch that may have bordered the anus; both reports locate the anus and the madreporite consistent with Table 2. An ophiuroid from the Silurian of Gotland that is reported to have an anal cone is under study by Regnéll (1973:fig. 4, cited by Franzén 1979:220). Accepting this report means that the anus was reacquired by a Silurian ophiuroid which appears not to have left any descendants (at least none with an anus). From examination of Ruedemann's specimen of *Stenaster salteri* (= *S. obtusus*) with a supposed anal pore (Ruedemann 1916:54, plate 11, fig. 1) (Kilfoyle 1954:199, specimen NYSM 7744), I think it probable that the pore is an artifact from weathering. A careful search for an anus in fossils of Paleozoic asteroids and ophiuroids should continue to be made. It should be looked for not only on the aboral surface, but also on the oral surface (as in edrioasteroids) and on the interradial margins of the disc, as found in the ophiocistioid *Gillocystis* (Jell 1983).

Note 5.—Evidence of multiple changes in symmetry in echinoids includes the markedly oval tests of the Echinometridae (Grabowsky 1994). The axis of elongation plainly differs from that of spatangoids and other exocyclic echinoids, yet does not alter the tendency for oculars I and V to become insert (Fell *in* Moore & Fell 1966:U124). Also in echinoids, the markedly oblique peristome in certain cassiduloids and holectypoids may be mentioned (Rose 1976:303). The oral side of *Amblypygus merrilli* figured by Clark & Twitchel (1915:plate 76) displays a very evident bilateral symmetry of the peristome and the ambulacra about the II-4 plane, whereas the periproct is elongate and symmetrical in the III-5 plane. [Roman (1957) pointed out that the bilateral symmetry of *Echinolampas* is just external: the internal organs are not bilaterally arranged, and upon taking measurements the test itself is found to be not perfectly symmetrical.]

In crinoids may be mentioned *Comatula pectinata* showing a relative elongation of most of the 'anterior' arms (i.e., those corresponding to the side of the disc opposite the anus) (Clark 1977:Fig. 6b). Also, the recumbent bent-crown Calceocrinidae are bilateral in the E-BC homocrinid plane (Lane & Webster 1967, Brower 1985). [In *Holopus rangii* the position of the bivium and trivium of shorter and longer rays differs among specimens (Donovan 1992:668).]

In holothurians may be mentioned the Antarctic psolid *Ekkentropelma brychia* which has the mouth and anus of the U-shaped body displaced at 90 degrees to the usual holothurian plane of bilateral symmetry, while the sole is morphologically ventral, as usual. "Thus, the sole is functionally lateral in position, and apparently the animal is well adapted to attaching itself to vertical surfaces" (Pawson 1971:113).

In asteroids may be mentioned reports of leading arms in locomotion, of arm preferences in righting behavior, and also bilateral patterns of ray addition in some multiradiate starfish (see review in Hotchkiss & Seegers 1976). Also, on the aboral surface of *Luidia clathrata* there is a conspicuous line of dark coloration on the midline of each arm and in just one interradius (the madreporic interradius); these dark lines connect not to a central point but in a bilaterally symmetrical pattern that suggests a trivium and a bivium of rays (Gray et al. 1968: 139, figure 8A).

In ophiuroids may be mentioned *Asteronyx loveni* with two nonadjacent thick and long arms and three intervening thinner and shorter arms, although their orientation relative to the madreporite has not been described (Fujita & Ohta 1988, Irimura 1991). [The orientation relative to the madreporite of a similar pattern found in early growth stages of *Ophiophragmus filograneus* and *Amphiura filiformis* differs among specimens (Turner 1974, Muus 1981).] As another example, the juvenile *Ophiomastix flaccida* illustrated by Clark (1921:138, plate 13, figure 2) shows a color pattern with unmistakable bilateral symmetry. The color pattern of *Sigsbeia lineata* suggests imperfect bilateral symmetry (Lütken & Mortensen 1899:plate 20, figure 8).

Note 6.—Concerning Paleozoic echinoids with 'irregular' tendencies, the orientation of the oblong test of *Hyattechinus beecheri* has not yet been determined (Jackson 1912). The supposedly posterior anus in the Silurian *Palaeodiscus* and *Echinocystites* was shown by Hawkins & Hampton (1927) to be in the usual aboral, endocylic position of the Regularia. The elongate shape of *Ectinechinus* and *Eothuria,* although questioned as possibly due to post-mortem distortion by Kier (1965:442), is provisionally accepted herein because of the exceptional interest that attaches to the observation of MacBride & Spencer (1938) that the plane of elongation follows von Übisch's primordial plane of symmetry. Also of interest is the observation by Fell (1965:6) that "The earliest Echinoidea, such as *Eothuria,* possessed a multiplated, flexible spirally twisted body wall, similar to that of the Helicoplacoidea, and perhaps inherited from a helicoplacoid ancestry."

Note 7.—Evidence of the axis of the bilateral larva in the adults of *Asterias rubens* has been adduced from behavioral studies

(Smith 1950:216): "The tendency for arm II to dominate the locomotory pattern is not to be ascribed to any obvious organizational feature such as greater arm length or a greater number of podia. It appears rather to reflect some intrinsic feature of nervous organization such as, perhaps, the retention of traces of the bilateral symmetry of larva." [I regret that I do not know how Smith assigned Roman numerals to the rays.]

From anatomy and embryology (Lane & Webster 1967): "The homocrinid (E-BC) plane of bilateral symmetry in the crown of some monocyclic inadunate and flexible crinoids is postulated to be a relict expression in adults of the dorso-ventral symmetry plane of the doliolarian, free-swimming, larval stage."

From embryology (Grave *in* Brooks & Grave 1899:89, pl. I, fig. 6): In *Ophioderma brevispina* stage "C" larvae the hydrocoele is "a horseshoe-shaped structure astride the oesophagus," and "half of it lies to the right of the median sagittal plane of the larva and half to the left. Radial canal 3 lies in this plane and points directly toward the anterior of the larva." [The relation of the lobes of the hydrocoele crescent and of the plane of hydrocoele closure to the axis of the larva may provide a means of tracing the larval axis through to the adult, and should be documented wherever possible; perhaps more of such data already exist.]

From teratology (Macurda 1980:1161): "Abnormalities which were present in the bilaterally symmetrical larvae would be carried forward during metamorphosis to the pentameral adult and should have a bilateral distribution. . . . The data from this study appear to be supportive of the AB-D plane as being the larval symmetry plane in blastoids." [See also Macurda 1964, 1978]

Note 8.—The left side of the larva becomes the oral surface, and the right side becomes the aboral surface. Hence the plane of symmetry of the echinopluteus is at right angles to von Übisch's plane of primordial symmetry in the adult. The axes of symmetry are coincident even though the planes are at right angles (Onoda 1931:126). Crystallographic studies of echinoid ocular and genital plates, summarized and extended by Emlet (1988, 1989), confirm von Übisch's plane of primordial symmetry in many genera for which the development has not yet been directly observed.

Note 9.—Fritsch (1908) interpreted the enigmatic Ordovician fossil *Furca bohemica* as a crinoid pluteus larva, but it was later shown to be a marellamorph (Arthropoda) (Perner 1919, Mortensen 1921:233, Prokop 1989:143–144). Echinopluteus skeletal rods and baskets were described by Deflandre-Rigaud (1946) from the Upper Jurassic of France. Emlet (1985) has shown that the crystallographic orientation of ocular and genital plates in echinoids is a reliable indicator either of indirect development with an echinopluteus (certain of these plates growing from the larval spicules of the echinopluteus) or of direct development without a pluteus (these plates then being formed de novo); he has used this technique to determine the mode of development of fossil echinoids.

Note 10.—The use by Smith (1984a) and Paul & Smith (1984) of the pluteus larva as a synapomorphy between ophiuroids and echinoids has been questioned by Smith (1984b:452–453). He concluded that "There is therefore a distinct possibility that elongation of the small processes common to all eleutherozoan larvae occurred independently in ophiuroids and echinoids." Here I consider an alternative to the proposal of Paul & Smith (1984:469) that the larval type of Ordovician ophiuroids was an ophiopluteus.

Note 11.—To the best of my knowledge, a planktotrophic larval stage is still not known in the Phrynophiurida (Fell 1967: S71–S72, Patent 1970, Strathmann 1975, Hotchkiss 1978:542–543, Hendler 1991). More research on the development of the Phrynophiurida is needed. Dowidar & El-Maghraby (1970:260) listed in their plankton the ophiopluteus of *Ophiomyxa pentagona,* but did not provide any evidence to support this identification. It is therefore very important that the embryology and larval type of *Ophiomyxa pentagona,* and of other ophiomyxine and euryaline phrynophiurids be worked out. Knowledge of the development of *Ophiocanops* could be particularly rewarding because it is thought to have retained the gonadal and stomachal characters of the Oegophiurida (Fell 1963c: 481, Hotchkiss 1977, Petr 1988:38). The egg size of *Ophiocanops fugiens* was judged by Hendler (1975) to indicate direct or abbreviated development. [Concerning the classification of *O. fugiens*: It does not have the "auluroid" vertebrae of the Oegophiurida. The presence of oral and adoral shields, a first ventral arm plate, and streptospondyline vertebrae verify that *Ophiocanops* is a phrynophiurid (Mortensen 1933, Hotchkiss 1977). The extraordinary soft part characters support family rank and suggest (following Fell 1962) that *O. fugiens* may be a living representative of the stem group for the Order Phrynophiurida.] Hendler (1975) and Strathmann (1993) caution against inferences based on assuming that if a species has primitive features as an adult that its larval traits are also primitive. Strathmann also cautions (in litt.) that there is a weakness in parts of the inferences of Fell and Patent. He mentions as counter examples: that *Pteraster tesselatus* has no trace of bilateral larval symmetry yet it is descended from an ancestor with a brachiolaria (McEdward 1992); and that those species of *Ophiolepis, Ophioderma* and *Ophionereis* that lack any vestige of a larval skeleton in their vitellaria larvae are, nevertheless, descended from ancestors with an ophiopluteus (Strathmann 1988, 1993). [Hendler's (1982) studies on *Ophionereis annulata* and Mladenov's (1985) studies on *Ophiocoma pumila* have now demonstrated a connection between the ophiopluteus and the vitellaria.] As another counter example, Emlet informs me (in litt.) that he has studied the development of an *Amphiodia* with a benthic egg capsule and a direct development with no vestige of a larval skeleton. These comments emphasize the speculative nature of attempting to deduce the characteristics of ancestral ophiuroid larvae.

Note 12.—Jackson (1912:33) observed that "the first oculars to become insert are the plates of the bivium, next the plates of the posterior pair of the trivium, and last, if at all, the anterior odd plate of the trivium. . . . The ocular plates therefore in many regular Echini express a bilateral symmetry in this group, and an orientation passing through ambulacrum III and interambulacrum 5, the plane of symmetry adopted by Lovén." Jackson extended this correlation to plates of the oral surface (1927:556): "The law of sequence of incoming oculars in Echini indicates an arrangement to the right and left of the anteroposterior axis through III-5. This is in support of Lovén's law of the orderly arrangement of primordial ambulacral plates in clypeastroids, spatangoids, and young regular Echini, the Ia, IIa, IIIb, IVa, Vb are larger, while the Ib, IIb, IIIa, IVb, Va are smaller. So that from them as with a key one can gather the true orientation of an echinoid." Fell (*in* Moore & Fell 1966) added the insight that the insert condition of oculars I and V is the result of rearward migration of the anus toward interambulacrum 5, and that this rearward migration was already evident in the Cidaroida. [It is also noteworthy that Onoda (1933) showed a physiological anterior-posterior axis in *Heliocidaris* that coincides with the III-5 axis of Lovén's plane.]

Note 13.—A close relation between echinoids and asterozoans, based on study of *Palaeodiscus, Aulechinus* and *Ectinechinus,* was proposed by Spencer (1904), Bather & Spencer (1934), and MacBride & Spencer (1938). Evidence for a close relation between echinoids and ophiuroids was developed in detail by Hyman (1955:699) and most recently by Smith (1984a). Smith's cladogram accounts for the similarity of the adult morphologies of asteroids and ophiuroids, and the (apparent) similarity of the larval morphologies of ophiuroids and echinoids, by showing the stem ophiuroid as most closely related to the asteroids, and the stem echinoid as most closely related to the ophiuroids. However, with the similarity of the larvae now reappraised as a homeomorphism, with Lovén's law comprehended as an ancestral character that was present in the edrioasteroids (symplesiomorphy), and with a new table of ray homologies showing numerous changes in the location of the madreporite, the cladogram of Smith is in need of revision.

As stated by Mooi (1989) it is the "interpretations of the homologies of characters deemed important" that will determine the resulting cladogram, and not the actual use of cladistic methods. I accept the conclusions of Fell (1963b, 1963c) that ophiuroids display vestiges of metapinnular structure; that ophiuroids therefore derive from somasteroids (which have metapinnules); and that echinoids derive from a stock with meridional growth gradients that did not have metapinnules. Therefore, I agree with Fell that ophiuroids do not qualify as ancestors to the echinoids. I agree with Fell that the Asterozoa and the Echinozoa are ancient and independent lineages, and I disagree with Smith's (1984b) combining ophiuroids with echinoids and holothurians in a new Superclass Cryptosyringida. [A recent study on mitochondrial gene arrangements supports grouping asteroids with ophiuroids into the Asterozoa, and grouping echinoids with holothurians into the Echinozoa (Smith et al. 1993).] I interpret the fact of sharing Lovén's law to mean that ophiuroids and echinoids belong to the same 2-1-2 clade as the edrioasteroids. Thus I agree with Smith's (1984b) reconstitution of the Subphylum Eleutherozoa, which he expands to include stromatocystitoid and other edrioasteroids.

Note 14.—The probability under the null hypothesis H0 that a out of n arms will have a specific character state (the A or the B that is needed to spell out Lovén's law) is given by the binomial distribution with $p = q = 0.5$. The probability of observing a or more of the specific character in a sample of n observations has been calculated for each of the data on arms in Table 7 [exact calculations under the null hypothesis].

Arm I: $P(a \geq 9, n = 9) = 1/512$

Arm II: $P(a \geq 10, n = 13) = 378/8192$

Arm III: $P(a \geq 12, n = 12) = 1/4096$

Arm IV: $P(a \geq 10, n = 11) = 12/2048$

Arm V: $P(a \geq 6, n = 8) = 37/256$.

Using a criterion of $P<0.05$, the null hypothesis is rejected for arms I, II, III and IV. Although the null hypothesis could not be rejected for arm V, undoubtedly that will change when more Set II observations become available. The working hypothesis that each arm position relative to the madreporite has a preferred character state, that the preferred character states spell out Lovén's law, and that this pattern identifies the madreporic interradius as III/IV is supported.

The working hypothesis does not assume that any subset of rays is more (or less) faithful to its predominant character state than any other subset. This allows pooling the 53 observations of Set II and the 60 observations of Set I. The number of ocurrences of the predominant character state is $a = 107$ in $n = 113$ observations. The observed frequency is therefore 0.947. The probability that a specimen will have the predominant character state in all five of its arms, and therefore spell out Lovén's law, is $(0.947)^5 = 0.762$. In my previous study (Hotchkiss 1978) I reported an estimated observed frequency of 0.617 [with a 0.99 confidence interval on the estimate spanning from 0.33 to 0.85].

Conference paper.—Portions of this paper were presented at the second North American Friends of Echinoderms conference and workshop at the Harbor Branch Oceanographic Institution, Inc., 9–11 July 1992, with the title "Footnotes on Lovén's law". In the excellent atmosphere of discussions among the scientists at the meeting, I learned from Dr. Richard Mooi that he and Dr. Bruno David had also discovered that Lovén's law applies to *Stromatocystites walcotti,* and that they had used Smith's published drawings is exactly the same way as I report here. Further, Dr. Mooi informed me that he concurs with the characterization of Lovén's law in echinoids as a recapitulation of the 2-1-2 organization of *Camptostroma* and the edrioasteroids.

Acknowledgments

I thank David L. Pawson for constant help for over 25 years, without which I would not have been able to do this or any other research on echinoderms. I thank Anita P. Hotchkiss, David L. Pawson, Václav Petr, Richard Strathmann, Richard Emlet, and Gordon Hendler for reading and commenting on drafts of this manuscript. I thank Andrew Smith for his stimulating papers, his extremely important and exact observations on *Stromatocystites,* and for correspondence on the subject of situs inversus; Peter A. Jell for help with photographs and observations on ophiuroids used in the Appendix, and for reprints and his extremely important and exact observations on *Gillocystis.* I thank S. K. Donovan and an anonymous reviewer for their helpful reviews. I thank S. K. Donovan for informing me of the suggestion by Conway Morris (1993) that *Echmatocrinus* is actually a coelenterate and not a crinoid. I thank J. Sprinkle for a verbal communication confirming that *Echmatocrinus* has plates and reaffirming his opinion that it is a crinoid and not a coelenterate. I thank Gordon Hendler for informing me of the bilateral symmetry in *Asteronyx* and of the paper by Muus (1981), and for general communications and encouragement over many years; Richard Emlet for correspondence on the relation of the larva to the adult in echinoids and for reprints; Richard Strathmann for his willing responses to my phone calls for help; Jon W. Branstrattor for correspondence, reprints and advice on locating specimens for this study; David L. Meyer for being a willing host during my visits to the University of Cincinnati; Richard Terry of the University of Cincinnati for showing me material that he collected; W. Bruce Gibson of Cincinnati, Ohio, Thomas Frushour of Temperance, Michigan, and Kevin Brett of West Hill, Ontario, for allowing me to examine Ordovician ophiuroid materials; Janet Waddington, Peter von Bitter and Desmond Collins for their kind reception and help during my visit to the Royal Ontario Museum; Greg Buckley for help during visits to the Chicago Field Museum; H. C. Klinger of the South African Museum and J. E. Almond of the S. A. Geological Survey for information on Bokkeveld ophiuroids under study by P. A. Jell; John Harper, J. Roman and E. P. F. Rose for correspondence and reprints; Václav Petr for his generous help through correspondence, latex casts of specimens, papers (including translating the paper by Perner on *Furca,* and for additional references on *Furca*); Kraig Derstler for latex casts of material in the North Museum at Franklin and Marshall College; Niles Eldredge and Melvin T. Hinkley for assistance with the collections at the American Museum of Natural History; Ivo Chlupac for information and references on *Furca bohemica*; David N. Lewis for latex casts of BM(NH) material; Christina Franzén-Bengtson for information on the anal cone in the Gotland ophiuroid; the Boxboro Library for introducing me to Polya's (1954) book on plausible inference; James Doherty and Alan Doherty for their expert help in preparing rubber casts for this study; Donna Nordberg for help in final preparation of the manuscript; Rita Vine for help in obtaining the copyright permissions for the figures. I thank Dan Blake, John Dearborn, Lee Ehrman, Julian Fell, Anita P. Hotchkiss, Grace M. Hotchkiss, Peter Jell, Caleb Kaufman, John Lawrence, David Pawson, Ira B. Perelle, Václav Petr and Richard Strathmann for help with literature. I thank: The Paleontological Society for permission to use Text. Figs. 1 & 2 of Hotchkiss 1978 as the basis for Figs. 1 & 2 herein; Cambridge University Press for permission to use Fig. 6 of Bather 1914b as the basis for Fig. 3; A. B. Smith and Cambridge University Press for permission to use Fig. 7 of Paul & Smith 1984 as the basis for Fig. 4; P. A. Jell and the Association of Australasian Palaeontologists for permission to use Fig. 14 of Jell 1983 as the basis for Fig. 5; D. L. Pawson for providing the final preparation of the figures.

Dedication

This paper is dedicated in memory of Prof. H. Barraclough Fell (1917–1994), whom I cherished as mentor and friend. Fell's enthusiasm and charisma, and the sincerity and collegiality with which he treated his young students (as experienced by James F. Clark and myself in the 1960s) made him one of the most important influences in my life, both personally and scientifically. I believe that these remarks would be readily echoed by his other students. To prepare this manuscript I reread papers by Fell that had ignited my interest in echinoderms while an undergraduate student. Part of the pleasure and the challenge of writing this paper has been to try to do justice to the seminal ideas of this great scholar. Thus, in the section of this paper where I discuss the ophiopluteus, an additional goal is to provide access to Fell's treatment of the topic by giving detailed page references.

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Table 4.—Key for processing specimens into two mutually exclusive sets for the study of Lovén's law and the location of the madreporite in Paleozoic ophiuroids.

A.	Oral view	B
	Aboral view	Exclude
B.	Specimen has recognizable madreporite	C
	Madreporite not found	Exclude
C.	One or more arms scorable	D
	No arms scorable	Exclude
D.	Five arms scorable	E
	One to four scorable arms	Set II
E.	Five arms conform to Lovén's law	Set I
	Five arms do not conform	Set II

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Appendix I

Additional Data on Lovén's Law and the Location of the Madreporite in Ophiuroids

Methods.—Evidence of Lovén's law is obtained by recording the arrangement of the ambulacral plates (Hotchkiss 1978). Examined from the oral surface, the ambulacral series on the anticlockwise side of each arm is either in advance (A) or behind (B) the series on the clockwise side of the arm. The arrangement AABAB is Lovénian, and the labels I, II, III, IV, V apply to the arms (Fig. 2).

Two methods of analysis, based on mutually exclusive categories of specimens, provide separate looks at the location of the madreporite in connection with Lovén's law in Paleozoic ophiuroids. Specimens were processed into two sets following the dichotomous key given in Table 4.

The SET I collection of specimens all obey Lovén's law. Hence the arms can be labeled I, II, III, IV, V according to Lovén's system. The location of the madreporite is then determined by inspection to belong to a certain interradius by name, i.e., I/II, or II/III, etc. The working hypothesis is that the madreporite occurs almost exclusively in the III/IV interradius (Hotchkiss 1978). The null hypothesis is that there is no preferred location.

The SET II collection of specimens all have a madreporite. We will assign interradius designation III/IV to the madreporic interradius. Hence the arms can be labeled I, II, III, IV, V, according to their placement with respect to the madreporite. The character state of each scorable arm can be determined by inspection to be either "A" or "B." The working hypothesis is that each arm is associated with a particular character state and that the pattern conforms with Lovén's law. The null hypothesis is that there is no preferred character state for any arm.

Materials.—This study can use only those Paleozoic ophiuroids that have alternating ambulacral plates. The preservation must permit individual recognition of the 1st, 2nd, 3rd, etc., plates of each half series of ambulacral plates in order to score the character state. In some specimens the lateral plates of the two sides of the arm can be used to assist in the interpretation. To assist in proper scoring of the ambulacrals, it is necessary to prepare latex or silicone rubber casts of specimens preserved as molds. In some specimens the aboral view can be scored. In exceptional circumstances data can be taken from published photographs. It is fairly common for published drawings to contain reconstructed detail that would not be reliable for this study.

The specimens comprising Set I and Set II all belong to the families Protasteridae and Encrinasteridae, suborder Lysophiurina, order Oegophiurida.

Set I: Twelve specimens. Details are as follows:

101. *Protaster sedgwickii* Forbes, lectotype, Sedgwick Museum No. A6374, Lower Ludlow (Upper Silurian), Lake District, England (oral view; seen) (Hotchkiss 1978:specimen no. 1)

102. Protasteridae sp., North Museum, Franklin and Marshall College No. PE38, Devonian, from roadside near Portland, New York (oral view; seen) (Hotchkiss 1978:specimen no. 6)

103. Hamling's ophiuroid = Protasteridae sp. juv. British Museum (Natural History) No. E13737a, Upper Devonian, Pickard's Down, near Barnstaple, North Devon (oral view; seen) (Hotchkiss 1978:specimen no. 11; 1980:fig. 2B; Lewis 1993:69 as *Drepanaster scabrosus*)

104. *Strataster ohioensis* Kesling & LeVasseur, paratype, University of Michigan Museum of Paleontology No. UMMP 58332a, Meadville Shale (Early Missippian), Cuyahoga County, Ohio (oral view; studied from the photograph: Kesling & LeVasseur 1971:pl. 7 fig. 4) (Hotchkiss 1978:542, 1993:65)

105. *Eugasterella logani* (Hall), Moscow Formation (Middle Devonian), near Earlville, Madison County, New York, the AAB*AB arm and madreporite arrangement reported by Harper (1985:367) is visible in his photograph of Carnegie Museum of Natural History No. CM 34422 (oral view; studied from the photograph: Harper 1985:fig. 7A) (The lateral plates help to score the arms.)

106. Protasteridae sp., South African Museum, Cape Town, SAM K1015 (formerly SAM 69d; originally from S.A. Geological Survey collections; plaster replica only), Gydo Formation (Devonian Bokkeveld Group), near Grootrivier, Cedarberg Mountains. (oral view; studied from photography supplied by Dr. P. A. Jell; under study by Dr. Jell; locality information from Dr. J. E. Almond) [an aged rubber pull of SAM 69d is in the Geology Museum of the University of Cincinnati]

107. Protasteridae sp., South African Museum, Cape Town, SAM K1014 (formerly SAM 203/67d; originally from S. A. Geological Survey collections), Gydo Formation (Devonian Bokkeveld Group), near Grootrivier, Cedarberg Mountains. (oral view; studied from photograph supplied by Dr. P. A. Jell; under study by Dr. Jell; locality information from Dr. J. E. Almond) [an aged rubber pull of SAM 203/67d is in the Geology Museum of the University of Cincinnati]

108–112. Protasteridae sp., Devonian Bokkeveld Group, South Africa. [oral views; studied from photographs loaned by Dr. P. A. Jell; material is under study by Dr. Jell; repository and registration numbers will be reported by Dr. Jell (information not available)]

Table 5.—Set I data. Location of the madreporite in specimens that obey Lovén's law.

I/II	II/III	III/IV	IV/V	V/I
0	0	12	0	0

Set II: Nineteen specimens. Details are as follows (specimen numbers according to Table 5):

201. *Encrinaster hamlingi* Spencer, holotype, Institute of Geological Sciences, Leeds, Nos. GSM 37360, GSM 37361, Lower Carboniferous, Croyde, North Devon (counterpart halves; seen) (Hotchkiss 1978: specimen no. 2)

202. *Taeniaster spinosus* (Billings), holotype of *Protaster? granuliferus* Meek, Museum of Comparative Zoology, Harvard University, No. MCZ 470, Richmond Group (Middle Ordovician), Moore's Hill, Indiana (oral view; studied from the photograph: Hotchkiss 1970:fig. 6) (Hotchkiss 1978:specimen no. 13)

203. *Strataster ohioensis* Kesling & LeVasseur, paratype L-25e, Meadville Shale (Early Missippian), Cuyahoga County, Ohio (oral view; studied from the photograph: Kesling & LeVasseur 1971:pl. 4 fig. 1; pl. 10, fig. 4) (Hotchkiss 1993:65)

204. *Strataster ohioensis* Kesling & LeVasseur, paratype L-25i, Meadville Shale (Early Missippian), Cuyahoga County, Ohio (oral view; studied from the photograph: Kesling & LeVasseur 1971:pl. 6 fig. 2) (Hotchkiss 1993:65)

205. *Strataster maciverorum* Hotchkiss, topotype, Panther Mountain Formation (Middle Devonian), near Cooperstown, New York; New York State Museum (uncatalogued Mclver collection: rock specimen DS12) (oral view; seen) (Mclver & Mclver 1955, Hotchkiss 1993:73)

206. *Strataster maciverorum* Hotchkiss, topotype, Panther Mountain Formation (Middle Devonian), near Cooperstown, New York; New York State Museum (uncatalogued Mclver collection: rock specimen DS70) (oral view; seen) (Mclver & Mclver 1955, Hotchkiss 1993:73)

207. *Taeniaster spinosus* (Billings), holotype of *T. schohariae* Ruedemann, New York State Museum No. 7784, Schenectady beds (Middle Ordovician), near Schoharie Junction, New York. (oral view; seen) (Kilfoyle 1954:204, 639; Hotchkiss 1970:fig. 3).

208. *Protasterina fimbriata* Ulrich, holotype, Economy Formation (Middle Ordovician), Covington, Kentucky, University of Cincinnati Geology Museum No. 25001 (oral view; seen) (Schuchert 1915:pl. 36 fig. 4) (Hansman et al. 1962)

209. *Protasterina fimbriata* Ulrich, Utica Slate, Cincinnati, Ohio, American Museum of Natural History

AMNH 13190 (labeled *Protaster flexuosa* Miller & Dyer; Faber exchange) (oral view; seen; madreporite partly covered by spines)

210. *Eugasterella logani* (Hall), Moscow Formation (Middle Devonian), near Earlville, Madison County, New York, photograph published by Harper (1985:fig. 2B, fig. 3), Carnegie Museum of Natural History No. CM 34421A (oral view; studied from the photograph)

211. *Protaster whiteavesianus* Parks, syntype, Middle Ordovician Trenton Group, Kirkfield, Ontario. Royal Ontario Museum No. 23846, inked #638T specimen B (oral view; fragmentary; seen) (Parks 1908:368, Waddington et al. 1978:132).

212. *Taeniaster ibericus* Hammann & Schmincke, holotype, Museum of the Instituto Geológico y Minéro, Madrid, No. S 587/2, "*Tristani*-beds" (Middle Ordovician), near Fontanosas, Spain (oral view; studied from the photograph: Hammann & Schmincke 1986:fig. 8d.)

213. *Taeniaster ibericus* Hammann & Schmincke, paratype, Museum of the Instituto Geológico y Minéro, Madrid, No. S 587/1, "*Tristani*-beds" (Middle Ordovician), near Fontanosas, Spain (oral view; studied from the photograph: Hammann & Schmincke 1986: fig. 10.)

214. *Taeniaster ibericus* Hammann & Schmincke, paratype, Museum of the Instituto Geológico y Minéro, Madrid, No. S 587/5, "*Tristani*-beds" (Middle Ordovician), near Fontanosas, Spain (oral view; studied from the photograph: Hammann & Schmincke 1986: fig. 7a, 7c.)

215–219. Protasteridae sp., Devonian Bokkeveld Group, South Africa. [oral views; studied from photographs loaned by Dr. P. A. Jell; material is under study by Dr. Jell; repository and registration numbers will be reported by Dr. Jell (information not available)]

Excluded: The following excluded specimens deserve special comment. For convenience of future reference they are numbered:

301. *Armathyraster paradoxis* Harper & Morris, Brush Creek Shale (Pennsylvanian), Punxsutawney, Jefferson County, Pennsylvania, ABA*AA arrangement described by Harper & Morris (1978:157) [Carnegie Museum of Natural History No. CM 33966; counterpart halves; the aboral view is easily scored.] Excluded because the location of the madreporite is doubtful: it is "not well enough preserved for complete identification" (Harper & Morris 1978:157). The reported score ABA*AA contains three disparities with the expected AAB*AB. An alternative possibility is that the hydropore is not associated with a visible madreporite, and that the specimen scores as AAB(*?)AA or AAA(*?)AB with only one disparity.

302. *Bohemura jahni* Jaekel, figured specimen, Letna Formation, Haj near Zahorany. National Museum [Narodni Museum], Prague, No. NM L 10172. Excluded because none of the arms are scorable; in the published drawing (Petr 1988:fig. 1a) details of ambs around the mouth opening were filled in for the purpose of illustration. (Oral view; latex pull supplied by Dr. Petr)

303. *Bohemura jahni* Jaekel, lectotype, Zahorany Formation, Zahorany near Beroun. National Museum [Narodni Museum], Prague, No. NM L 10066 [formerly registered as No. EH 146]. Excluded because none of the arms are scorable; the drawing published by Spencer (1934:473, text-fig. 305; reproduced in Spencer & Wright 1966:U86 fig. 75,2a) was found by Petr (1989:1) to be incorrect. This specimen was reillustrated by Petr (1989:6, text-fig. 2, pl. I) and was designated the lectotype. (Oral view; latex pull supplied by Dr. Petr)

304. *Euzonosoma orbitoides* Spencer, holotype, Thraive Glen Starfish Bed. British Museum (Natural History) No. BMNH E52424b [formerly No. D. 52c in Mrs. Gray's colln.] (Owen 1965:552, Lewis 1993: 69). Excluded because the location of the madreporite is doubtful: it is not distinct enough from the other disc plates for certain identification in this specimen. The detail of amb IV in the drawing published by Spencer (1930:414, text-fig. 265, indicating the amb arrangement ???*B?; drawing reproduced in Spencer & Wright 1966:U85 fig. 74,4b) is not confirmed by the fossil. I score the fossil as AA?(*?)A?. (Oral view; latex pull supplied by D. N. Lewis)

305. *Protaster piltonensis* Spencer, holotype, Lower Carboniferous of Top Orchard Quarry, Pilton, Devon. British Museum (Natural History) No. BMNH E13835b [formerly No. 1292 in the Torquay Natural History Society Collection] (Owen 1965:549, Lewis 1993:75). Excluded because none of the arms are scorable. The detail of amb IV in the drawing published by Spencer (1934:470, text-fig. 304, indicating the amb arrangement ???*B?) is not present in the fossil. (Oral view; latex pull supplied by D. N. Lewis)

Results and analysis of Set I data.—The plate arrangements of the twelve Lovénian specimens are used to label the arms as I, II, III, IV, V. The madreporite is found only in interradius III/IV (Table 5). Under the null hypothesis of no preferred placement of the madreporite, the probability of observing the madreporite in the same interradius (not specifically the III/IV interradius, but any interradius) in all twelve specimens is

$$(0.2)^{11} = 0.00000002$$

Therefore the null hypothesis is rejected. The madreporite occurs in interradius III/IV more frequently than can be accounted for by chance alone.

Results and analysis of Set II data.—The madreporite is used to label interradius III/IV. The remaining arms are labeled according to their placement with respect to the madreporite. This before-the-fact label-

Table 6.—Set II data. The madreporite is used as a landmark to label the arms I, II, III, IV, V. The A or B score of each scorable arm is recorded in the table.

	Specimen	I	II	III	*	IV	V
201	*Encrinaster hamlingi*	—	B	B	*	A	A
202	*Taeniaster spinosus*	—	B	B	*	A	—
203	*Strataster ohioensis*	A	—	B	*	A	B
204	*Strataster ohioensis*	—	A	—	*	—	—
205	*Strataster maciverorum*	A	A	—	*	A	B
206	*Strataster maciverorum*	—	—	B	*	—	—
207	*Taeniaster spinosus*	—	—	B	*	—	—
208	*Protasterina fimbriata*	A	A	—	*	A	B
209	*Protasterina fimbriata*	A	B	—	*	B	A
210	*Eugasterella logani*	A	A	B	*	A	—
211	*Protaster whiteavesianus*	—	—	B	*	—	—
212	*Taeniaster ibericus*	—	—	—	*	A	—
213	*Taeniaster ibericus*	—	—	—	*	—	B
214	*Taeniaster ibericus*	A	A	B	*	—	—
215	Protasteridae sp.	—	A	B	*	A	—
216	Protasteridae sp.	A	A	—	*	A	B
217	Protasteridae sp.	A	A	B	*	—	—
218	Protasteridae sp.	—	A	B	*	—	B
219	Protasteridae sp.	A	A	B	*	A	—

ing is based on having a working hypothesis and provides the convenience of not having to relabel the arms after doing the analysis. The A or B score of each arm is entered in Table 6. The working hypothesis is that the arms have predominant character states, these states spell out Lovén's law, and ray numbering based on Lovén's law places the madreporite in interradius III/IV.

The data of Table 6 are summarized in Table 7. The predominant character states occur more frequently than can be accounted for by chance alone (one sided test; see Note 14). It is seen that the predominant character states of the arms spell out Lovén's law. Numbering the rays based on recognizing Lovén's law shows that the madreporite occurs in interradius III/IV.

Table 7.—Analysis of Set II data. The working hypothesis is that the observed character states will spell out Lovén's law in a way that places the madreporite in interradius III/IV. Table entries record the number of times that the working hypothesis is fulfilled and the probability (P) of observing this many or more of the stated character under the null hypothesis HO of chance alone.

Arm I has arrangement A in 9 out of 9 specimens, $P = 0.00195$
Arm II has arrangement A in 10 out of 13 specimens, $P = 0.0461$
Arm III has arrangement B in 12 out of 12 specimens, $P = 0.000244$
Arm IV has arrangement A in 10 out of 11 specimens, $P = 0.00586$
Arm V has arrangement B in 6 out of 8 specimens, $P = 0.145$
Lovénian arrangement found in 47 out of 53 arms

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(3):436–450. 1995.

Alloeocomatella, a new genus of reef-dwelling feather star from the tropical Indo-West Pacific (Echinodermata: Crinoidea: Comasteridae)

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Abstract.—*Alloeocomatella,* a new genus of comasterid feather star from tropical Indo-West Pacific reefs, contains two species: *A. polycladia,* a new species, and *A. pectinifera* (A. H. Clark), the latter reassigned from the genus *Comissia.* Both are cryptic during the day; at night they extend their arms for feeding or emerge completely. *Alloeocomatella* differs from other genera in the family Comasteridae in its pattern of development of first brachial syzygies, and in the structure of its oral pinnule combs. *A. pectinifera* has rays up to 500 mm long, the longest recorded for any extant feather star.

Recent collections of shallow-water crinoids from tropical western Pacific reefs include a new species of Comasteridae that cannot be assigned to any named genus. The species exhibits the same arm branching pattern as *Comatella* A. H. Clark, but differs in pinnule and cirrus structure, and in the placement of initial brachial syzygies. The latter changes with growth, a trait apparently unique among comasterids. In specimens with 11–20 arms, the first syzygy is as in *Comanthus* and several other genera. In specimens with >20 arms, placement of syzygies approaches that of *Comatella.* Comparison with co-occurring *Comissia pectinifera* A. H. Clark indicates that the two species are congeneric. In fact, specific assignment of small ten-armed specimens is problematic. The two differ substantially from the type species of *Comissia* (*C. luetkeni* A. H. Clark) and so warrant a new genus.

Material used in this study is housed in the National Museum of Natural History, Smithsonian Institution (USNM), British Museum (Natural History)(BMNH), Museum national d'Histoire naturelle, Paris (PM), Los Angeles County Museum of Natural History (LACM), and the Institut Royal des Sciences naturelles de Belgique (BELG). Terms, abbreviations, measurements and symbols are as follows: Centrodorsal: central aboral plate. Cirri: aboral, segmented hooks attached to centrodorsal; Roman and Arabic numerals indicate numbers of cirri/individual and segments (cirrals)/cirrus, respectively (a range of values is usually given); LW of cirral: length to median width ratio (:1) when viewed laterally. Ray: one of five branched series of ossicles radiating from center of specimen; three rays arising closest to the mouth (displaced to one side of visceral mass in comasterids) are anterior. Radial: (n.) first ossicle of a ray or (adj.) a structure associated or oriented with a ray. Axil: ossicle at which a ray branches. Brachitaxis: series of ossicles following radial or axil and including the next axil; I-IIIBr: first through third brachitaxes; Arabic numeral immediately following indicates number of ossicles in that brachitaxis (e.g., IIBr2). Arm: unbranched series of ossicles following distalmost axil; brachial (br; plural, brr): arm ossicle; subscript numbers indicate specific ray ossicle (brachitaxis or arm) counting from first ossicle after preceding axil or radial (e.g., $IIBr_2$, br_7); WL of ray ossicle: median width to midaboral length ratio when viewed aborally. Synarthry: articulation between first two ossicles of a brachitaxis or arm consisting of two ligament bundles separated by an aboral-oral fulcral ridge, sometimes with midaboral swelling. Syzygy (+): articulation between two successive ray ossicles consisting of radiating ridges and grooves and appearing externally as a perforated line (e.g., br_{3+4}); intersyzygial interval: number of articulations between successive syzygies. Pinnules (P): unbranched segmented appendages arising from alternate sides of successive brachials; subscripts count pinnules from the most proximal; numbers and letters refer to pinnules along exterior and interior side of an arm, respectively (that is, the sides away from and toward the extrapolated axis of the ray) (e.g., P_4, P_c); LW of pinnule ossicles (pinnulars): length to median width ratio. Comb: modification of distal pinnulars of proximal (oral) pinnules producing comblike profile. Disk: central visceral mass or, specifically, its oral surface; anal interambulacral area: large area on disk surrounded by food grooves and bearing anal papilla. For further discussions and examples of comatulid morphometrics, meristics, abbreviations and symbology, see A. M. Clark & Rowe (1971), Breimer (1978), Hoggett & Rowe (1986) and Messing & Dearborn (1990). In all illustrations, sparse uniform stippling indicates articulations.

Genus *Alloeocomatella,* new genus

Diagnosis.—A genus of Comasteridae with all brachitaxes of two ossicles articulated by synarthry; arms 10–30, always arranged in single plane (rays never twisted); when present, IIIBr series developed exteriorly; first syzygy at br_{3+4} on arms arising from IBr series; in specimens with <20 arms, first syzygy also chiefly at br_{3+4} on arms arising from IIBr series; in specimens with ≥20 arms, syzygies at $br_{1+2,3+4}$ or br_{3+4} on arms arising from IIBr, and chiefly $br_{1+2,3+4}$ on interior arms and br_{3+4} on exterior arms arising from IIIBr; br_{1+2} occasionally present alone; middle brr with raised axial lines; oral pinnule combs long, of 20–37 teeth, occurring from P_1 to between P_4 and P_8; teeth confluent with lateral margin of pinnular, ≥2× taller than their greatest width at mid-comb, remaining tall to pinnule tip, and arising from side of pinnular away from arm; proximal tooth not transverse; basal carinae absent; cirri up to 26 segments, cylindrical proximally, compressed and wider distally; transitional and following cirrals with transparent distal rim, and with distally-directed midaboral spine located distally or subdistally initially, gradually moving to middle of segment and becoming more erect on more distal cirrals; spine usually sharp, sometimes blunt on large cirri, sometimes broadened as a narrow transverse ridge, occasionally forked (especially opposing spine); mouth excentric; anal papilla close to mouth.

Type species.—*Alloeocomatella polycladia,* new species.

Other included species.—*Comissia pectinifer* A. H. Clark, 1911.

Distribution.—Maldive Islands, Christmas Island (Indian Ocean), Indonesia, New Guinea, Bismarck Archipelago, Great Barrier Reef (Lizard I.), Fiji, Palau, New Caledonia, Chuuk Atoll. From 3 to at least 25 m [one record of 100 m (A. H. Clark 1931)].

Etymology.—From the Greek *alloios* (αλλοιος) "of another kind, different" (Brown, 1978) and *Comatella,* a comatulid genus that it resembles. Gender is female.

Remarks.—Both species of *Alloeocomatella,* when handled alive, are less "sticky" and more flexible than many other comasterids; lack of stickiness is perhaps due to relatively weak development of spines and hooks on distal pinnulars.

Features of *Comatella* distinguishing it from *Alloeocomatella* are as follows: arms 10 to >80; rays in single plane or twisted, with exterior branches curved to oral side of radial plane; first syzygy at br_{1+2} on arms arising from IIBr and following brachitaxes with one exception: first syzygy at br_{3+4} on exteriormost arm of IIIBr and following brachitaxes; br_{3+4} often absent following br_{1+2}, even in specimens with 40 arms. Single confluent comb teeth arising from interior side of pinnule (side closest to arm); individual teeth $<2\times$ taller than greatest width at mid-comb, usually 14–18/comb, and strongly reduced on last one or two pinnulars; sharp rounded carina usually present on basal segments of proximal pinnules. Cirri bearing aboral transverse ridges (sometimes shallow V- or Y-shaped in aboral view), sometimes narrowing to erect rounded or triangular prominence or spine on more distal cirrals.

The type specimen of *Comissia luetkeni* A. H. Clark, the type of *Comissia,* differs from *Alloeocomatella* as follows: cirri stout; aboral distal margins of all but basal and distal few cirrals strongly flared and sometimes dentate; IBr2 series and arm bases as far as br_2 closely apposed and flat-sided; no raised axial lines on brr; pinnule combs of fewer than 20 teeth, arising abruptly on all oral pinnules; most pinnulars of middle and distal pinnules with strong distal spine; distal pinnulars with $LW \leq 3.0$; mouth subcentral; anus marginal.

Alloeocomatella polycladia, new species

Figs. 1–2, 3a–d, h, 4

Comatella maculata.—Meyer & Macurda, 1980, pp. 63, 68, 83, 96 (part); Meyer, 1986, pp. 203, 208–209 (part?).

Diagnosis.—A species of *Alloeocomatella* with up to 30 arms; ray length up to 205 mm; anterior:posterior ray length ratio 1.1–1.5:1; longest segments on distal pinnules with LW usually 3.0–5.0; longest cirrals (on mature cirri) with LW 1.3–2.0; anal interambulacral area usually crowded with rounded or irregular, knobbed or molariform nodules, but not often on anal papilla itself. [Small ten-armed specimens may have more elongated cirrals and distal pinnulars.]

Type series.—Holotype: USNM E44632, N side of Northeast Pass, S of Quoi I., Chuuk Atoll, Federated States of Micronesia, 7°31′32″N, 151°58′11″E, ≈18 m, 11 Jun 93, night. Paratypes: Chuuk Atoll: USNM E44633 (1 specimen) N side of NE Pass, S of Quoi I., ≈18 m, 11 Jun 1993, night. USNM E44636 (1), N side of NE Pass, S of Quoi I., 9-18 m, 11 Jun 1993, night, Patrick Colin, coll. USNM E44634 (1), N side of NE Pass, S of Quoi I., 6 m, 8 Jun 1993, Larry Sharron, coll. BMNH 1994.5850 (1), barrier reef S of Otta I., 07°08′45″N, 151°53′11″E, 11 m, 9 Jun 1993. LACM 93-95.1 (1), barrier reef S of Otta I., 9 m, 9 Jun 93, Larry Sharron, coll. Papua New Guinea: PM ECCh-16 (1), fringing reef, N side Nagada Harbor, Madang, 05°09′29″S, 145°49′21″E, 9 m, 10 Jul 1991, night. USNM E44642 (1), Nagada Harbor area N of Madang, no field data, Jul 1991. USNM E44635 (1), fringing reef drop off, Cape Croisilles, 4°51′30″S, 145°48′E, ≈30 km N of Madang, 6 m, 13 Jun 1992, Bert Hoeksema, coll. USNM E44637 (1), barrier reef E of Wongat I., Madang, 05°08′09″S, 145°50′51″E, 3 m, 11 Jul 1991. (All collections by the author except where noted.)

Other material examined.—Caroline Islands: USNM E44770 (4 specimens), E34983 (2), E44693 (18), E44694 (21), Palau Is., D. L. Meyer, coll. Australia: USNM E44771 (3), E44768 (3), Lizard I., Great Barrier Reef, D. L. Meyer, coll. Fiji: USNM E44769 (2), D. L. Meyer, coll. Indonesia: USNM E35033 (1), Marsegoe I., N end of Ceram I., Moluccas (2°59′48″S, 128°03′E), 15 m, D. L. Meyer, coll. Papua New Guinea: BELG-418 (1), Platier, Laing I., night, 23 Jul 1989, 20 m, M. C. Lahaye, coll.

Description of holotype.—Centrodorsal a thick pentagonal disk with sloping sides; diam. = 9.3 mm; aboral surface rugged with deep central depression and traces of former cirrus sockets. Cirri LXV, 21–25, 16–26 mm long, of variable length and robustness, crowded two or three deep around centrodorsal margin, with few sockets encroaching on aboral surface. First segment very short; second wider than long; third squarish; fourth or fifth to eighth, ninth or tenth cirrals longest, LW = 1.3, slightly constricted. Following cirrals gradually decreasing in length; cirrals in distal third of cirrus shorter than wide, LW = 0.7. Twelfth to fifteenth cirral (on larger cirri) transitional, shiny distally. Tip of sharp aboral spines occasionally finely divided into several tiny teeth. Antepenultimate cirral with transverse aboral ridge, sometimes with prominent ends forming a pair of spines. Spine on preceding cirral (fourth from end including claw) may also be slightly widened transversely. Opposing spine also a transverse ridge. Transverse ridges may be irregularly denticulate.

Anterior rays 150–160 mm, posterior rays 140 mm long. Arm number 30. Radials hidden by centrodorsal. Rays separated proximally; aboral surface of disk visible between adjacent rays. Brachitaxes with low midaboral synarthrial swelling straddling articulation of first and second ossicles. IBr_1 short, partly hidden by centrodorsal (mostly hidden by cirri). Axil (IBr_2) with very short, diverging lateral margins, WL = 2.0. IIIBr uniformly developed exteriorly. II and $IIIBr_1$ and br_1 slightly longer exteriorly and united interiorly; articulations with low midaboral synarthrial swellings; each brachitaxis with gently concave lateral margin. Br_1 and br_2 (or br_{1+2}) longer exteriorly. Br_{3+4} oblong, WL = 1.4–1.7, diam. = 1.9–2.1 mm. Br_{5-7} oblong, with well-developed alternating articular tubercles, WL = 1.7–2.0. Br_{8-9} cuneate. Following brr triangular, WL = 2.3, diam. = 2.1–2.4 mm (slightly wider than arm base). Brr become shorter by mid-arm, very strongly cuneate or triangular, WL = 2.6–3.0; distal margins thickened (raised but not everted) and spinose; thickening best developed along middle portion of arm. Distal brr almost oblong (slightly longer on one side), WL = 1.5; thickening of distal margins reduced; spines present only midaborally. Aboral surface of arms beyond the proximal several brr with numerous fine raised axial lines projecting beyond distal margin of ossicle as distal rim of spines; these spines fewer and midaboral on distal brr. On arms arising from IIBr, syzygies at $br_{1+2,3+4}$ or br_{3+4} alone. Br_{3+4} on exterior arms and $br_{1+2,3+4}$ on interior arms arising from IIIBr. Following syzygy br_{15+16} to br_{19+20}. Next intersyzygial interval chiefly 4–5 (few 3); distal intersyzygial interval chiefly 3 (some 4, 5).

P_1 of 64 segments, 25 teeth, L = 23 mm; basal several segments shorter than wide; most segments about as long as wide, with distal rim of spines best developed on side of pinnular facing arm tip (when pinnule extends outward from arm); middle and distal pinnulars also with cluster of spines on side of pinnular facing arm tip; lateral spines consolidating to form rudimentary proximal comb teeth; comb teeth tall, narrow and usually triangular. P_2 and following oral pinnules similar to P_1 but decreasing in length through last comb-bearing pinnule (P_7–P_8); with comb teeth developing more abruptly, few middle pinnulars longer than wide (LW to 1.3), and comb occupying relatively more segments per pinnule. P_2 of 54 segments, 33 teeth, L = 16 mm; P_3 of 45 segments, 27 teeth, L = 13 mm; P_7 of 30 segments, 20 teeth, L = 9 mm. P_8 or P_9 without a comb, 24 segments, L = 9 mm; basal segments short; most middle segments squarish to somewhat longer than wide, LW to 1.4; all segments except basal 3 with numerous spines on side of pinnulars facing arm tip. Middle pinnules (e.g., P_{20}) with 29 segments, L = 14 mm; similar to P_9 but more robust; segments with LW up to 1.4. Distal pinnules much slenderer, with up to 28 segments, L = 13 mm; basal two segments short; following segments longer than broad (except near tip), becoming very slender in mid-pinnule, LW to 3.5; proximal segments with few distal spines; middle and distal segments with few weak lateral spines; last four segments with typical strong hooks.

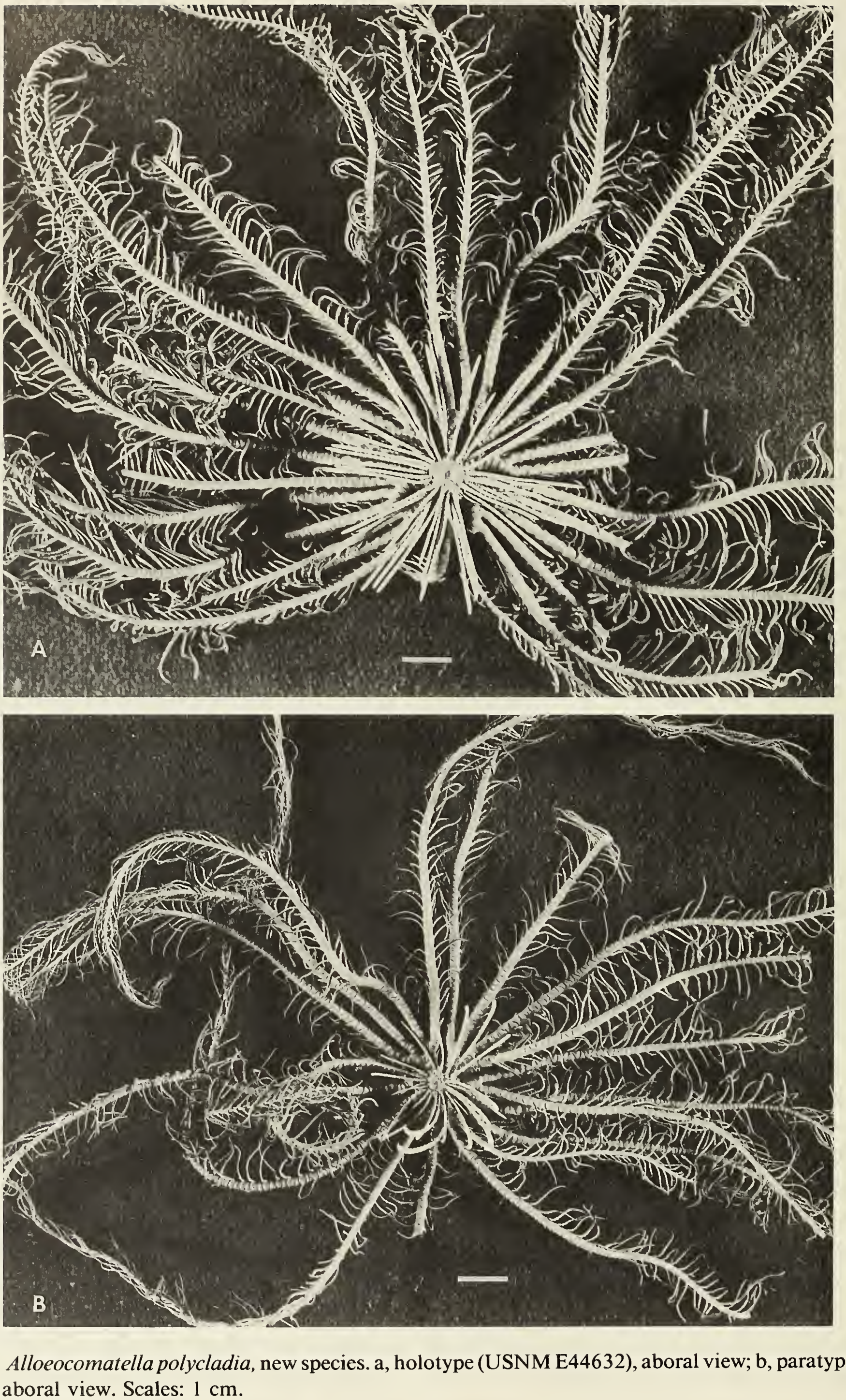

Fig. 1. *Alloeocomatella polycladia,* new species. a, holotype (USNM E44632), aboral view; b, paratype (LACM 93–95.1), aboral view. Scales: 1 cm.

Few large irregular nodules on large swollen anal interambulacral area; some almost foliose. Nodules more compact on anal papilla; some molariform. Anal papilla adjacent to mouth.

Other specimens.—One paratype (USNM E44633) collected with the holotype and three collected by D. L. Meyer at Lizard Island (USNM E44771) as large or larger than the holotype: centrodorsal diameter 9–10 mm; cirri LX–LXX, the largest with 24–25 segments, 23–27 mm long; ray length 150–205 mm; arms 28–30; P_1 up to 63 segments.

Most material smaller: 15–21 arms, ray length 105–150 mm (mostly <125 mm), and centrodorsal diameter 5.5–7.0 mm. Anterior:posterior ray length ratio 1.3–1.5:1. Central aboral depression shallower on smaller specimens. As in the holotype, cirri usually varying substantially in length, number of segments and robustness in individual specimens; chiefly XXXV–LV, with largest cirri of 16–20 segments, 15–18 mm long. Longest cirrals usually fourth and fifth or sixth, with LW = 1.5–2.0 (to 2.3 on smaller cirri).

P_1 usually 43–54 segments, 22–30 teeth, 14–20 mm long. P_4 or P_5 usually the last comb-bearing pinnule. Middle and distal pinnules correspondingly smaller than those of holotype (e.g., middle pinnules with 21 segments, 9 mm long; distal pinnules with 24–25 segments, 11–12 mm long). Middle pinnules of 20–21 segments, 9.0 mm long, not especially more robust than more proximal (non-combed) pinnules; LW of middle pinnulars up to 1.7. Distal pinnules differing from those of holotype in having one or few strong distal spines on both proximal and middle pinnulars, LW = 2.7–5.0, and only 0–3 weak lateral spines on distal few pinnulars (not including distal hooks).

Anal interambulacral area often crowded with rounded or irregular nodules except on anal papilla itself. Nodules usually with a knob; several sometimes coalesced into larger ridged or molariform structures, sometimes forming an irregular pavement. Nodules sometimes also present on several small peripheral interambulacral areas. Oral surface completely naked in a few specimens.

Smaller ten-armed specimens differ as follows: centrodorsal diameter 2.9–4.6 mm; central depression slight or absent; ray length up to about 110 mm; cirri usually XXIX–XXXVI (rarely less), the largest of 16–19 segments; longest cirral with LW = 1.7–2.6; only the opposing spine widened or forked; segments of distal pinnules with LW to ≈6.0.

Two small specimens from Palau have 6 rays and 12 arms.

Description of an immature specimen.—(USNM E44693) Centrodorsal a thin disk, 3.0 mm across; aboral surface slightly convex, without central depression; cirri XXIII, 12–16, 11.4 mm, third to sixth segments elongated with expanded ends, fourth to fifth or sixth segments longest, with LW = 2.2–2.4 (3.0 on a much smaller cirrus); sixth or seventh segment transitional, shorter and wider, LW = 1.6; distal several segments slightly wider than long; opposing spine slightly widened transversely.

Most rays broken; anterior ray 65 mm, posterior ray ≈ 45 mm; radials visible in interradial angles; IBr_1 completely exposed, oblong, WL = 2.2; axil pentagonal with diverging lateral margins, WL = 2.0; br_1 and br_2 oblong, WL = 1.7; br_1 united interiorly only proximally; br_{3+4} oblong, WL = 1.2, diameter = 1.0 mm; br_{5-6} oblong, WL = 1.3–1.4; following brr becoming cuneate, none triangular; middle brr cuneate, WL = 1.0, with distal margins raised, spinose, no axial lines; distal brr almost oblong, with few coarse midaboral distal spines; WL = 0.7.

P_1 of up to 35 segments, 19 teeth, 9.7 mm long; P_2 the last comb-bearing pinnule, smaller and slenderer than P_1, up to 29 segments, 19 teeth, 7.6 mm long; P_3, P_c and P_4 much smaller and slenderer than P_2 not present on all remaining arms; middle pinnules of 15 segments, 6.1 mm long; distal

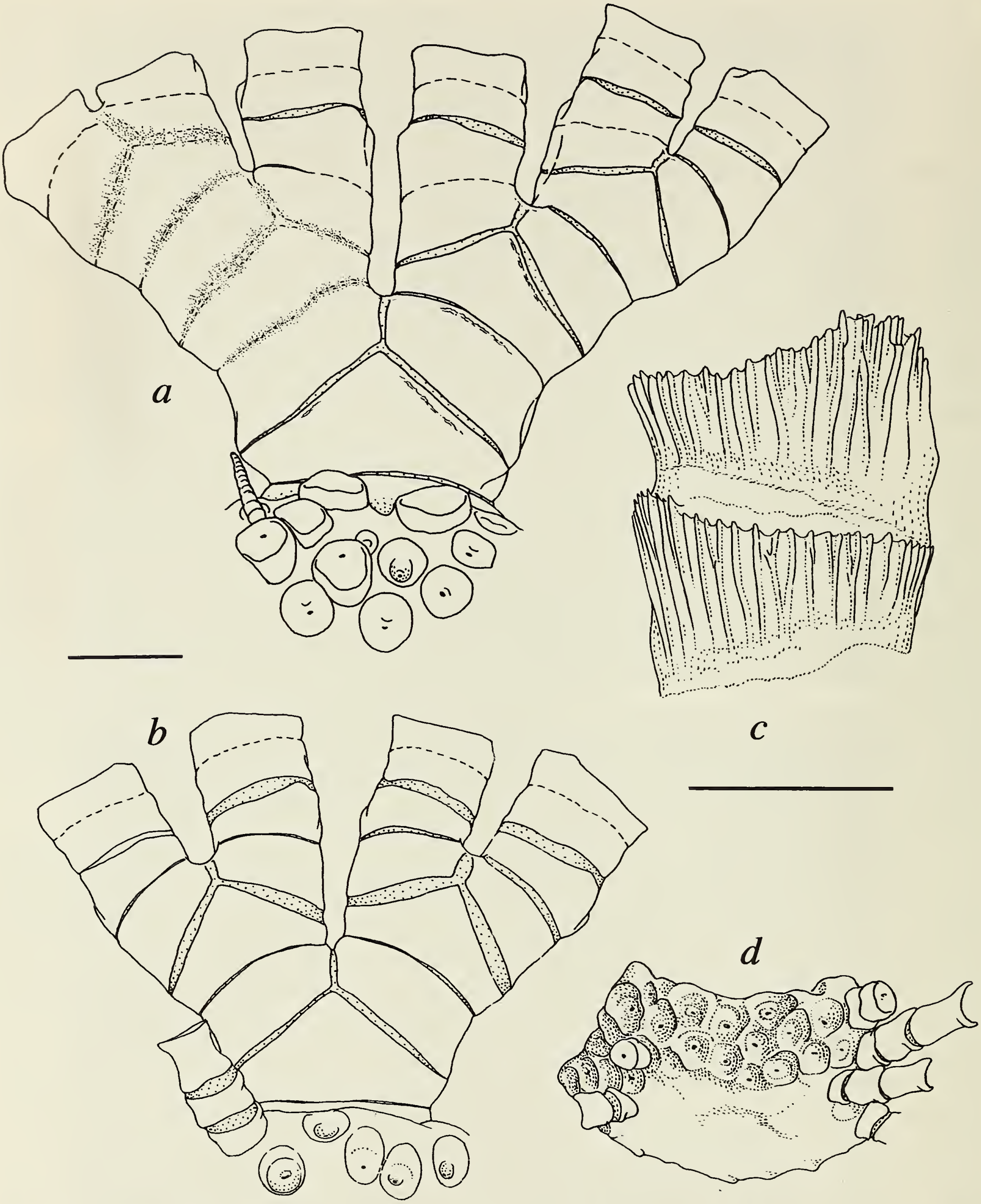

Fig. 2. *Alloeocomatella polycladia,* new species. a–b, margin of centrodorsal and base of one ray; a, large paratype with 30 arms (USNM E44633) (stippling on left side indicates reticulated tissue that obscures articulations; typical of proximal portions of rays of both species); b, smaller paratype with 20 arms (USNM E44636). c, two middle brachials showing raised axial ridges and distal spinose margins, paratype (PM ECCh-16). d, centrodorsal with several cirrus bases, oblique view, paratype (USNM E44637). Scale: (left) a, b, d, 2 mm; (right) c, 1 mm.

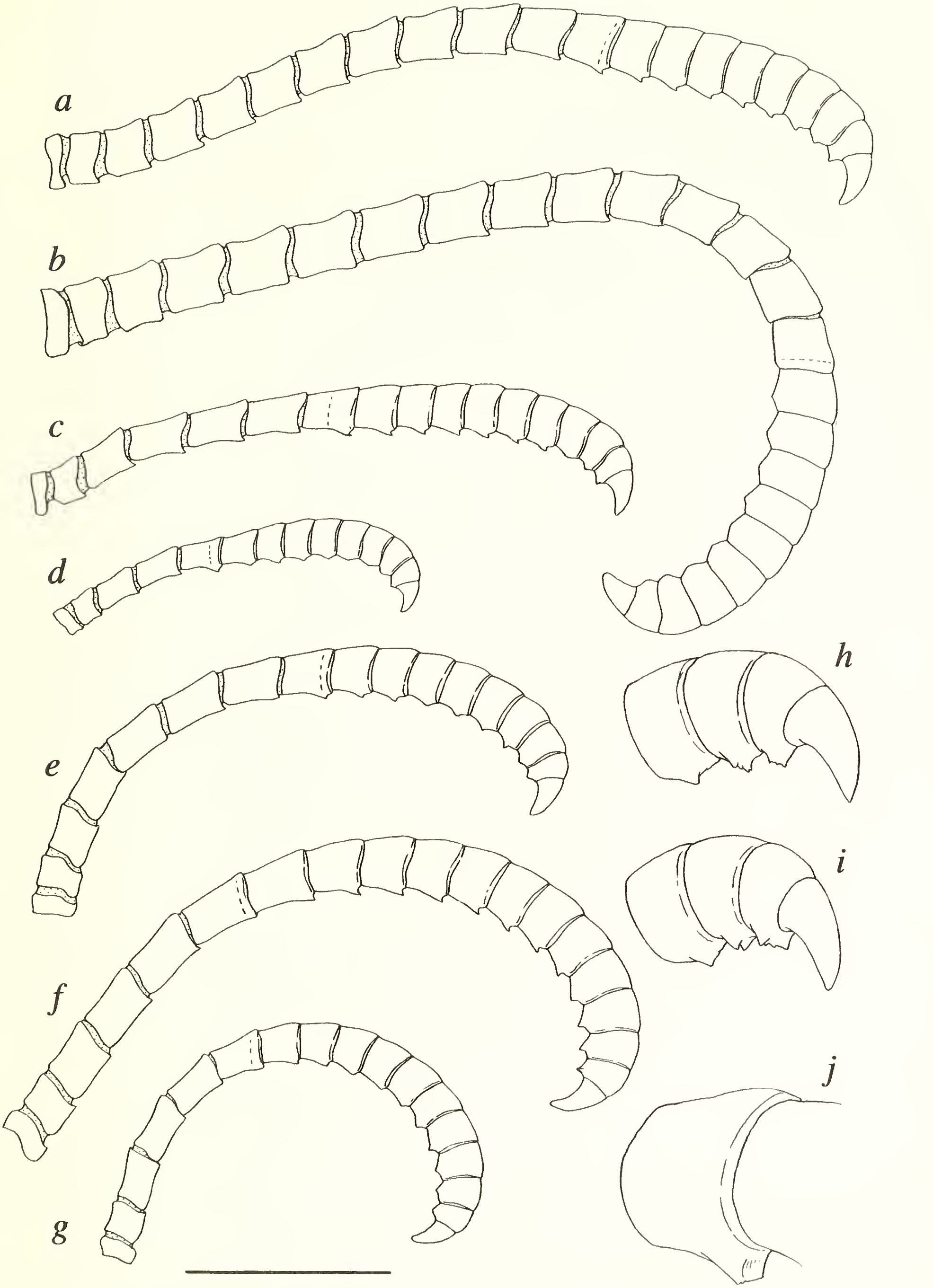

Fig. 3. Cirri. a–d, h. *Alloeocomatella polycladia,* new species. a–b, large paratype (USNM E44633); c–d, smaller paratype (USNM E44642); h, cirrus tip showing aboral spines on distal two segments (preceding terminal claw) widened as dentate transverse ridges. e–g, i, j. *Alloeocomatella pectinifera* (A. H. Clark). e, holotype (BMNH 87-4-26-9); f–g, (USNM E44640); i, cirrus tip showing forked aboral spine on antepenultimate cirral, and opposing spine widened as transverse dentate ridge; j, cirral following transitional cirral with aboral spine widened as sharp, narrow transverse ridge (LACM 92–160.1). Dashed lines (a–g) indicate transitional segments. Scale: a–g, 4 mm; h–i, 2 mm; j, 1 mm.

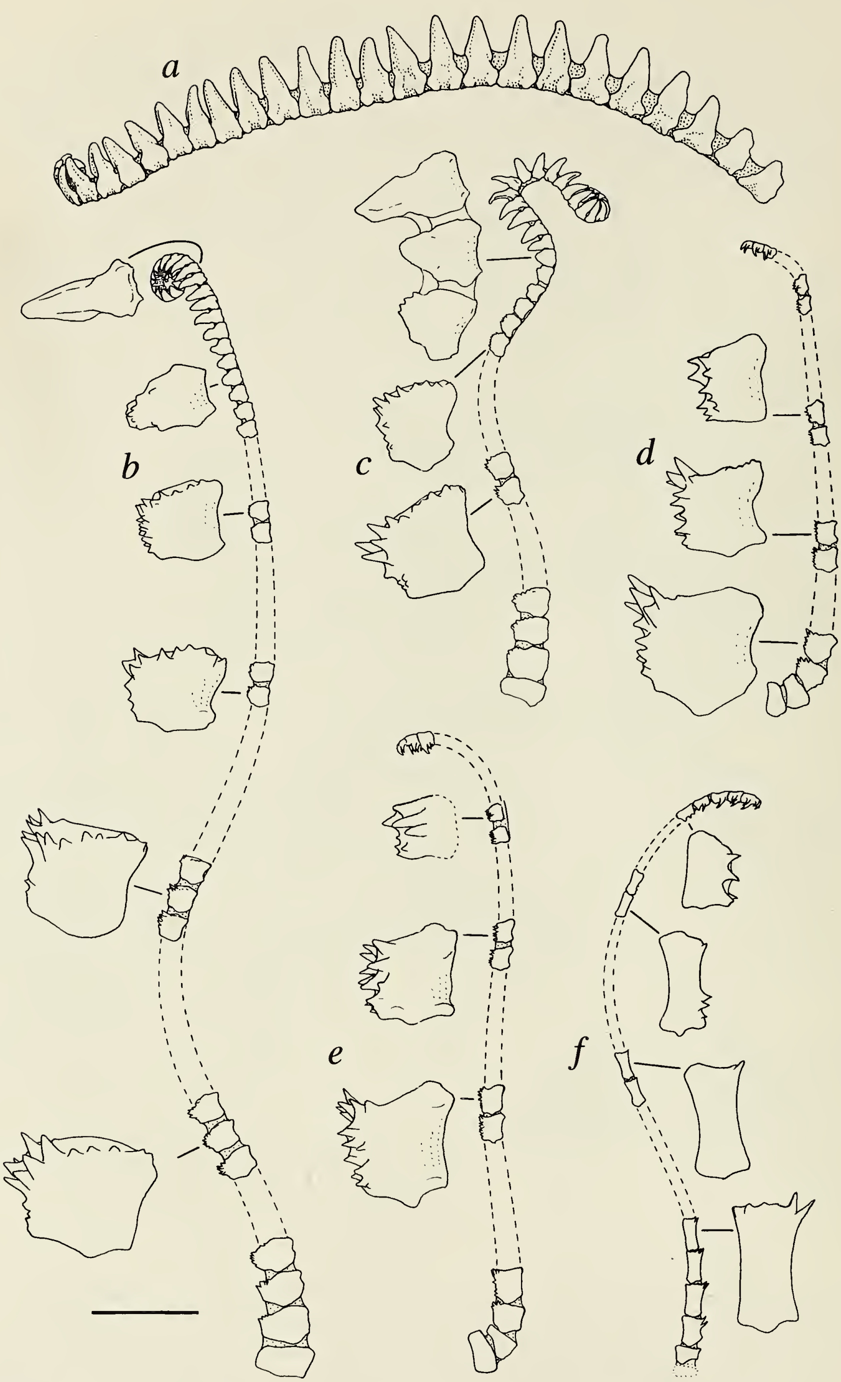

Fig. 4. *Alloeocomatella polycladia,* new species. a, comb of P_1, paratype (PM ECCh-16); b–f, holotype (USNM E44632); b, P_1; c, P_3; d, P_9; e, P_{20} (dotted portion of distalmost enlarged pinnular obscured by tissue); f, P_{distal} (different arm) [first pinnular (dotted) lost]. Scale: 2 mm; enlarged pinnulars, 0.5 mm.

pinnules slender, up to 20 segments, 9.9 mm long.

Disk with numerous round nodules on anal interambulacral area.

Color pattern.—Dark red or purplish red; pinnules sometimes beaded purplish red and pink, sometimes with yellow, orange or pink tips.

Habits.—All specimens collected by SCUBA on inshore fringing reefs, lagoonal patch reefs, and barrier reefs. Cryptic during the day, often found curled under slabs of coral rubble. At night: specimens with about 20 or fewer arms concealed in crevices, with several arms extending into the water column and with pinnules arranged in single plane; withdrawing rapidly and completely when illuminated; large specimens completely exposed, perched on corals, forming arcuate or radial fan, also with pinnules arranged in single plane. The photograph identified as *Comatella maculata* on p. 208 of Meyer (1986) is almost certainly this species.

Distribution.—Indonesia (Ceram I.), Papua New Guinea, northern Australia (Lizard I., Great Barrier Reef), Palau Is., Fiji, New Caledonia, Chuuk Atoll; 3–18 m.

Etymology.—From the Greek *polys* (πολυς) "many" and *klados* (κλαδος) "branch," because this species has more than the ten arms of *A. pectinifera.*

Remarks.—In the past, specimens of *A. polycladia* have been identified as *Comatella maculata* due to similarities among brachitaxes, arm number and general cirrus structure in the two species (Meyer & Macurda 1980, Meyer, 1986). In Hoggett & Rowe's (1986) key to the genera of Comasteridae, large specimens (>20 arms; first syzygy on IIBr arms at br_{1+2}) run down to *Comatella* while smaller multibrachiate specimens (11–20 arms; first syzygy on IIBr arms at br_{3+4}) run down to either *Comanthus* or *Clarkcomanthus.* These smaller specimens lack the diagnostic features of either of the latter two genera and cannot be assigned to a genus using this key.

Several small specimens of *Alloeocomatella* collected by D. L. Meyer at Palau (included in USNM E44693, E44694) are difficult to assign to species. These individuals resemble *A. pectinifera* in having ten arms, and cirri and distal pinnules with more elongated segments. They are referred to *A. polycladia* because: 1) when measurable, the anterior:posterior ray length ratio is 1.1–1.5:1, less than in *A. pectinifera,* and 2) most specimens have large, crowded disk nodules except on the anal papilla itself. These specimens were also collected with larger specimens clearly identifiable as *A. polycladia,* but both species have been collected in the same local reef habitat. It is not surprising that small specimens may be difficult to identify. It is often impossible to identify juvenile ten-armed comasterids to genus (Hoggett & Rowe 1986).

Alloeocomatella pectinifera
(A. H. Clark, 1911),
new combination
Figs. 3e–g, i, j, 5, 6

Comissia pectinifer A. H. Clark, 1911, p. 644; 1912, p. 78; 1918, p. 19; 1931, p. 255–256, pl. 25.—Messing, 1994, p. 239.

Comissia pectinifera.—A. M. Clark & Davies, 1965, pp. 598, 603–4.—A. M. Clark & Rowe, 1971, pp. 6, 14.—Zmarzly, 1985, pp. 348, 350–2.—Meyer, 1986, p. 203.—Bradbury et al., 1987, pp. 190–191.

Comissia sp. cf. *pectinifera.*—Zmarzly, 1985, pp. 348, 351–2, 354–6.—Meyer, 1986, pp. 206–7.

Diagnosis.—Ten arms; anterior ray length up to 500 mm; anterior:posterior ray length ratio 2.0–2.9:1; longest segments on distal pinnules (anterior rays) with LW up to 7.0; longest cirrals (on mature cirri) with LW = 1.6–2.3; anal interambulacral area usually naked, with few scattered nodules, or with numerous nodules on anal papilla.

Holotype.—BMNH 87-4-26-9; Christmas Island, Indonesia (south of the Sunda

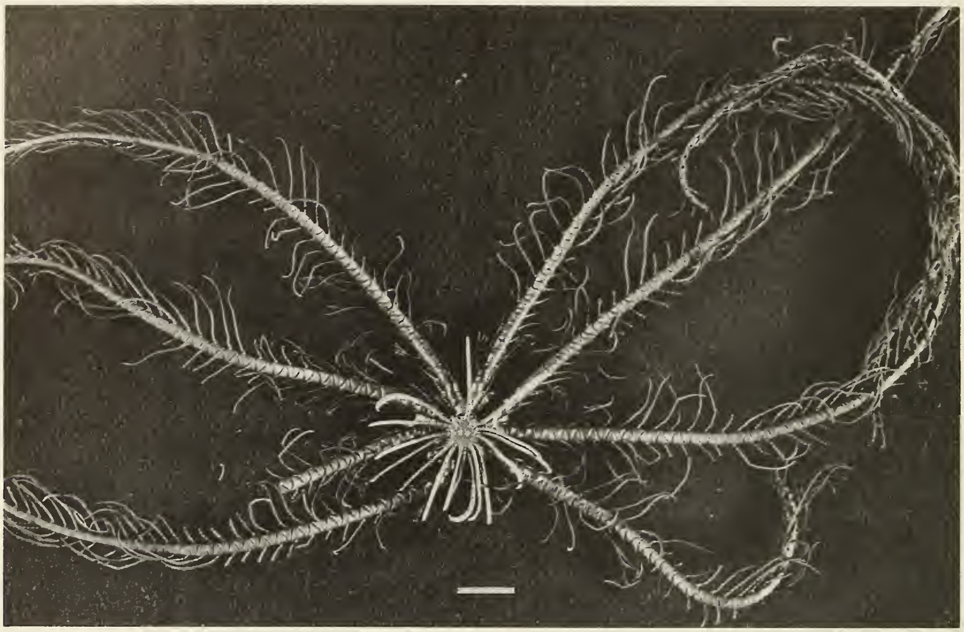

Fig. 5. *Alloeocomatella pectinifera* (A. H. Clark) (USNM E44640), aboral view. Scale: 1 cm.

Straits, between Sumatra and Java), H. M. S. Flying Fish (A. H. Clark, 1911, 1931).

Other material examined.—Chuuk Atoll: USNM E44802 (2 specimens), N side NE Pass, S of Quoi I., Chuuk Atoll, 7°31′32″N, 151°58′11″E, 18-23 m, 11 Jun 1993, P. Colin/C. G. Messing, coll. Papua New Guinea: USNM E44639 (1), fringing reef, N side Nagada Harbor, Madang, E of wading beach, 05°09′29″S, 145°49′24″E, 3 m, 4 Jun 1992. USNM E44638 (1), near top of barrier reef SE of Pig I., SE of Nagada Harbor, Madang, 05°10′21″S, 145°51′47″E, 14 m, 16 Jul 1991. LACM 92-160.1 (1), fringing reef, N side Nagada Harbor, Madang, 05°09′29″S, 145°49′21″E, 8 m, 12 Jun 1992. USNM E44640 (1), wall off Barracuda Rock, SE of Nagada Harbor, Madang, 05°10′20″S, 145°51′53″E, 23 m, 14 Jul 1991. USNM E44803 (1), near top of barrier reef SE of Pig I., SE of Nagada Harbor, Madang, 14 m, 16 Jul 1991. USNM E44804 (1 immature). Nagada Harbor area, Madang, no field data. USNM E44641 (1), Cape Croisilles, exposed fringing reef, 4°51′30″S, 145°48′E, ≈30 km N of Madang, 6 m, 13 Jun 1992, B. Hoeksema, coll. Indonesia: USNM E8959 (2), Duroa Strait, Kei Is., 5°24′20″S, 132°55′E, 100 m, 15 Apr 1922, T. Mortensen, coll. (sta. 24). (All collections by the author except where noted.)

Description of holotype.—Poor condition; most rays broken near their bases. Centrodorsal a thick pentagonal disk with sloping sides, diameter = 4.6 mm; aboral surface with shallow central depression; cirri crowded around margin, 2–3 deep, XLIV, 14–17, maximum length 14 mm; segments increasing in length from very short first to fifth; fifth and sixth segments longest, LW = 1.9; following segments decreasing in length; seventh or eighth and following segments with sharp erect or distally-directed spine (blunt on some cirri); first spine-bearing segment with LW = 1.2, next as wide as long; following segments wider than long and becoming shorter distally; antepenultimate with LW = 0.7; spines on few distal

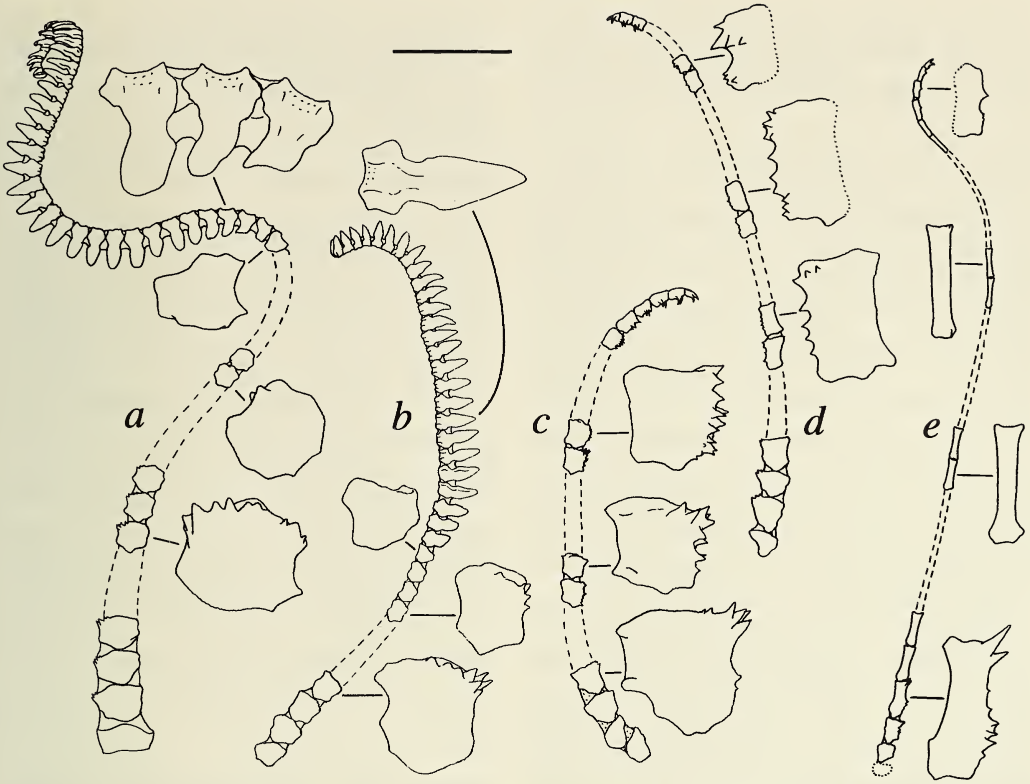

Fig. 6. *Alloeocomatella pectinifera* (A. H. Clark) (USNM E44803). a, P_1; b, P_5; c, P_9; d, P_{20} (dotted portions obscured by tissue); e, P_{distal} [first pinnular (dotted) lost]. Pinnules taken from different arms. Scale: 2 mm; enlarged pinnulars, 0.5 mm.

segments, including opposing spine, sometimes widened as a transverse ridge which may be forked, dentate or serrate.

Radials visible in interradial angles; IBr_1 short and separated, WL = 4.0; axils wider than IBr_1, with short, diverging lateral margins, WL = 1.8; br_1 oblong or slightly wider exteriorly, united interiorly only proximally, WL = 2.8; br_2 wider exteriorly, WL = 2.2; br_{3+4} diameter = 2.0–2.2 mm; br_{5-6} oblong, WL = 2.3; proximal brr with strongly developed alternating articular tubercles; brr triangular or almost so by br_{8-9}, WL = 2.5; second syzygy at br_{11+12}; brr with thickened, raised, spinose distal margins and raised axial lines; middle brr strongly cuneate, WL = 1.7; distal intersyzygial interval 3. Most arms broken; longest intact to br_{23}.

Most pinnules broken. P_1 of 47 segments, with ≈ 26 tall narrow teeth, 15.3 mm long; comb developing gradually (comb coiled–tip may be lost; another P_1 bears 32 teeth); P_b of 39 segments, about 27 teeth; comb developing more abruptly. Proximal and middle segments of oral pinnules short, with distal fringe of spines; middle segments also with few lateral spines coalescing on more distal segments to form comb rudiment. Middle pinnule of 22 segments, 9.3 mm long; segments beyond short basal few squarish or little longer than wide, with dense lateral cluster of spines.

Disk absent.

Description of other material.—Centrodorsal usually a thick rounded pentagonal or circular disk with steeply sloping sides; diam. = 4.1–6.1 mm; aboral surface with shallow central depression and at least a trace of radiating interradial ridges. Cirri crowded, of varying length and robustness, one or two deep around centrodorsal margin; XXIX-XLVI, 16–22 (mature), maximum length on any individual 12–19 mm (chiefly 13–16 mm); only one or two segments, from the fourth to seventh, longest; LW of longest segments on largest cirri = 1.6–2.3 (chiefly 1.8–2.0); sixth to eighth segment transitional; second segment following transitional, LW = 0.9–1.1; following segments slightly shorter; antepenultimate segment with LW = 0.6–0.8; aboral spine widened as a sharp narrow transverse ridge on some or most segments in some specimens; when present, transverse ridge may be forked (rarely trifid), eroded and blunt, or restricted to penultimate segment.

Maximum ray length chiefly 200–275 mm; anterior to posterior ray length ratio 2.0–2.5:1; one specimen with anterior rays 500 mm, posterior rays 200 mm; radials hidden or visible in interradial angles; IBr$_1$ short, oblong, separated or just touching proximally, partly hidden by centrodorsal or completely exposed, WL = 2.8–4.0; axil with short diverging lateral margins, WL = 2.0–2.2; IBr and br$_{1\text{-}2}$ with or without small synarthrial swelling; br$_1$ oblong or slightly longer exteriorly, united interiorly at least partly, WL = 2.0–2.8; br$_2$ longer exteriorly, usually shorter than br$_1$, WL = 2.3–3.1; br$_{3+4}$ oblong, WL = 1.5–1.9, diameter = 1.6–2.4 mm; br$_5$ to br$_6$ or br$_7$ oblong, WL = 1.9–2.3; proximal brachials with moderately to strongly developed alternating articular tubercles; brr triangular by br$_{9-11}$, WL = 1.9–2.6; brr with raised, spinose distal margins and raised axial lines first appearing by br$_{7-11}$; brr strongly cuneate in proximal third of arm, WL = 1.8–2.4, becoming moderately cuneate by mid-arm, WL = 1.5–1.9, with raised, spinose distal margins and axial lines; distal brr moderately or weakly cuneate (almost oblong), often longer than wide, WL = 0.7–1.1, usually with distal margins weakly raised, spines strongest midaborally, and axial lines weak or absent; brr near arm tip slender and elongated, WL = 0.5–0.8, with few coarse midaboral spines. Syzygies at br$_{3+4}$, usually br$_{11+12}$ to br$_{14+15}$ (rarely br$_{10+11}$ to br$_{16+17}$); distal intersyzygial interval usually 3 (sometimes 2 or 4; rarely 5 to 7).

Pinnules generally similar to those of *A. polycladia*. P$_1$ of 49–60 segments, 23–37 teeth, L = 18–26 mm; P$_2$ of 44–57 segments, 29–39 teeth, L = 13–20 mm; P$_3$ of 43–58 segments, 29–39 teeth, L = 12–18 mm; P$_4$ to P$_6$ the last comb-bearing pinnule, up to 42 segments, 31 teeth, L = 11 mm. P$_9$ of 22 short segments (max. LW = 1.3), up to 9 mm long; proximal segments (except basal two) with distal rim of spines; most segments with numerous spines on side of pinnule facing arm tip. Middle pinnules of 19–25 segments, L = 8–13 mm; similar to P$_9$ but with middle pinnulars more elongated; LW = 1.3–1.9. Distal pinnules up to 32 segments, L = 11–17 mm; basal two segments short; remaining segments (except near tip) elongate, LW = 3.0–7.0; proximal segments with one or two strong distal spines; most segments (especially on pinnules near arm tip) smooth with expanded ends; distal segments with one or two small mid-lateral spines; distal hooks weak.

Disk usually lost; when present, naked, or with few scattered conical nodules on anal interambulacrum; nodules numerous on anal papilla in one specimen.

Description of an immature specimen.—(USNM E44804) Centrodorsal a thin disk, 2.1 mm across; aboral surface slightly convex, with traces of juvenile sockets, and without central depression; cirri XXIV, 13–15, 10 mm; third to fifth segments elongated with expanded ends; fourth segment longest, with LW = 2.8–3.0; transitional sixth segment shorter and wider, LW = 1.6; distal several segments slightly wider than long; opposing spine slightly widened transversely on one or two cirri.

Anterior rays 130 mm, posterior rays ≈ 45 mm; radials just visible beyond centrodorsal; IBr_1 completely exposed, oblong, WL = 2.0; axil pentagonal with diverging lateral margins, WL = 1.5; br_1 and br_2 slightly longer exteriorly, WL = 1.6; br_1 united interiorly only proximally; br_{3+4} oblong, WL = 0.9, diameter = 0.9 mm; br_{5-6} oblong, WL ≈ 1.0; following brr becoming cuneate, none triangular; middle brr cuneate, longer than wide, WL = 0.7, with distal margins raised, slightly everted, spinose and with spines strongest midaborally; no axial lines; distal brr slender, constricted in middle, with few coarse midaboral distal spines; WL = 0.3.

P_1 up to 43 segments, 29 teeth, L = 10.7 mm; P_2 smaller and slenderer than P_1, up to 34 segments, 22 teeth, L = 7.4 mm; P_3 and P_c not developed; P_4 the last comb-bearing pinnule, much smaller and slenderer than P_2, about 16–23 segments, 7–14 teeth, max. L = 4.0 mm; middle pinnules of 13–15 segments, L = 5 mm; distal pinnules extremely slender, up to 21 segments, L = 9.2 mm.

Disk naked.

Color patterns.–Rays variously deep red, red-orange, reddish- or pinkish gray, maroon or dark red-brown, often with differently pigmented articulations (red, orange or white), or a paler midaboral stripe. Some specimens with articulations and ossicle margins white. Pinnules same color as arms or darker, sometimes with paler or yellow tips, sometimes with white aboral stripe; in specimens with white-bordered ossicles, tissue dark brown on proximal pinnules, becoming orange or yellow on distal pinnules; centrodorsal sometimes with white center; cirri sometimes with white aboral stripe; disk dark red, red-brown, sometimes with narrow white stripes. At New Caledonia (Meyer 1986), yellowish or banded yellowish and brown, with brown pinnules.

Habits.—Cryptic during the day. At night, calyx remains hidden, with four to eight arms extended more or less in parallel; pinnules arranged in a single plane. Withdraws rapidly and completely when illuminated.

Distribution.—Maldive Is., Indonesia, northern Australia (Lizard I., Great Barrier Reef), Papua New Guinea, Palau Is., New Caledonia, Chuuk Atoll, Kwajalein Atoll. 3–23 m.

Remarks.—As mentioned under *A. polycladia,* small ten-armed specimens of *Alloeocomatella* may be difficult to identify to species. The greater difference between anterior and posterior ray lengths even in small specimens appears to separate *A. pectinifera* from *A. polycladia.* The nature and distribution of disk nodules should be used cautiously as a diagnostic character because specimens of both species may lack them.

Anterior:posterior ray length ratios vary within several comasterid taxa (Messing 1994), which suggests that this may not be a useful diagnostic feature. *Comanthus parvicirrus* (Müller), for example, tends to develop longer anterior rays and higher ratios in deeper and quieter habitats. Specimens from shallow (<8 m), higher-energy habitats tend to have rays of more nearly equal lengths. However, ray length ratio does not appear to vary with habitat in *Alloeocomatella.* At Madang and Chuuk Atoll, I found both species in the same local reef habitat and observed that both extend arms or emerge completely only under relatively low energy conditions, either in deeper water (14–23 m) or on shallow (3–4 m) sheltered inshore reefs. A single specimen from a shallow, high-energy habitat was cryptic. At New Caledonia, Meyer (1986) recorded *A. polycladia* (as *Comatella maculata*) from "relatively sheltered reefs" (p. 209), and *A. pectinifera* from "reefs subject to weak currents" (p. 206).

Most specimens of *A. pectinifera* described here are larger than previously recorded material. The largest collected (and several measured in the field) has a maximum ray length of about 500 mm, the longest recorded for any comatulid. Because posterior rays are substantially shorter (about 200 mm), the total span approximately equals that of the largest comatulid previously noted; the Arctic/boreal antedonid *Heliometra glacialis* var. *maxima* has rays up to 350 mm in length (Clark & Clark 1967).

Acknowledgments

I want to thank the following: the Christensen Fund (Palo Alto, California) for awarding me the fellowship that permitted me to carry out research at the Christensen Research Institute (CRI), P.O. Box 305, Madang, Papua New Guinea (1991–1992); Matthew Jebb, former director of CRI, who smoothed the waters, parted the seas and made life and science at the antipodes a piece of cake; Patrick and Lori Colin, directors of the Coral Reef Research Foundation (Weno, Chuuk, Federated States of Micronesia), for similar extraordinary efforts and accommodations at Chuuk Atoll (1993); David Pawson and Cindy Ahearn (USNM), Sheila Halsey (BMNH), Michel Jangoux (BELG) and Nadia Cominardi (PM), for making specimens available from their respective institutions; James D. Thomas for first recommending CRI to me, and Kim Norton and the Deep Ocean Society for providing research equipment. Many others contributed diving and boat handling support. Part of this research was carried out under the National Cancer Institute Contract for Collection and Taxonomy of Shallow-water Marine Organisms (P. Colin, principal investigator). This is Contribution No. 75 from the Christensen Research Institute and Contribution No. 7 from the Deep Ocean Society, Inc., Hollywood, Florida.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(3):451–457. 1995.

Morellia dendropanacis, a new species, and other species with spotted wings: characterization and comparison (Diptera: Muscidae: Muscinae)

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Abstract.—The description of a new species of *Morellia* Robineau-Desvoidy (1830) (Diptera, Muscidae, Muscinae) with spotted wings, morphologically similar to *M. couriae* Pamplona and *M. maculipennis* (Macquart), is given and compared with other Neotropical species with spotted wings.

Among the 18 Neotropical *Morellia* species, 13 have spotted wings. Some species have conspicuous markings, others have faint markings. The latter includes *M. affinis* Malloch, with a spot on the apex of Sc and *M. concacata* Pamplona, *M. ochricornis* (Wiedemann), *M. roppai* Pamplona and *M. sinopensis* Pamplona with a spot on the humeral crossvein. As the spots are almost imperceptible in these species, identification using Pamplona's key (1986) (couplet 3) requires careful comparison of the wing with the figures. The remaining eight species, *M. couriae* Pamplona, *M. humeralis* (Stein), *M. lopesae* Pamplona, *M. maculipennis* (Macquart), *M. nigricosta* Hough, *M. semimarginata* (Stein), *M. xanthoptera* Pamplona and *M. dendropanacis,* new species have conspicuous spots, facilitating their identification.

The new species described here was collected among flies that were pollinating *Dendropanax cuneatum* (Araliaceae) (Pombal & Morellato 1995). According to these authors *M. humeralis* and *M. dendropanacis* were the main pollinators of this plant, being specially observed from 10am until 1pm, in groups of up to 24 on an inflorescence. Pombal & Morellato considered them to be effective pollinators due to their small size, the high frequency of visitations, their visiting behavior and the large number of flies.

Morellia dendropanacis, new species
Figs. 1–11

Type material.—Holotype ♂ [MNRJ], labeled: Faz. Sta. Genebra [Fazenda Santa Genebra]/Campinas-SP [São Paulo]/03/VII/1992/Pombal, E.C.P. On the underface of the label: coletado em *Dendropanax cuneatum* [collected on *D. cuneatum*]; "HOLOTIPO" [red label]. Left mid- and hindlegs broken; the abdomen is dissected and preserved in glycerin in a microvial that is attached to the pin. Paratypes: 1 ♂, 4 ♀ [MNRJ] with same label data as the holotype: "PARATYPE" [green label]. All in good condition; male paratype with right hindleg glued on label, abdomen broken; one female paratype dissected and preserved in glycerin in microvial.

Diagnosis.—Wings with cloudlike spots on humeral crossvein, basal radial cell, subcostal apex, cell r_1 apex and crossveins r-m and dm-cu; hindtibia of ♂, at anteroventral, ventral and posteroventral surfaces with many bristles at apical half.

Coloration.—Metallic black-bluish with a faint whitish pruinescence on mesonotum near the head. Frons, lower half of parafacials and lower half of face with whitish pruinescence, upper half of fronto-orbital plate and gena blackish shining. Lower half of fronto-orbital shining yellowish; pedicel and flagellum yellow-brownish; arista with basal half yellow and apical half black; proboscis brown and palpus yellow. Wing with spots on humeral crossvein, on the adjacent area of basal radial cell, on subcostal apex connected to a spot on r-m, on the apex of r_1 cell and on dm-cu (Fig. 1). Calypteres faint brownish. Halter white. Legs brown, with femur-tibial articulations yellowish. Both spiracles white.

Male: Length; body, 4.5–5.0 mm; wing, 4.5–5.0 mm

Head.—Eyes bare with divergent margins larger at vertex; distance between eyes at anterior ocellus level about 6–7 times less than head width; anterior-inner ommatidia larger than others. 11–13 frontal bristles. Antenna inserted below mid eye level, with flagellum about 2.2–2.4 the pedicel. Arista plumose with 11–14 hairs. Palpi a little enlarged apicad with about 10–14 setae along margin.

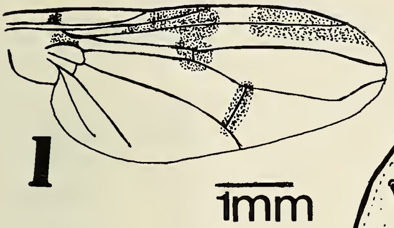
Thorax.—Dc 0:2; Acr 0:1; 3 humeral bristles; posthumeral absent; one prs; one ia; one pra; 3 sa; 2 psa; ipal absent. Notopleuron with 2 bristles. Scutellum with 1 pair of basal bristles; 2 pairs of laterals; 1 pair of apical. Prosternum wide and bare (with anterior pubescence difficult to observe). Several proepisternal and proepimeral bristles. Propleuron bare. Anterior spiracle vertical, oblong. Anepisternum covered with long setae and with 11–13 bristles on the posterior border. Ctps 1:2, supraposterior one, much larger than others. Anepimeron setulose. Lower calypter about 2.3–2.4 times the upper. Wing with M_1 curved to R_{4+5} apicad; veins bare. Foreleg with femur at anterior surface bare; posteroventral and posterodorsal surfaces with a row of bristles. Tibia at dorsal surface with a row of setulae; posterodorsal surface with 1 preapical bristle; ventral surface with several setae on apical half. Tarsomeres with short setae. Midfemur bearing some weak bristles along apical half of ventral surface; dorsal surface with 3 apical small spurs. Tibia at ventral surface with two apical bristles. Tarsomeres as in foreleg. Hindleg with femur at anterodorsal and anteroventral surfaces with a row of weak and short bristles; posterior surface bare. Tibia at anteroventral surface with 4 bristles on apical third, ventral to anteroventral surface with 5 larger parallel bristles; ventral to postero-ventral surfaces with several setae on apical half; anterodorsal surface with 3 bristles on middle third; dorsal surface with a row of very small bristles. Tarsomeres as in foreleg.

Abdomen.—With few bristles on laterally areas of segments. Sternite V as in Fig. 2. Terminalia: Cercal plate small, with a ventral plate with 2 lateral projections with spines along inner margin (Figs. 3 and 5); surstylus with an apical projection (Fig. 4); hypandrium large (Fig. 6); aedeagal apodeme with many spines in center, gonostylus membranous with small bristles, gonocoxite with a strong bristle; paramere with long bristles at apex (Figs. 7–8).

Female: Length; body, 4.5–5.0 mm; wing, 4.5–5.0 mm. Similar to male except as follows: 4 fronto-orbitals, 2 proclinate and 2 lateroclinate. All ommatidia of same size. Distance between eyes at anterior ocellus level about 2.7–2.8 times smaller than head width. Midfemur, at dorsal surface without spurs; hindtibia at anteroventral and posterodorsal surfaces with respectively 2 and 1 bristles on apical half. Terminalia: Ovi-

→

Figs. 1–7. *Morellia dendropanacis.* 1, wing; 2, sternite V, holotype; 3, cercal plate, holotype, dorsal view; 4, surstylus, holotype; 5, cercal plate, holotype, lateral view; 6, hypandrium, holotype; 7, aedeagus, holotype, dorsal view.



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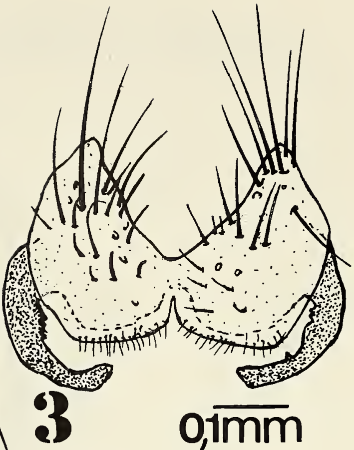

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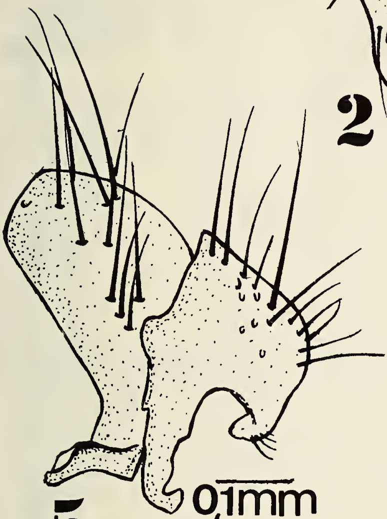

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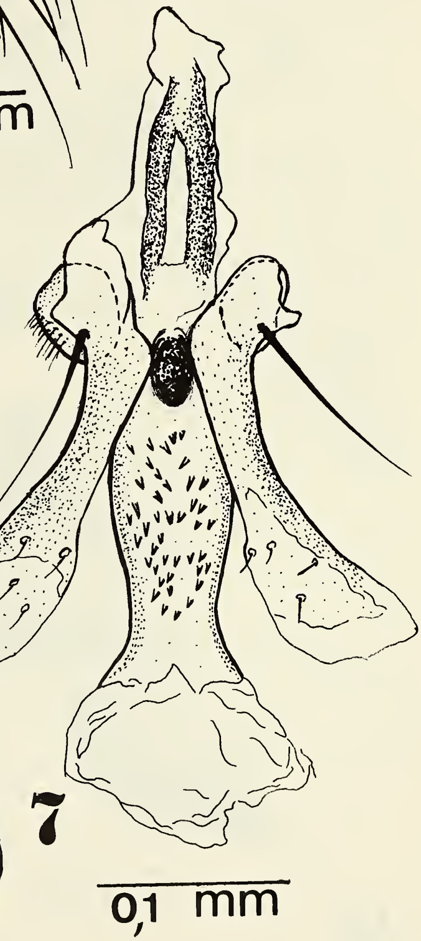

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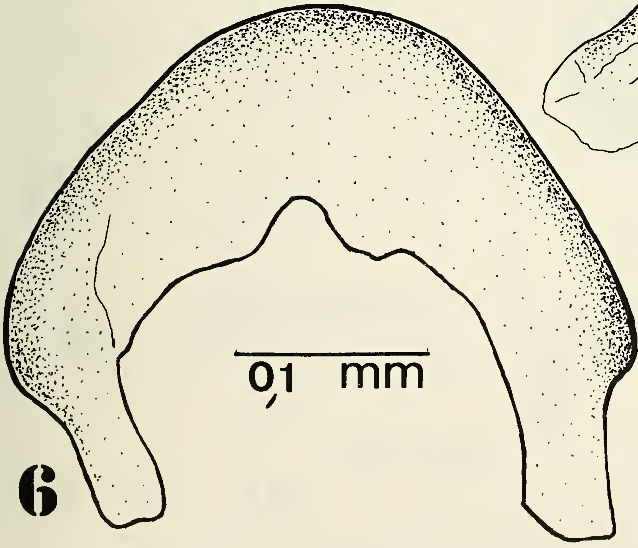

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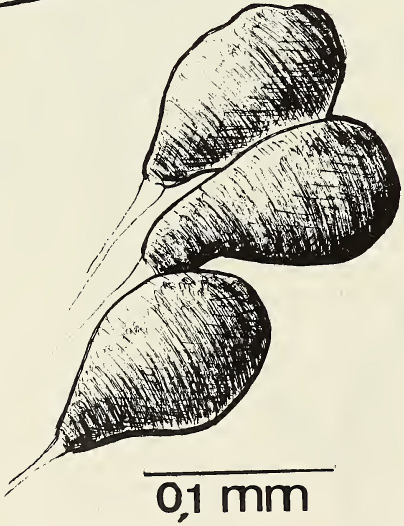

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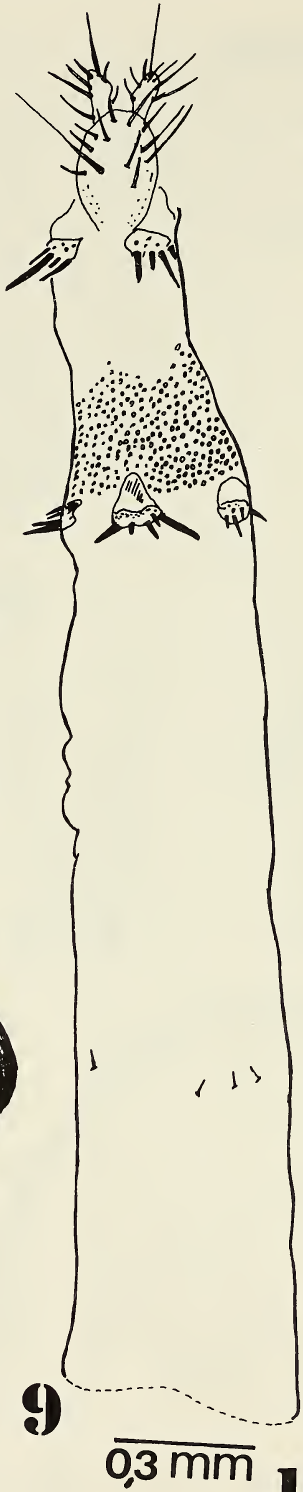

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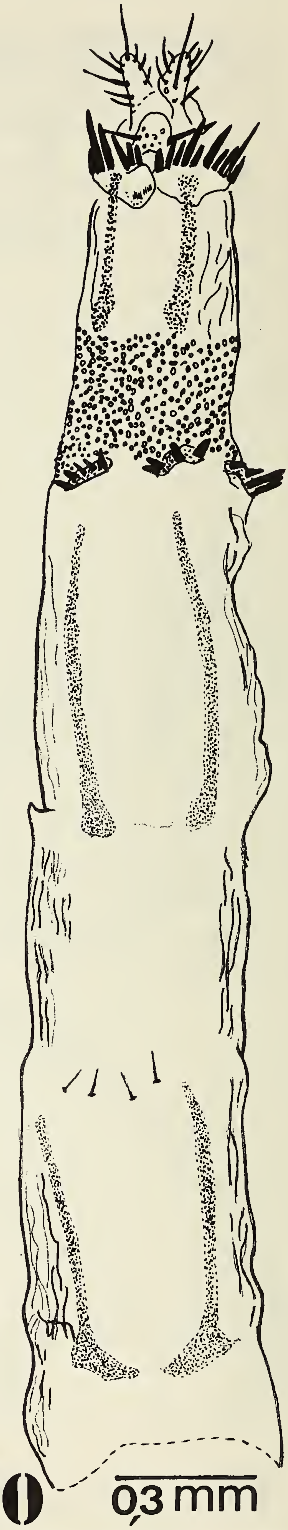

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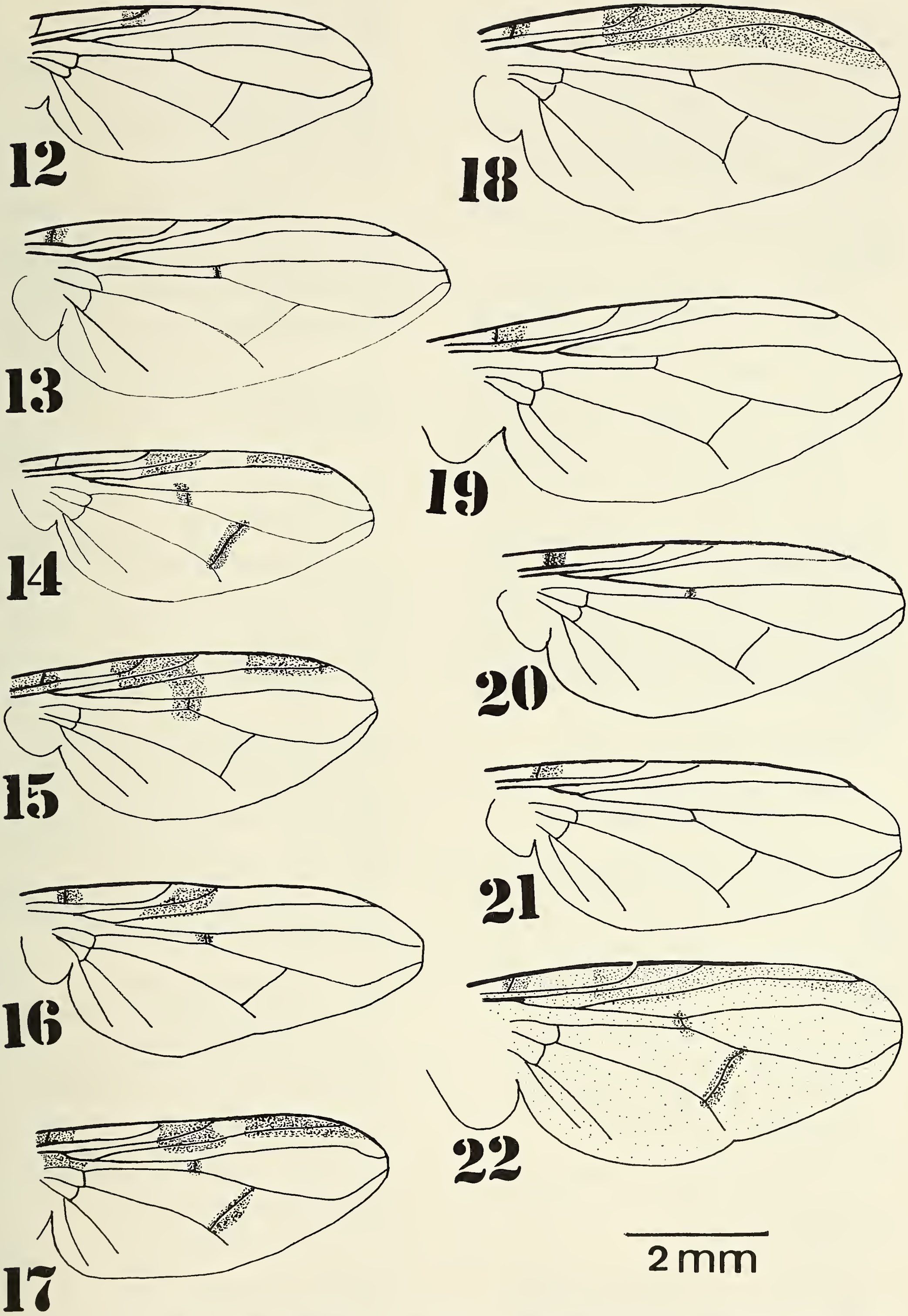
Figs. 8–11. *Morellia dendropanicus.* 8, aedeagus, holotype, lateral view; 9, ovipositor, paratype ♀, dorsal view; 10, ovipositor, paratype ♀, ventral view; 11, spermathecae, paratype ♀.



Figs. 12–22. Wings of species of *Morellia:* 12, *M. affinis*; 13, *M. concacata*; 14, *M. couriae*; 15, *M. humeralis*; 16, *M. lopesi*; 17, *M. maculipennis*; 18, *M. nigricosta*; 19, *M. ochricornis*; 20, *M. roppai*; 21, *M. sinopensis*; 22, *M. xanthoptera.*

positor long; tergite VI enlarged at base, tergites VII and VIII elongate; series of strong spines at sclerites above tergite VII and tergite VIII; cercus longer than epiproct (Fig. 8); sternite VII and VIII with 4 strong spines each (Fig. 9); spermathecae pear-shaped.

Etymology.—The specific adjectival name *dendropanacis* refers to the plant *Dendropanax cuneatum* where the specimens were collected.

Comments.—The wing maculation of *M. dendropanacis* n. sp. is similar to that of *M. couriae* and *M. maculipennis.* It differs from *M. couriae* mainly by the presence of a spot on the humeral crossvein and another one adjacent to it on the basal radial cell. The new species differs from *M. maculipennis* in having the cloudlike spot on the Sc apex connected to the one of r-m crossvein. Although the new species can easily be distinguished from these two species by the number of frontal bristles, chaetotaxy of hindtibia and hind spiracle shape and ciliation, the similarity of the male terminalia of these three species suggests a close relation among them.

Distribution: Brazil. São Paulo.

Key to Species of *Morellia* with Spotted Wings

Most species of *Morellia* with spotted wings can be easily distinguished by the distribution of the spots in association with other characters of chaetotaxy legs and thorax. The following key is to aid in their identification:

1. Wing with no more than 2 faint small spots (Figs. 12, 13, 19–21) 2
– Wing with at least 2 conspicuous spots (Figs. 1, 14–18, 22) 7
2. Flagellum yellow .... *M. ochricornis* (Wiedemann)
– Flagellum brown 3
3. Prosternum haired 4
– Prosternum bare 5
4. Hindtibia at anterodorsal surface with 4 bristles from the base to the apex and at posterodorsal surface with 1 bristle on basal third .... *M. affinis* Malloch
– Hindtibia at anterodorsal surface with 2 bristles on apical half and at posterodorsal surface with 1 bristle on apical third .... *M. concacata* Pamplona
5. Dc 1:2; hindtibia at posteroventral with 6 bristles .. *M. roppai* Pamplona
– Dc 0:2; hindtibia at posteroventral without bristles .... *M. sinopensis* Pamplona
6. Wing brown from base to apex along costa and connected with a dark cloud over the r-m .... *M. semimarginata* (Stein)
– Wing not as above 7
7. Postpronotum yellow .... *M. humeralis* (Stein)
– Postpronotum background colored 8
8. dm-cu crossvein without spot (Figs. 16, 18) 9
– dm-cu crossvein spotted (Figs. 1, 14, 17, 22) 10
9. Wing with a long cloudlike spot from a little before Sc apex till wing apex (Fig. 18) .. *M. nigricosta* Hough
– Wing without the above cited cloud (Fig. 16) ...... *M. lopesae* Pamplona
10. Cell r_1 with 1 spot (Fig. 22) .... *M. xanthoptera* Pamplona
– Cell r_1 with 2 spots (Figs. 1, 14, 17) 11
11. Dc 1:2; prosternum haired .... *M. maculipennis* (Macquart)
– Dc 0:2; prosternum bare 12
12. Flagellum brownish yellow with yellow spot at the base; hindfemur at anteroventral surface with weak and short bristles only on apical third; male: anteroventral, ventral and posteroventral surfaces with few setae on apical half .... *M. couriae* Pamplona
– Flagellum brownish yellow without yellow spot at the base; hind-

femur at anteroventral surface with weak and short bristles from base to apex; male: anteroventral, ventral and posteroventral surfaces with a great number of setae on apical half .. *Morellia dendropanacis*

Acknowledgments

We are grateful to Ellen C. P. Pombal for the specimens of *M. dendropanacis.* Also to "Fundacáo Uniprectória José Bonifácio" (proc. 5295–7) for the financial support.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(3):458–464. 1995.

Within-species variation in *Periclimenes yucatanicus* (Ives), with taxonomic remarks on *P. pedersoni* Chace (Crustacea: Decapoda: Caridea: Palaemonidae)

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Abstract.—The spotted cleaner shrimp *Periclimenes yucatanicus* is found to vary in the number of rostral teeth, length/width ratio of the carpus of the major cheliped, color pattern and cnidarian host. Similar variation has been found in other species of *Periclimenes.* Morphological features and type of host have been used to distinguish between *P. anthophilus* Holthuis & Eibl-Eibesfeldt, and *P. pedersoni* Chace, but these features overlap extensively; therefore, *P. anthophilus* is herein considered to be a junior synonym of *P. pedersoni.*

Shrimp of the genus *Periclimenes* Costa, 1844 are among the most colorful carideans of coral reefs. Species inhabiting cnidarian hosts are among the best known. Four species of *Periclimenes* have been reported to live with cnidarians in the western Atlantic, Gulf of Mexico and Caribbean: *P. yucatanicus* (Ives 1891), *P. pedersoni* Chace, 1958 *P. anthophilus* Holthuis & Eibl-Eibesfeldt, 1964 and *P. rathbunae* Schmitt, 1924. (See Chace 1972, for a key to the species of *Periclimenes* in the area).

During studies of cleaning behavior of shrimp and fish, species of *Periclimenes* were observed on coral reefs near Key Largo, Florida, U.S.A., and Bonaire, Netherlands Antilles. The shrimp were identified from photographs and by sight. However, during night dives at Bonaire, shrimp with an unusual color pattern, unlike that of known species in the area, were observed. These shrimp were found in association with the giant sea anemone, *Condylactis gigantea* (Weinland).

To identify this unknown shrimp, specimens were collected and compared with previously identified material. Photographs of live animals were examined to compare color patterns of the unknown shrimp with those of species of *Periclimenes* known to inhabit sea anemones in the area. Records of shrimp species and their hosts were quantified. The results indicate that there is considerable within-species variation in at least two species of *Periclimenes.*

Methods

During studies of cleaning behavior, this writer and volunteer divers from the nonprofit organization CEDAM International, counted numbers of shrimp per species of host in Key Largo, Florida, U.S.A., during 11–17 July 1992, and Bonaire, Netherlands Antilles, during 25 July–5 August 1993 and 30 July–12 August 1994. Shrimp were observed during SCUBA dives at depths of 3–22 m between 0600–2200 hours. Twenty-four photographs of all species of *Periclimenes* were taken in Florida and 110 in Bonaire. Species were identified in the field according to the color patterns shown in the popular book by Humann (1992:151); unidentified ones were reported as *Periclimenes* sp.

Five specimens (the maximum number allowed as stated on the collecting permit) of the unidentified shrimp were collected at

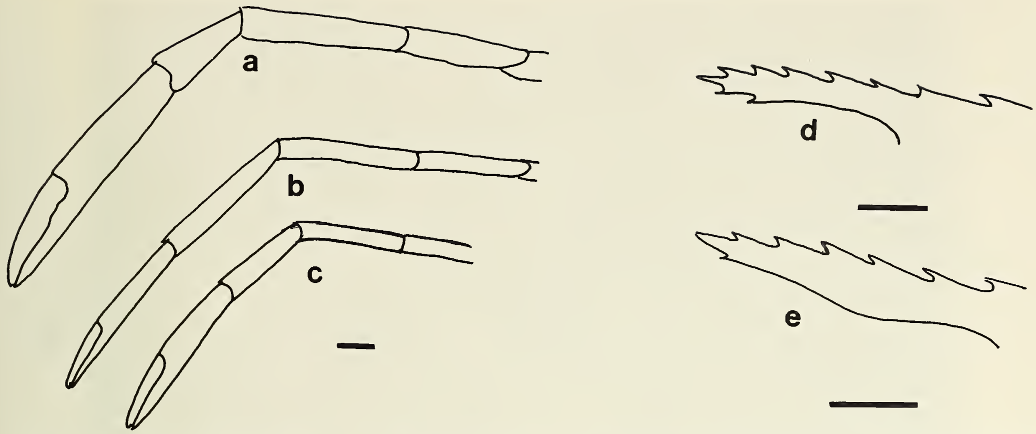

Fig. 1. Variation in the rostrum and second pereopod of *Periclimenes yucatanicus.* a, left second pereopod from individual 29.8 mm in total length; b, c, left and right second pereopods from individual 16.5 mm in total length; d, rostrum from individual 29.8 mm in total length; e, rostrum from individual 13.0 mm in total length. Scales are 1 mm and refer to the drawings immediately above them.

Calabas Reef, near Kralendijk, Bonaire, during 1994. An additional 13 were photographed in their natural habitat, but not collected. The animals were kept alive for 5–7 days and their color patterns recorded. These specimens were compared with descriptions of known species and also with 13 specimens of *P. yucatanicus* from the collections of the National Museum of Natural History Smithsonian Institution, Washington, D.C. The color patterns also were compared with those shown in photographs of *P. yucatanicus* from Grand Cayman, British West Indies (two slides showing three shrimp), Isla Cozumel, Quintana Roo, Mexico (three slides showing two shrimp), the U.S. Virgin Islands (one photograph of one shrimp) and Discovery Bay, Jamaica (photograph by Colin 1978).

Results

The unidentified shrimp are a previously unreported color variety (hereafter called the nocturnal color phase) of *P. yucatanicus.* Their bodies closely match the description of *P. yucatanicus* as given by Holthuis (1951: 38, pl. 10, figs. a–l). In these specimens and previously collected material of the species, there is variation in the number of rostral teeth and the length-width ratio of the carpus of the second (major) cheliped (Fig. 1). The rostrum can have 5–8 dorsal and 0–3 ventral teeth in addition to an acute apex. The length/width ratio of the carpus ranges from 2.3–7.5. A more slender carpus (4× longer than wide or more) usually occurs in smaller shrimp (total length 16 mm or less). (The largest specimen measured 29.8 mm in total length, orbit-telson.) In three specimens, the second pereopods were asymmetrical.

The 18 shrimp of the nocturnal color phase had translucent bodies with a few small spots of brown or white on the dorsal surface, and a translucent turquoise blotch near the gastric region. In two, there was a pale white stripe along the dorsal midline; in another two, there was a small dorsal pale brown spot on either the carapace or third abdominal somite. The pereopods were banded. Most had white antennae, but two had the outer antennal flagella banded and the inner ones white. In two, the uropods ended in faint white spots; in the others, there either were no such spots or the tail

Fig. 2. Color variation in *Periclimenes yucatanicus,* drawn from photographs in life. a, entire animal, showing banded appendages, from Florida, day; b, individual from Bonaire, day; c, individual from Bonaire, night; d, individual from Bonaire, day; e, same individual as seen in drawing d, night; f, individual from Bonaire, day.

fan could not be observed in the photograph.

Two of the individuals that were collected at night are shown in the nocturnal color phase in Figs. 2c and 2e. By day, both changed their color pattern to that of large white, tan, green or purple blotches, spots and saddle marks on a translucent body. The same individual is shown in Figs. 2d and 2e, illustrating the marked change in color pattern. Examination of the live specimens and photographs revealed considerable color variation in *P. yucatanicus.* Some of the patterns are shown in Figure 2. Of the 82 photographs identifiable as *P. yucatanicus* taken at Bonaire, all showed shrimp with the pereopods banded with white and a contrasting darker shade of red, purple or violet. Thirty-two shrimp (39%) had entirely white antennae; 34 shrimp (41%) had the outer flagella banded and the inner white, and 16 shrimp (20%) had both antennal flagella banded. Eleven photographs showed only the front of the animal, and thus only the color of the appendages and antennae could be seen. In the other 71 photographs, at least the carapace and first three abdominal segments were visible. The

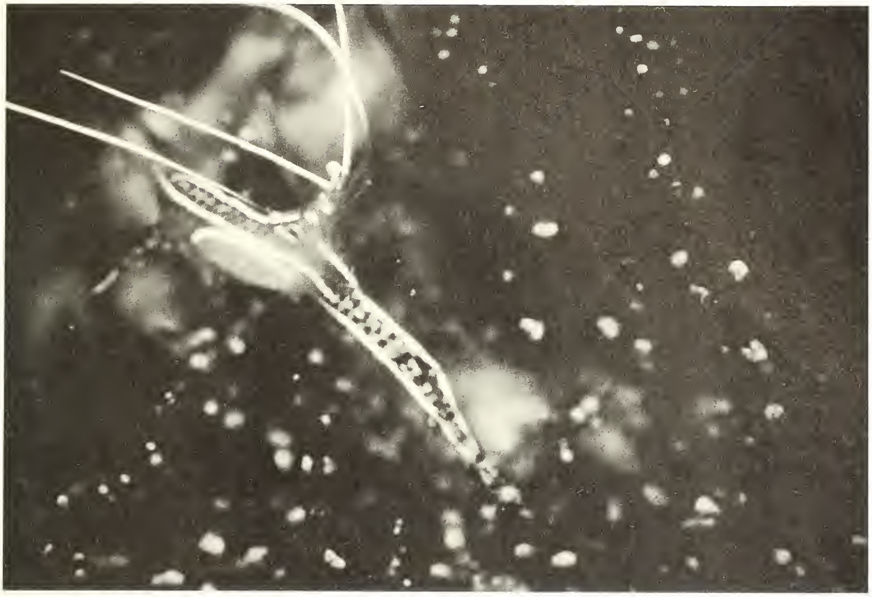

Fig. 3. *Periclimenes pedersoni* at Bonaire.

color pattern typically included a large dorsal "saddle" of pure white or pink, tan or green with a white border on the dorsal surface of the carapace, (seen in 31 shrimp, or 44% of the total), a saddle (sometimes in a figure-eight pattern) of similar color on the dorsal surface of the first and/or second abdominal somite (seen in 30 shrimp, or 42% of the total), and a large saddle on the third abdominal somite (seen in 46 shrimp, or 65% of the total). The tips of the uropods often were marked with white and dark spots shaped like eyespots; however, the tail fan was visible in only 21 photographs. The lower surface of the carapace or abdomen often had spots of white or white and dark pigment and the anterior parts of the cephalothorax could be speckled; however, it was difficult to see these marks in many photographs. Many shrimp also had "saddle" marks on the fourth abdominal somite, or had marks that overlapped two abdominal somites. Two of the largest shrimp (total body length approximately 30 mm, as estimated from photographs) had a body background color of brownish pigment; most of the shrimp were translucent except for the bands and spots. Similar color patterns were observed in photographs of shrimp from other areas except for one photograph from Grand Cayman, which showed two shrimp with the same color pattern as the nocturnal color phase from Bonaire. The photograph of *P. yucatanicus* by Humann (1992) shows a shrimp with a brown background pigmentation.

Another common shrimp, *Periclimenes pedersoni,* had very different markings which were not observed to change at night. This species was marked with white, blue or purple-violet lines running the length of the body, similar marks on the major chelipeds, purple speckles on the maxillipeds and other pereopods, and pure white antennae. The white lines and antennae are readily visible at a distance (Fig. 3).

Of 302 total *P. yucatanicus* observed in the wild (whether photographed or not), 283 were among the tentacles of *Condylactis gigantea,* 13 were on the sea anemone *Bartholomea annulata* (Lesueur) and six were away from a cnidarian host. Usually, only one shrimp was observed per host, but as many as five could be found per anemone. All of the unidentified shrimp at night were found on *C. gigantea. Periclimenes pedersoni* was more abundant. Of a total of 938 observed, 555 were on *C. gigantea,* 315 on *B. annulata* and 68 on other hosts or away from a cnidarian. As many as 13 *P. pedersoni* could be found living in a single sea anemone. The two species never coexisted on the same host. The hippolytid shrimp *Thor amboinensis* (De Man) often occupied the same individual of *C. gigantea* with one of the two species; snapping shrimp (*Alpheus ? armatus* Rathbun) lived along the stalks of *B. annulata* under the tentacles where the *Periclimenes* lived.

No individuals of *P. rathbunae* were observed at either Key Largo or Bonaire.

Discussion

Holthuis (1951) noted variation in the length/width ratio of the carpus of the second pereopod in specimens of *P. yucatanicus,* and speculated on whether this might be due to sexual difference, a growth form or geographic variation. This asymmetry also could be due to loss and regeneration of an appendage. The results given here suggest that variation in the proportions of the carpus of the second pereopod exists within *P. yucatanicus.* Holthuis noted similar variation in *P. infraspinis* (Rathbun). Chace & Bruce (1993) noted that several Indo-Pacific species of *Periclimenes* had subequal to grossly unequal second pereopods.

The pattern of spots and lines in specimens from Bonaire and Florida was consistent with that shown in photographs of *P. yucatanicus* from other areas. Less variation was seen in the color pattern of *P. pedersoni* (Humann 1992:151; Sefton & Webster 1986:77, figs. 117, 118; Colin 1978: 339–341; Voss 1980:87 and color plate). *Periclimenes rathbunae* has a pattern of white and brown dots and lines, with white dots at the tips of the uropods (Spotte et al. 1991:fig. 1; Colin 1978:344 as "unidentified species of *Periclimenes*"). It is possible that slight regional differences in color pattern may exist in these species, but such differences would be difficult to see or photograph in the natural habitat.

Marked changes in color patterns from day to night have been reported previously in the hippolytid shrimp *Hippolyte varians Heptacarpus pictus* and *Heptacarpus paludicola* (Green 1961, Bauer 1981). In these species, the shrimp showed a tranluscent blue color by night, regardless of the color pattern displayed by day. Divers at Key Largo noticed a similar color change in *Thor amboinensis,* which had a pattern of white spots against a chocolate brown background by day, and a blue background at night. There are few observations of the nocturnal coloration of shrimp, especially in their natural habitat, so it is difficult to determine how common diurnal/nocturnal color changes are among species of *Periclimenes.*

Spotte et al. (1991) reviewed associations of shrimp with cnidarians in the West Indies and Bermuda, and reported that neither *P. yucatanicus* nor *P. pedersoni* was confined to a single host. *Periclimenes yucatanicus* was listed to live with six species of sea anemones (Order Actiniaria), the jellyfish *Cassiopeia xamachana* (Bigelow) and the corallimorpharian, *Rhodactis sanctaethomasae* (Duchassaing & Michelotti). *Periclimenes pedersoni* was reported to live with six species of sea anemones, the same jellyfish and a tube anemone, *Cerianthus* sp.. At Key Largo, diver Rick Sammon photographed *Periclimenes yucatanicus* in association with another corallimorpharian, *Ricordea florida* (Duchassaing & Michelotti). I photographed the same association at Grand Cayman.

Evidently, *P. yucatanicus* and *P. pedersoni* can live on multiple hosts. However, most records of either species come from the anemones *C. gigantea* and *B. annulata.* Goy (1990) found that more larval *P. yucatanicus* completed metamorphosis successfully if exposed to exudates of *C. gigantea* than to those of other species or none at all; larval *P. pedersoni* showed better survival if exposed to exudates of *B. annulata.* Levine & Blanchard (1980) reported that species of *Periclimenes* could be stung by sea anemones to which they were not acclimated.

Periclimenes anthophilus Holthuis & Eibl-Eibesfeldt (1964) was described as a distinct species from Bermuda. The original authors, and Chace (1972) remarked that it was very similar to *P. pedersoni,* but could be distinguished by the position of the hepatic spine in front of the most posterior dorsal carapace spine; the carpus of the second pereopod being less than half the length of the chela and the host being *Actinia bermudensis* or *C. gigantea.* Other morphological features and the color pattern were indistinguishable from those of *P. pedersoni.*

Chace (1972) remarked on the close morphological similarity between the two supposed species, and re-examined specimens. The only differences he found between them were the "different habits" and the "proportionately shorter carpus of the major second pereopod". However, proportions of the carpus of the second pereopod vary in species of *Periclimenes* as well as in other palaemonids. In species of freshwater shrimp of the genus *Macrobrachium,* for example, the entire second pereopod is markedly longer and more robust in adult males than in juveniles or females. As shown in Fig. 1, the length/width ratio of the carpus can vary in specimens of *Periclimenes* spp., as does the length of the carpus relative to the chela.

Although species of *Periclimenes* apparently have preferred hosts, they are not restricted to a single species of cnidarian. The review by Spotte et al. (1991) shows this lack of specificity, as does a study of shrimp living with sea anemones in central Japan (Suzuki & Hayashi 1977). Both *P. pedersoni* and *P. anthophilus* have been reported to live with *C. gigantea* and *B. annulata,* as well as with other hosts (Spotte et al. 1991). Lacking additional evidence of distinctive coloration or species-specific behavioral or morphological distinguishing features, *P. anthophilus* should be considered a junior synonym of *P. pedersoni* Chace, 1958.

Acknowledgments

I am grateful to Kalli de Meyer, Bonaire Marine Park, and the government of the Netherlands Antilles for permission to conduct studies and collect specimens. Volunteer divers from CEDAM International, especially Rick Sammon, Dave Downs and Stella Covre, and Nancy Sefton of the Cayman Islands aided immensely in photographing and documenting shrimp in the natural habitat.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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Dittosa, a new genus of leucosiid (Crustacea: Decapoda: Brachyura) from southern Australia and New Zealand

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Abstract.—A new genus, *Dittosa,* is established for two southern Australian species of *Philyra* Leach, 1817: *Philyra laevis* Bell, 1855, *P. murrayensis* Rathbun, 1923, and the New Zealand *Ebalia cheesmani* Filhol, 1886, on the basis of the male first and second gonopods which are of equal length, presence of two fissures on the roof of the orbit, structure of the male abdomen, form of the front and third maxilliped exopod, and appearance of the intestinal region of the carapace.

There are 41 known species in the genus *Philyra* Leach, 1817 (Bell 1855, Serène 1968, Rathbun 1924, Takeda & Nakasone 1991). These are generally characterized by their rounded carapaces, massive chelipeds, expanded exopod of third maxilliped and rather broad front which is not produced.

For the species of *Philyra* in which the male first gonopod is known, this structure is stiff and stout, and about twice to three times the length of the second gonopod (Stephensen 1946, Dai & Yang 1991). Recently, in the course of examining leucosiids in the Smithsonian Institution collection, I found that two southern Australian species, *P. laevis* Bell, 1855, and *P. murrayensis* Rathbun, 1923, and a New Zealand species, *Ebalia cheesmani* Filhol, 1886, have the male first and second gonopods of almost equal length, with the first gonopod long and sinuous, and the second gonopod elongate and slender. In addition, the number of fissures on the orbital roof, male abdominal segmentation, the form of the front, appearance of the intestinal region and, to a lesser extent, form of the third maxilliped exopod in these two species differ from those in typical *Philyra* species. In this paper, a new genus, *Dittosa,* is established for *P. laevis, P. murrayensis,* and *Ebalia cheesmani* on the basis of this unique suite of characters.

For purposes of comparison, eight other species of *Philyra* were studied and these are listed in the Appendix. The following abbreviations are used in the text: G1, G2, the male first and second gonopods respectively; APE, U.S. "Albatross" Philippine Expedition and USARP, United States Antarctic Research Program. Measurements are given in the order carapace length times width in millimeters (mm), exclusive of the posterior intestinal spine and lateral tubercles. Specimens examined are deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington D.C., U.S.A., and the Zoological Reference Collection (ZRC), Department of Zoology, National University of Singapore.

Family Leucosiidae Samouelle, 1819
Dittosa, new genus

Type species.—*Philyra laevis* Bell, 1855, by present designation.

Diagnosis.—Carapace rounded, with widely spaced tubercles or granules along the margins, surface smooth or granular, intestinal region with raised region (ridge, tu-

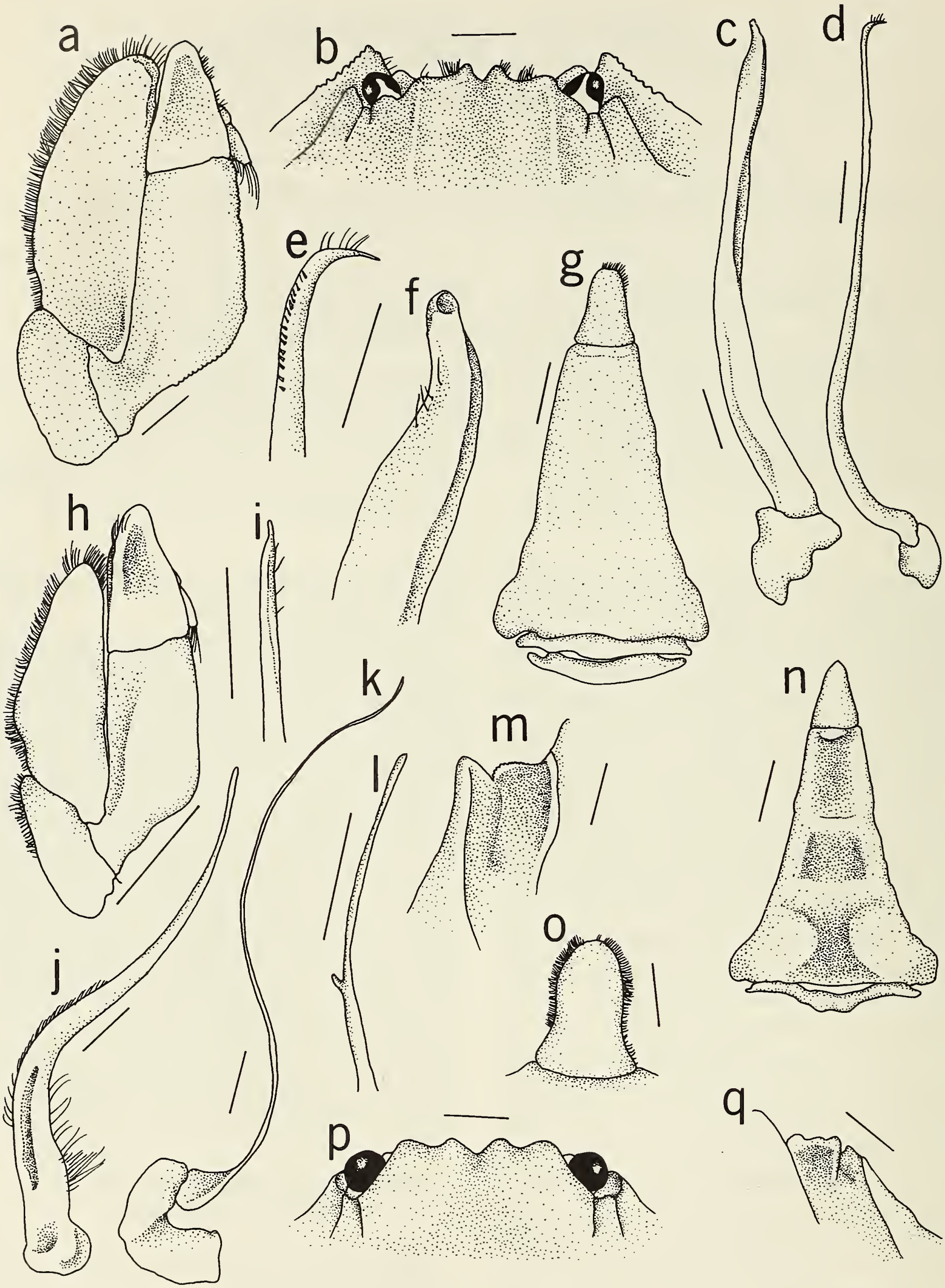

Fig. 1. *Dittosa murrayensis,* male, 18.8 × 18.4: a, right third maxilliped; b, front, dorsal view; *c,* right G1; *d,* right G2; *e,* right G2, apex; *f,* right G1, apex; *g,* abdomen. *Dittosa laevis,* male, 14.2 × 13.5: h, right third maxilliped; i, right G1, apex; j, right G1; k, right G2; 1, right G2, apex. *Dittosa murrayensis,* male, 18.8 × 18.4: m. right pterygostomian region, ventral view, with third maxilliped removed. *Dittosa laevis,* male, 14.2 × 13.5, female, 14.0 × 13.6. n, male abdomen excluding segment 1; o, telson, female abdomen; p, front, dorsal view;

bercle or spine). Front bilobed, lobes separated by V-shaped notch, inner angle of each lobe extended and denticulate, giving front a 4-toothed appearance. Eyes medium sized, visible from dorsal view, roof of orbit with 2 sutures, floor of orbit with 1 suture. Antennules folded obliquely. Antennae occupying orbital hiatus, basal segment fixed, other segments movable. Third maxilliped with exopod not strongly dilated (sometimes dilated proximally), merus triangular, not narrowed. Chelipeds more massive than ambulatory legs, palm broad, fingers longer than palm. Male abdomen with segments 3–6 fused, suture between segments 5–6 discernible to absent, or if present, laterally interrupted. G1 elongate, usually sinuous; G2 elongate, as long as or slightly longer than G1, usually more slender.

Remarks.—In general appearance, *Dittosa* bears a close resemblance to *Philyra* sensu stricto. The massive chelipeds, form of the fingers, rounded shape of the carapace, granulation on the lateral borders of the carapace and broad front that is not produced are characters common to both genera. The most significant difference between *Dittosa* and *Philyra* is that in *Dittosa,* the G1 and G2 are almost equal in length. Such a condition is relatively rare in the Leucosiidae, being previously reported in only six other species: *Ebalia longimana* Ortmann, 1892 (Stephensen 1946), *E. fasciata* Ihle, 1918, *Praebebalia longidactyla* Yokoya, 1933, *P. mosakiana* Sakai, 1965, *P. taeniata* Takeda, 1977, and *P. kumanoensis* Sakai, 1983 (Nagai 1992).

The male abdomen in *Dittosa* has the third to sixth segments fused. The suture between the fifth and sixth segments is indistinct and the sixth segment has no mobility whatsoever. In *Philyra* sensu stricto, there may be limited mobility of the sixth segment as the suture between the fifth and sixth may reach the lateral margins of the abdomen and may be rather deep. In general, the sixth segment of the male abdomen in *Philyra* has its proximal end wider than the distal end of the fifth segment. In this way, a wide notch between the fifth and sixth segments is formed on either side of the abdomen (Fig. 3a, b) and the sixth segment may have a flattened, distal, transverse tubercle. In *P. globus* (Fabricius, 1775), the type species of *Philyra* (fide H. Milne Edwards 1837), the suture between the fifth and sixth segment is deep and the lateral notch between these segments is present on either side (Stephensen 1946:fig. 11 I). There is a median denticle on the sixth segment in this species.

The type species of *Philyra, Cancer globus* Fabricius, 1775, is a senior synonym of *Leucosia globulosa* Bosc, 1802. Thus, *P. globulosa* (Bosc, 1802) (sometimes wrongly attributed to H. Milne Edwards 1837) should be referred to as *P. globus* (Fabricius, 1775) (see Manning & Holthuis 1981:66).

Another useful character in *Dittosa* is that the roof of the orbit has two clear sutures corresponding to the α and β sutures described by Ihle (1918:52). In *Philyra globus* and in all other species of *Philyra* examined (see Appendix), the α suture is absent. In the case of *D. murrayensis,* the β and γ sutures are deep and open anteriorly, thus forming a prominent extra-orbital lobe (Fig. 1b).

In species of *Philyra,* the front is generally almost straight with a shallow median groove on the dorsal surface, or trilobate, with two outer lobes formed by the inner supra-orbital angle and a smaller, median triangular lobe. The former condition is true for *P. globus.* The three species of *Dittosa* have the front distinctly bilobed, each lobe being separated by a moderately deep,

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←

q, left pterygostomian region, ventral view, with third maxilliped removed. Scales: e, f, i, l = 0.5 mm, others = 1 mm.

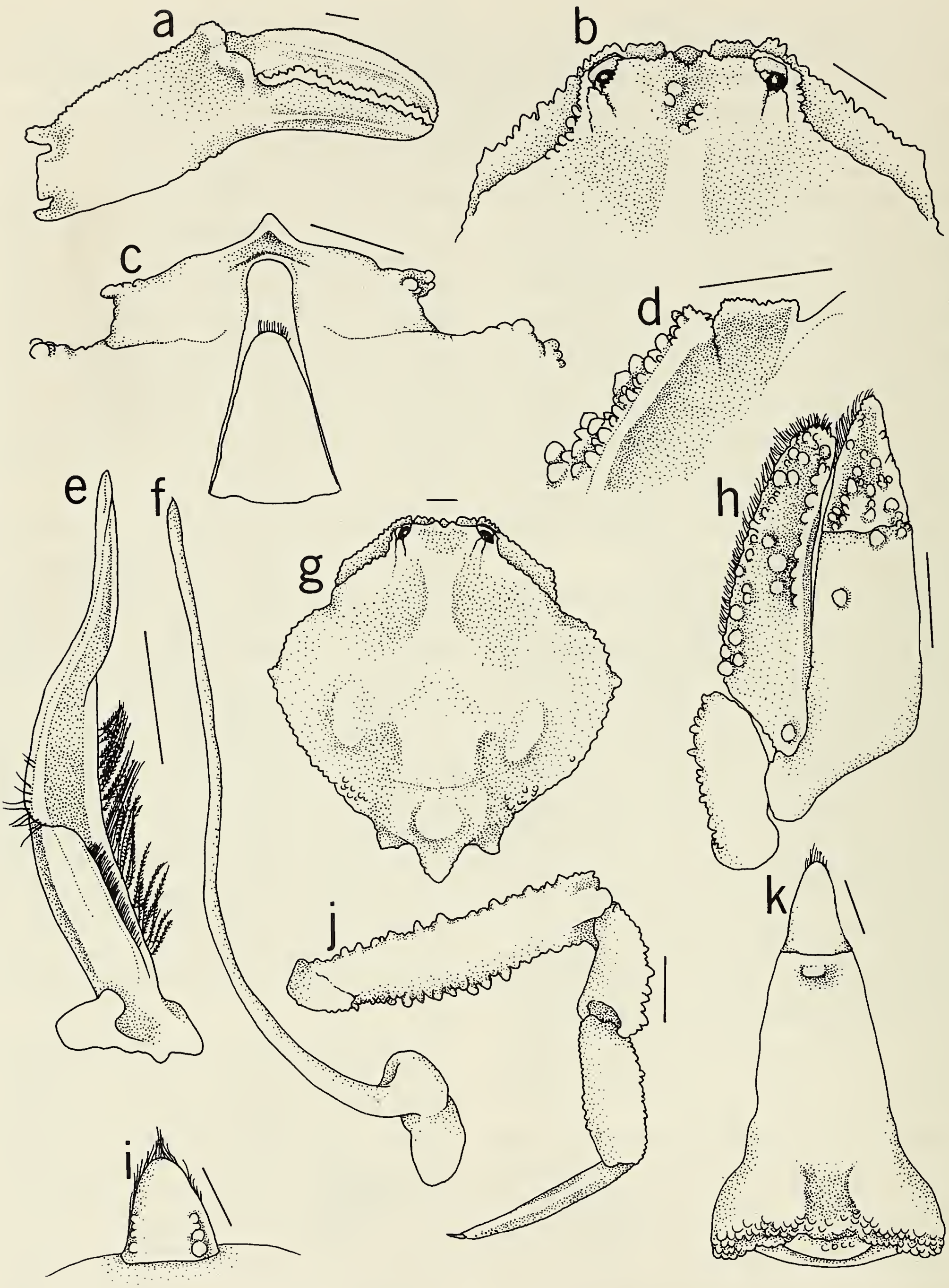

Fig. 2. *Dittosa cheesmani* (Filhol, 1886) male, 11.4 × 11.6, female: a, Male left cheliped upper surface; b, Male front, dorsal view; c, male sternum; d, male right pterygostomian region, ventral view, with third maxilliped removed; e, right G1; f, right G2; g, male carapace, dorsal view; h, male right third maxilliped; i, female abdomen, telson; j, male right last ambulatory leg; k, male abdomen. Scale = 1 mm.

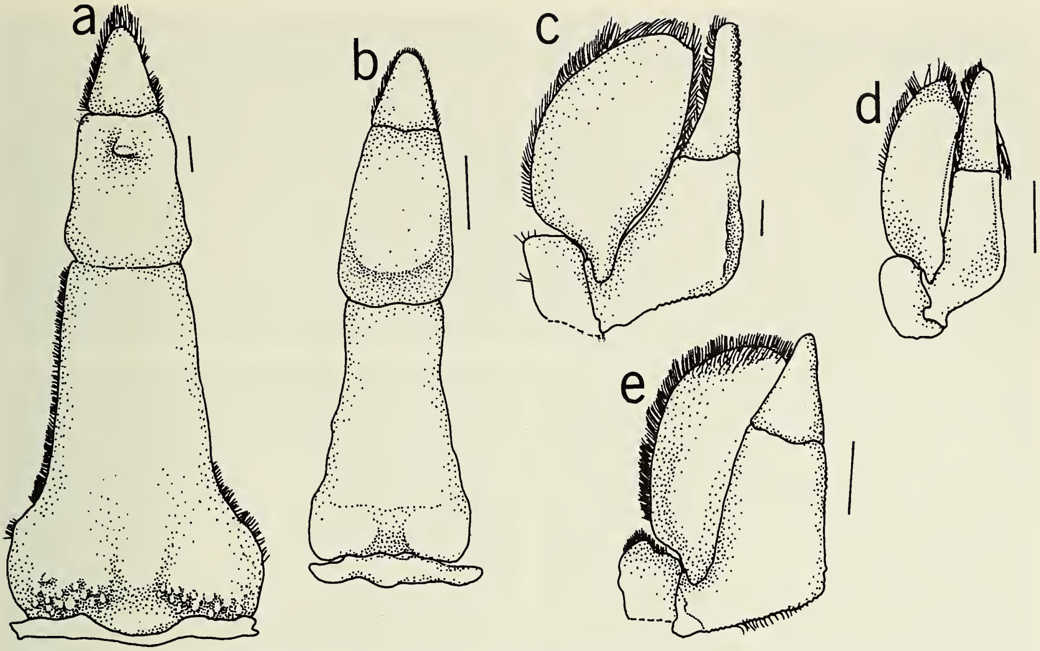

Fig. 3. Male abdomen showing notch on lateral margin between fifth and sixth segments: a, *Philyra globus,* USNM 42756, male; b, *P. olivacea,* USNM 62038, male. Right third maxillipeds: c, *P. globus,* USNM 42756, male; d, *P. olivacea,* USNM 62038, male; e, *P. syndactyla,* USNM 56781, male. Scale = 1 mm.

V-shaped median notch. The inner angles of each lobe are pointed and denticulate, conferring a "four-toothed" appearance to the front (Figs. 1b, p, 2b). The variability in this character within *Dittosa* cannot be ascertained as there are currently only three species. This character should be used in conjunction with the other characters as the front has been shown to be variable in some congeneric leucosiids. Nevertheless, generally, the "four-toothed" front is absent in *Philyra.*

In *Dittosa,* a protrusion of some sort is present on the posterior intestinal region, be it a spine or a transverse ridge (see Figs. 2g, 4A, C, E). For *Philyra,* the intestinal region, though it may be covered in granules, and swollen, does not possess spines or raised ridges. In *P. globus,* it is finely granular.

The form of the exopod of the third maxillipeds appears to gradate in *Philyra* (Fig. 3c–e). In *P. globus, P. globosa* (Fabricius, 1798), and *P. heterograna* Ortmann, 1892, the exopod is greatly expanded proximally, with the outer edge describing a semi-circular arc and the merus is very narrow and is shaped like a right-angled triangle (see Stephensen 1946, Fig. 11C, D). In others, e.g., *P. scabriuscula* (Fabricius, 1798), the exopod is expanded and the merus is not narrowed but rather regularly triangular. In *P. olivacea* Rathbun, 1909 (Fig. 3d), and *P. biprotubera* Dai & Guan, 1986, the exopod is less expanded but the outer edge still describes a curve and the merus is narrow. The fourth condition is shown in species such as *P. granigera* Nobili, 1906, and *P. syndactyla* Ortmann, 1892 (Fig. 3e), where the outer edge of the exopod may be straight, the distal portion only slightly dilated and the merus broad. In *Dittosa,* however, the exopod is expanded slightly proximally (Figs. 1a, h, 2h), but never as in *P. globosa*

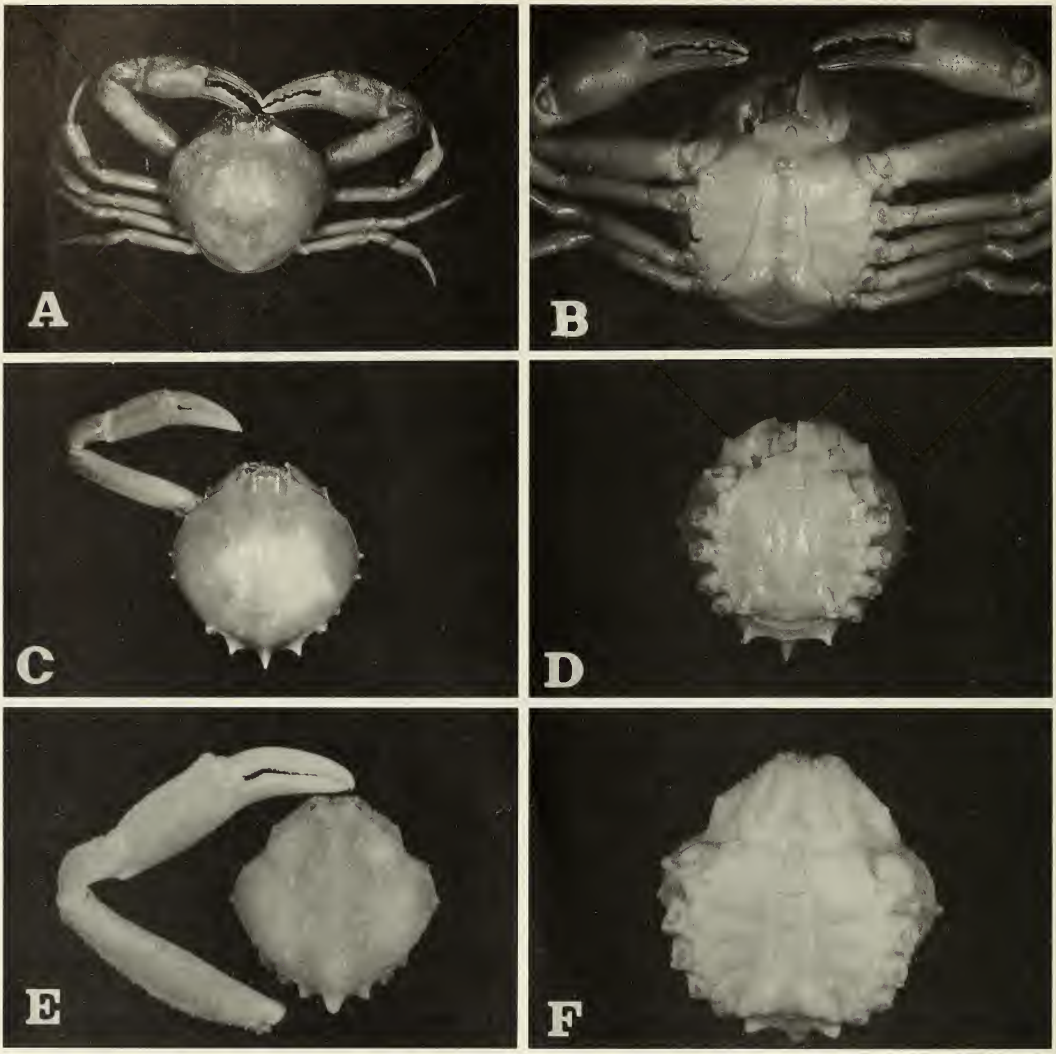

Fig. 4. *Dittosa laevis,* male, 16.6 × 15.8: A, dorsal view; B, ventral view. *Dittosa murrayensis,* male, 18.8 × 18.4: C, dorsal view; D, ventral view. *Dittosa cheesmani,* male, 11.4 × 11.6: E, dorsal view; F, ventral view.

or *P. globus,* and the merus is triangular and not narrowed. However, the third maxillipeds in *Dittosa* are rather similar to those of *P. olivacea* and *P. granigera.* Due to the variation exhibited by this character, it is advisable to use it in conjunction with other characters such as the gonopods and the number of orbital roof sutures.

The variation shown by the structure of the third maxilliped exopod and the merus in *Philyra* sensu stricto suggests the possibility that the genus, as it presently stands, is heterogeneous and in need of a revision. Specimens of *Philyra* species examined here sometimes differ significantly from *P. globus* in terms of the structure of the male G1, form of the abdomen, extent to which the front edge of the buccal cavity extends beyond the front, structure and ornamentation of the sternum, form of the front and as discussed above, structure of the third maxillipeds.

Dittosa resembles also the genus *Praebebalia* Rathbun, 1911. The carapace in *Praebebalia* has lateral projections similar to that found in *Dittosa,* the chelipeds are longer than the carapace, the edge of the buccal frame projects beyond the front and there are two fissures on the upper orbital roof. Again, the chief difference between the two genera is the relative length of the G1 and G2. I have examined specimens of the type species, *Praebebalia extensiva* Rathbun, 1911, and have found that its G1 is much longer than the G2. Fusion of the male abdominal segments is also different, with segments 3–5 fused in *Praebebalia* and segments 3–6 fused in *Dittosa.* Also, in *Praebebalia,* the palms of the chelipeds are slender and about twice the length of the fingers. In *Dittosa,* the chelipeds are massive, the palms are broad and as long as the fingers. *Praebebalia* also lacks the lateral projections on either side of the intestinal projection found in *Dittosa.*

Nagai (1992) figured the G1 and G2 of *Praebebalia longidactyla* Yokoya, 1933, *P. mosakiana* Sakai, 1965, *P. taeniata* Takeda, 1977, and *P. kumanoensis* Sakai, 1983. These differ from *Praebebalia extensiva* in that they have G2 as long as or slightly longer than G1 (Nagai 1992, Fig. 2) and the abdominal segments 3–6 are fused. Their relatively smaller size (4.3–6.5 mm length, 4.3–6.5 mm width) also separates them from *P. extensiva* (12.7 × 13.0). This suggests that a group distinct from *Praebebalia* sensu stricto should perhaps be recognized and that a review of the genus is necessary. From Nagai's (1992) figures, the form of the front (broadly bilobed), absence of lateral projections on the carapace, slender chelipeds, and absence of posterior projections of the four *Praebebalia* species are characters that serve to distinguish them from *Dittosa.*

Etymology.—The name is arbitrarily derived from the Greek "dittos" (dissos; dixos) which means "two-fold, double", alluding to the equal length of the male first and second gonopods. The gender is feminine.

Dittosa laevis (Bell, 1855)
Figs. 1h–l, n–q, 4A, B

Philyra laevis Bell, 1855:300, pl. 32, fig. 7 (type locality: Port Adelaide, South Australia).—Hale, 1927:194, fig. 192, 195.

Material examined.—USNM, 1 male, 14.3 × 13.6, 1 female, 14.1 × 13.6, South Australia, Kangaroo Island, coll. C. M. Hoy, 10 Jan 1920.—USNM, 2 males, 16.4 × 16.0, 16.6 × 15.8, 2 females 17.7 × 17.4, 18.1 × 17.4, South Australia, Victoria, Swan Bay, Queenscliffe, 100 yards north of railway station, *Zostera* flats. coll. C. F. E. Roper & B. Burn, 7 Feb 1976.—USNM 64650, 1 male, 1 female, Ralph's Bay, Tasmania, dredge, 1.8–5.5 m, oyster fishermen coll., Aug 1926.—USNM 64723, 7 males, 1 female, near entrance to Port Phillip, Victoria, Australia, sandy bottom, don. Australian Museum, Jan 1926.

Description of male.—Carapace slightly longer than broad, surface rather smooth, with minute punctae, regions not well-demarcated, hepatic and subhepatic margins raised to form facet, anterolateral margin with short oblique fissure immediately after margin of hepatic region, followed by obtuse triangular angle, junction of antero- and posterolateral margins with rounded tubercle, margin between tubercle and obtuse triangular angle on anterolateral margin straight, posterior margin with smoothly curving ridge, subhepatic region with large, obtuse triangular angle, posterior intestinal region with flat, rounded transverse ridge.

Front bilobed; edge of buccal cavern, particularly outer angle, slightly visible beyond front, extending beyond orbital margin. Outer surface of third maxillipeds smooth, margins setose, exopod slightly dilated at base, tapering to rounded point distally, merus triangular, with shallow longitudinal depression on distal half.

Chelipeds minutely punctate as on carapace, fingers longer than palm, inner and outer surfaces of fingers each with 2 distinct rows of large punctae, cutting edges with rounded blade-like teeth; anterior edge of propodus of ambulatory legs carinate, dactylus flattened, both edges carinate.

Outer surface of male abdomen minutely punctate, distal end of segment 6 with median, transverse, low, rounded tubercle, short median, transverse groove present at base of segment 6, telson triangular, apex pointed. G1 long, sinuous, proximal half setose, stout, gradually tapering to slender, pointed apex, apex simple, sparsely covered with short setae; G2 very thin, slightly longer than G1, slender throughout, tip bifid with one branch reduced to pointed lobe, other branch long.

Female: Telson elongate, bell-shaped. Non-sexually dimorphic characters similar to male.

Remarks.–The ridge on the posterior intestinal region of the carapace varies in form in individual specimens. It may be nearly indistinct, particularly in larger specimens. Hale (1927:195) remarks: "The ridge of the intestinal region may be obsolete in old examples, but in juveniles it is often prominent and produced upwards in the form of a subtriangular tooth; the carapace of the young sometimes bears large scattered granules". Hale (1927:195) also gives an interesting account of their behavior, noting that the crabs probably remain buried in the mud at high water and during rough weather, only commencing their activities at low-tide. During mating, the male performs a kind of courtship dance during which the female becomes quiescent. The male then grasps the female and moves off, presumably to a burrow. The specimens I examined are from South Australia (type locality of *D. laevis*) and match Bell's (1855) description and figures well.

Dittosa murrayensis (Rathbun, 1923)

Figs. 1a–g, m, 4 C, D

Philyra murrayensis Rathbun, 1923:136, pl. 34 [type locality: Off Murray river mouth, South Australia].—Hale, 1927:195, Fig. 196.

Material examined.—USNM, 1 male, 18.8 × 18.4, South Australia, Victoria, Port Phillip Bay, 3 miles west of Brighton Pier, Stn. 5 and 6, 11 m, very shelly bottom, colls. C. F. E. Roper, S. Stevenson & R. Plant, 10 Feb 1972.

Description.—Carapace slightly broader than long, surface with minute punctae and granules, regions not well-demarcated, shallow, oblique groove present immediately behind margin of hepatic region, intestinal region defined by groove anteriorly and laterally; hepatic and subhepatic margins raised to form facet, anterolateral margin with small denticle immediately after hepatic margin, junction of antero- and posterolateral margin with 2 denticles, posterolateral margin with denticle close to posterior margin, posterior margin with flattened, upward pointing spine on either side of median line, posterior intestinal region with large backward and upward pointing spine on higher level than posterior marginal spines; subhepatic region with median denticle.

Front bilobed; extraorbital lobe rather pronounced. Edge of buccal cavern slightly visible beyond front, outer angle projecting beyond orbital margin. Surface of third maxilliped ischium smooth, inner margin finely granular, setose along margins, exopod slightly dilated proximally, tapering gradually distally. Chelipeds very long, stout, surface finely granular, fingers longer than palm, flattened, cutting edges finely denticulate; anterior edge of propodus of ambulatory legs carinate, dactylus flattened, both edges carinate.

Outer surface of male abdomen smooth, telson triangular, distal end rounded, edges setose. G1 stouter and slightly shorter than G2, long, rather straight, tapering to narrow tip distally; G2 slender, elongate; with curved tip, tip sparsely setose.

Remarks.—The presence of spines on the intestinal region and posterior margin of the carapace, the structure of the G1 and G2, the absence of a tubercle on the penultimate segment of the male abdomen, the long chelipeds of the male, the prominent outer angle of the buccal frame and the relative size of this species distinguishes it from *D. laevis.* Hale (1927:196) remarks that "the small tubercles of the carapace are much more distinct in some specimens than in others, and the obsolete median carina may bear scattered tubercles." This is the only specimen of *D. murrayensis* found in USNM and it matches Rathbun's (1923) description and plate well. Moreover, it was collected from Port Philip Bay, South Australia, close to the mouth of the River Murray, which is the type locality of the species.

Dittosa cheesmani (Filhol, 1886)

Fig. 2, 4 E, F

Ebalia laevis McLay, 1988:94, fig. 18a-c (see McLay, 1988 for complete synonymy).

Material examined.—USNM 270105, male, 11.4 × 11.6; "*Eltanin,*" Cruise 23, Stn. 1709, 43°31′S–43°30′S, 176°10′W–176°08′W, 143–183 m, Blake Trawl, 24 May 1966, coll. USARP; USNM 270106, 15 males, 14 females; ZRC, 1 male, 1 female.

Description of male.—Carapace slightly broader than long, surface covered with granules, those at the edges mushroom shaped, intestinal and cardiac regions demarcated by shallow grooves, hepatic and subhepatic margins raised to form facet, anterolateral margin with shallow notch immediately after hepatic margin, junction of antero- and posterolateral margins with pointed tubercle, posterior margin with flattened, triangular projection on either side of median line, subhepatic region with obtuse triangular projection, mid-intestinal region with rounded tubercle, posterior intestinal region with rounded spine.

Front bilobed, lobes separated by u-shaped notch; edge of buccal cavern visible beyond front, extending beyond orbital margin. Outer surface of third maxillipeds with large, round granules, outer margins setose, exopod slightly narrower than ischium, anterior surface of merus with shallow depression, without elevated granules.

Outer edge of chelipeds with pointed granules of varying sizes, surface with flat pavement of granules, palm broader than merus, outer edge carinate, distal edge with ridge just at base of movable finger, fingers slightly shorter than palm, immovable finger cutting edge with large, triangular tooth close to proximal end, movable finger with corresponding notch, cutting edges denticulate; anterior edge of first to third pairs of ambulatory legs with acuminate granules, last pair of legs with acuminate granules lining both anterior and posterior edges, dactylus flattened, carinate and setose on both edges.

Proximal end of abdomen with raised granules, distal end of penultimate segment with transverse tubercle, telson triangular, with rounded apex. Proximal end of G1 rather stout, gradually tapering to simple point, proximal half with long setae, G2 slender, elongate, slightly longer than G1.

Paratype females: Telson triangular, with rounded tip. Projections on posterior margin less pointed than that in males. Other non-sexually dimorphic characters similar to males.

Remarks.—There has been some confusion concerning the identities of *Ebalia laevis* Bell, 1855 (formerly *Phlyxia laevis*) and *Ebalia cheesmani* Filhol, 1886. Bennett (1964) synonymised both species, noting that in specimens of *E. laevis* which he examined, the degree of variability was high, particularly with respect to ". . . the posterodorsal projections, the anterolateral outline and the granulation . . ." (Bennett, 1964:21), making it difficult to distinguish it from *E. cheesmani.*

Additional confusion has been created due to the fact that Bell's (1855) *Phlyxia laevis* (now *Ebalia laevis*), differs considerably from what other authors have called *Phlyxia* (or *Ebalia*) *laevis* or *E. cheesmani* (for complete listing of authors, see McLay, 1988). From Bell's (1855) figures, it can be seen that the front is narrow and projected forwards, and the anterior margin of segment six of the abdomen is shown to have a median forward pointing denticle, followed by a flat tubercle. This is not mentioned by Bennett (1964) in his reasons for synonymysing *E. cheesmani* with *E. laevis.* Although it is known that characters such as granulation, structure of the carapace anterolateral margins and posterior projections are highly variable within leucosiid species, characters such as elongation of the front and particularly, the presence of a median, anteriorly-directed denticle on the anterior margin of the male sixth abdominal segment, seem to be constant and reliable. The latter character has been used in defining other leucosiid taxa such as *Drachiella* Guinot, 1976. Thus, *E. laevis* sensu stricto, may be a true *Phlyxia* or even a *Praebebalia,* but this can only be determined after the type specimens are examined. It is unlikely to be a species of *Dittosa,* due to the reasons mentioned above. It is certainly very unlikely to be a synonym of *P. cheesmani.*

Therefore, it is best to refer the present specimens to *E. cheesmani,* as they agree, in general, with what has been described.

Bennett's (1964) remarks concerning the large degree of variation found in specimens of *E. laevis* may perhaps suggest the presence of more than one species. In the specimens I observed, the variation in characters is not as substantial.

Acknowledgments

This study was carried out as part of the author's Graduate Student Fellowship at the Department of Invertebrate Zoology, Division of Crustacea, National Museum of Natural History, Smithsonian Institution. The author acknowledges funding from the Smithsonian Institution, R. B. Manning for his supervision, R. Lemaitre for his encouragement and advice, A. Rajaguru, K. Reed, P. Rothman, L. Ong (Museum Support Center), J. Maret and C. Walter for their help and support, W. Moser for his expert advice on photography, and the other staff at the Department of Invertebrate Zoology for their kind assistance. The author thanks P. Davie, Queensland Museum, for reviewing the manuscript, and P. K. L. Ng, Department of Zoology, National University of Singapore, for his advice and comments.

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Appendix

List of *Philyra* species examined

Philyra anatum (Herbst, 1782)

USNM 39653, 1 male, East of Koh Chang, Thailand, 11m, seine, 25.i.1900; USNM 39654, 1 juvenile, Sound at Koh Chang, Thailand, 5.5-9 m, soft clay bottom, coll. 1900.

Philyra globus (Fabricius, 1775)

USNM 42756, 3 males, 2 females, Ganges Delta, India; 2 females, Stn. GVF 53, channel between Songkhla and Goh Gnu Island, 3 Nov 1957.

Philyra olivacea Rathbun, 1909

USNM 62038, 1 male, tideflats, Tsimei, China, don. S. F. Light (University of China), Jun 1923; USNM 57505, 1 young female, San Mun Bay, East Coast of China, coll. M, Maki, 11 Jun 1922; 1 female, of Tachalom, Gulf of Thailand, 28 Jul 1923.

Philya pisum de Haan, 1841

USNM 55381, 2 males, 2 females, Kagi, Taiwan, Taihoku Normal School coll., Aug 1918; USNM 54522, 4 males, Chiba Prefecture, coll. M. Sasaki; 1 male, no data; USNM 45859, 1 male, Japan, exchange, no other data; USNM 18865, 1 male, Atami Province, Japan, "Mr. Sakamoto," no other data; 2 males, 2 females, Chemulpo, Korea, coll. P. L. Jony.

Philyra platychira de Haan, 1841

USNM 73207, 1 male, 1 female, Iloilo, Panay Island, Philippines, Ilo Ilo '*Eclipse*' Expedition, coll. H. C. Kellers, April 1929; USNM 65350, 1 female, Lubig Bay, Port Binanga, Philippines, coll. APE, 8 Jan 1908; 1 female, near Mariveles, Luzon, Philippines, coll. A. M. Reese, 8 Jan 1908.

Philyra punctata Bell, 1855

USNM 252713, 1 male, 1 female, between Mossel Bay and Algoa Bay, South Africa, 32 m, coll. R/V '*Thomas B. Davie,*' 15 Feb 1980; USNM 221770, 1 male, 1 female, between Port Elizabeth and Mossel Bay, South Africa, R/V '*Thomas B. Davie,*' 15 Feb 1980.

Philyra syndactyla Ortmann, 1892

USNM 56781, 12 males, 1 female, mouth of Jeddo Bay, Yenosima, Japan, coll. E. L. Morse; USNM 45863, 20 males, 2 females, Yenoshima, Japan.

Philyra tuberculosa Stimpson, 1858

USNM 57768, 1 male, Tsimei, China, coll. S. F. Light (University of China), Jun 1923.

Praebebalia extensiva Rathbun, 1911

USNM 041064, Holotype male, Seychelles Providence, West Indian Ocean, Stn. D8, 229 m, coll. R/V *Sealark,* 4 Oct 1905.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(3):477–490. 1995.

Neocallichirus cacahuate, a new species of ghost shrimp from the Atlantic coast of Florida, with reexamination of *N. grandimana* and *N. lemaitrei* (Crustacea: Decapoda: Callianassidae)

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Abstract.—Diversity of infaunal crustaceans remains poorly known, even for macrofaunal forms from accessible shorelines that have been urbanized for decades and studied extensively. *Neocallichirus cacahuate,* new species, is described from sparsely vegetated intertidal flats of Peanut Island just inside Lake Worth Inlet on the Atlantic coast of Florida, where it occurs as a minor constituent of a thalassinid fauna dominated by the callianassids *Neocallichirus rathbunae* (Schmitt), *Sergio mericeae* Manning & Felder, and *Callichirus major* (Say). This new species, at first confused with *Neocallichirus grandimana* (Gibbes) which also occurs occasionly in this habitat, bears a general resemblance to the young of that larger congener in carapacial features, chelae, telson, and uropods. However, in addition to the much larger body size attained by *N. grandimana,* this species and *N. cacahuate* can be distinguished on the basis of differences in body coloration, eyes, proportions of cheliped articles, shape of the uropodal endopods, and sculpture of the first and second male pleopods. At present known from only four small specimens, all from the type locality, *N. cacahuate* appears to mature at a much smaller size than does *N. grandimana.*

In the early 1980's, we initiated studies to document exhaustively the coastal decapod crustacean diversity in the Indian River Lagoon and adjacent embayments of southeastern Florida, a task in which we remain engaged. We chose to focus initially on intertidal and shallow subtidal infaunal groups because the habitats were readily accessible, these groups were not well represented in local collections, and both the assemblage and the habitats appeared vulnerable to continuing shoreline development in this rapidly urbanizing region. Our experience in sampling with yabby pumps (see Manning & Felder 1995, and citations therein) facilitated our obtaining large samples of macroinfaunal forms, especially of the more deeply burrowed thalassinid ghost shrimp. In the course of our subsequent studies of these large series of materials collected, we have come to recognize the divergent morphology which characterizes genera of the western Atlantic Callianassidae, the subtle characters that often separate closely related western Atlantic species, and the remarkable diversity of this taxocene in southern Florida (Manning & Felder 1986, 1991, 1992, 1995, Manning & Heard 1986, Manning 1987, 1993, Rodrigues & Manning 1992, Felder & Rodrigues 1993, Felder & Manning 1994, Manning & Lemaitre 1994).

We herewith report yet another previously unrecognized thalassinid species from this region, the third new thalassinid and fifth new infaunal decapod that we have reported from this southeastern region of Florida. This new species, at first confused with juveniles of a sympatric congener, *Neocallichirus grandimana* (Gibbes, 1850), represents the fifth species of that genus (sensu Manning & Lemaitre 1994) to be described from the western Atlantic. As with several other new callianassids we have found, the atypical coloration of fresh specimens first suggested that they may represent a unique form. In order to definitively distinguish the new species, our present analyses includes detailed comparisons with juveniles and adults of *N. grandimana* from southern Florida, a markedly larger species at maturity.

Material examined is listed by location followed by date, collector, number of specimens per sex and condition (mutl = mutilated, ov = ovigerous, immat = immature), and museum number. Size is expressed as postorbital carapace length (cl) or postorbital total length (tl) measured in millimeters (mm). The holotype and two paratypes of *Neocallichirus cacahuate* have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). A paratype has been deposited in the University of Southwestern Louisiana Zoological Collections, Lafayette, Louisiana (USLZ). As the single small female specimen of *N. cacahuate* appeared to be immature, the description was based primarily upon the larger male specimens. Comparative studies of *N. grandimana* are based upon males of that species from the Atlantic coast of Florida, some of which were immature stages (USLZ 3554) and of carapace lengths approximating those of *N. cacahuate,* others of which were much larger and fully mature (USLZ 3553). *Neocallichirus cacahuate* was also compared with two topotypic juvenile females of *N. grandimana* from Key West, Florida (USLZ 3555) and to the male holotype specimen of *Glypturus siguanensis* Boone, 1927 from Isle of Pines, Cuba (YPM 8160), obtained on loan from the Yale University Peabody Museum of Natural History. From our examination, the latter specimen was confirmed as a junior synonym of *N. grandimana* (see Manning 1987). The types of *N. cacahuate* were compared with fresh, comparably sized topotypic material of *N. lemaitrei* Manning, 1993 obtained recently in the Islas del Rosario, Colombia by DLF and R. Lemaitre (USLZ 3556). Publication figures were prepared by DLF.

Family Callianassidae Dana, 1852
Subfamily Callichirinae
Manning & Felder, 1991
Neocallichirus Sakai, 1988
Neocallichirus cacahuate, new species

Figs. 1a–c, 2, 3a–e, 4a–c, 5

Type material.—Holotype: North side of Peanut Island, sparsely vegetated sandy to shelly sand intertidal flats, Lake Worth, West Palm Beach County, Florida, 26°46.7′N, 80°2.9′W, 23 Jul 1994, coll: D. L. Felder, J. M. Felder, R. D. Felder and W. D. Lee, 1 ♂ (cl 13.2 mm; photographic voucher) USNM 268770.

Paratypes: Same site as holotype, 4 Mar 1987 (RBM station 87-5), coll: R. B. Manning and W. D. Lee, 2 ♂ (cl 9.9 mm) USLZ 3552, (cl 10.5 mm) USNM 268861, 1 ♀ (cl 7.2 mm) USNM 268769.

Diagnosis.—Front of carapace with 3 small angular anterior projections, medial usually more acute and anteriorly advanced than laterals. Eyestalks broad, with large swollen cornea occupying more than half of stalk width. Third maxilliped with arched dactyl and broad propodus, height of propodus greater than length of dactyl; maximum diagonal length of merus-ischium more than twice width at joint between these articles. Major cheliped with inferior margin of merus lacking distinct spine, regularly rounded in outline and armed with line of small slightly hooked or distally-directed denticles; carpus greater than or equal to ⅔ length of palm, inferior margins of both unarmed; dactylus with bilobed subrectangular tooth in proximal half, separated by deep cleft from broad subtriangular tooth distally, terminally with acute hooked tip. Minor cheliped with fingers subequal to or slightly longer than palm, palm subequal to or slightly longer than carpus. Uropodal endopod broadly subrectangular, posterior margin truncate, nearly straight; uropodal exopod with superior plate not reaching distal margin of inferior plate. Telson broader than long, posterior margin truncate to weakly sinuous.

Description.–Size small, males maturing at relatively small size; cl <15 mm and tl <65 mm in known specimens.

Frontal margin of carapace (Figs. 1a, 5a) with 3 anterior prominences, lateral of which are usually lobiform or obtusely angular, overlying inner margins of antennal peduncles; median prominence advanced slightly beyond laterals, forming short rostrum, not extending to cornea. Rostrum usually terminating in acute or slightly spiniform projection, lateral prominences sometimes terminating similarly in smaller specimens. Carapace lacking rostral carina, with distinct linea thalassinica, and with defined dorsal oval marked posteriorly by deep transverse cardiac furrow, latter extending anteroventrally to either side above linea thalassinica as shallow groove demarcating posterior half of dorsal oval. Frontal margin of carapace continued ventrolaterally beyond intersection with linea thalassinica and onto branchiostegite as thickened oblique ridge terminating at anterior end of prominent rounded hepatic boss and lower, more elongate swelling. Subantennular region of epistome forming calcified socket for antennal peduncle, bearing dense tuft of long setae below peduncle.

Eyestalks subtriangular, with large, bulbous, hemispherical, darkly pigmented corneas; swollen cornea occupying more than half of stalk width and markedly distending anterolateral margin of eyestalk. Length of exposed eyestalk in dorsal view slightly exceeding basal width, lobate to obtusely angular tips reaching to or nearly to distal end of basal antennal article; mesial surfaces of eyestalks closely appressed over proximal portion of midline, slightly divergent terminally; base of eyestalk with mesial sensory punctae on either side of rostrum.

Antennular peduncle shorter and heavier than antennal peduncle, terminal article about 1.5 times length of penultimate and not exceeding midlength of terminal article of antennal peduncle; penultimate and terminal articles of peduncle with ventromesial and ventrolateral rows of long setae, those of ventrolateral row longer; rows of setae continued onto ventral ramus of flagellum, proximal articles of which also bear very long midventral setae; rami of flagellum subequal in length or with ventral slightly exceeding dorsal, 5–6 times length of terminal article of peduncle; dorsal ramus with sparse setae in proximal half, distal half with dense tufts of short ventrolateral setae, articles comprising tapered tip with dense line of ventral aesthetascs. Antennal peduncle with terminal article subequal to or slightly longer than penultimate article; short basal article forming slightly produced, setose lip above laterally produced excretory pore; second article with deep, diagonal ventral suture, distolaterally with single tuft of setae, small, distinct, dorsal scale articulated at joint with third article; third article elongate, much narrower than second, distinctly longer than combined lengths of first two, proximolaterally with partially fused condylar process articulated to distolateral extreme of second article; fourth article slightly narrower than third; antennal flagellum about 2.5 times length of antennular flagellum.

Mandibles (Fig. 2a) with large, 3-segmented palp, elongated third article of palp slightly tapered and terminally rounded, concave on external surface, long setae distally on second article and on proximal extensor surface of third, field of short,

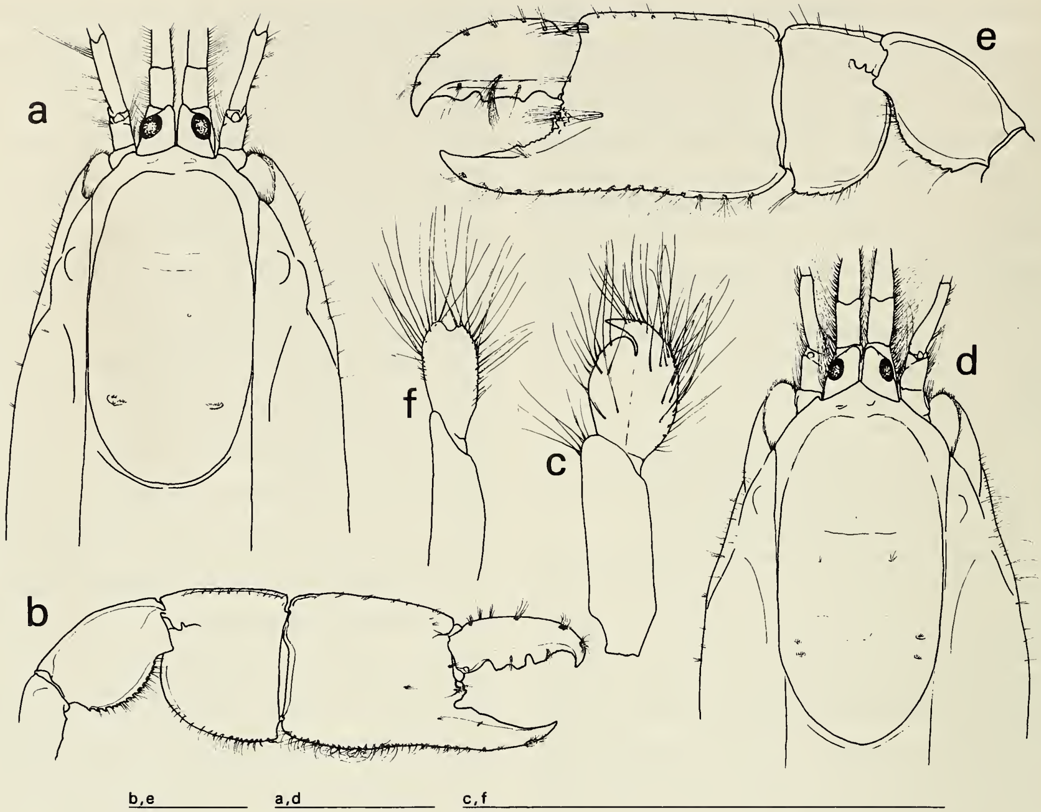

Fig. 1. *Neocallichirus cacahuate,* new species, male holotype (cl 13.2 mm) from Peanut Island, Lake Worth, Florida, USNM 268770: a, Carapace front, eyestalks, and basal antennal segments, dorsal view; b, Major cheliped, internal surface; c, First pleopod, posterolateral surface. *Neocallichirus grandimana* (Gibbes), immature male (cl 13.2 mm) from just north of St. Lucie Inlet, Florida, USLZ 3554: d, Carapace front, eyestalks, and basal antennal segments, dorsal view; e, Major cheliped, internal surface; f, First pleopod, posterolateral surface. Scale lines indicate 5 mm.

weakly hooked setae on most of extensor surface of third article, setae heavier and less hooked terminally; incisor process with well defined, terminally corneous teeth on cutting margin, teeth largest on proximal ⅔ of cutting margin, internal surface with lip giving rise to molar process proximal to incisor teeth, molar process with about 6–7 small marginal teeth, 1 of which may be spaced proximally on internal margin apart from others; paragnath (Fig. 2b) rounded, scaliform, poorly sclerotized, set against and below molar process. First maxilla (Fig. 2c) with endopodal palp long, narrow, terminal article deflected proximally at articulation and narrowed to terminal tip; proximal endite with very dense fine setation on most of lower mesial margin, terminal lobe with field of large, terminally bifurcate setae; distal endite elongate, proximally narrow, broadening terminally where armed with short stiff bristles, distalmost bristles may be weakly bifurcate; exopodite low, truncate and setose. Second maxilla (Fig. 2d) with endopod acute distally, first and second endites each longitudinally subdivided and densely setose terminally; first endite with low arcuate setose crest across external surface of lower lobe, internal surface fused to broad, rounded, plate bearing long marginal setae; exopod forming large, broad, scaphognathite. First maxilliped (Fig. 2e) with proximal endite narrowly produced, dentiform, marginally setose; distal endite robust, subquadrate, mesial half of external surface and margins heavily setose, long dense setae of outer surface overreaching and obscuring stout bifurcate bristles on mesial margin, longest setae terminal, internal surface concave; exopod ovoid, divided by transverse suture marking notch on mesial margin, longest setae in field on external surface and mesial margin proximal to notch; epipod large, posterior lobe broad, anterior end tapered to narrow terminus. Second maxilliped (Fig. 2f) with long, narrow endopod; endopodal merus length about 4 times width, flexor margin with dense fringe of long, close-set setae; carpus short; propodus slightly arcuate, heaviest distally, greatest width about ⅖ length; dactylus more than ⅓ length of propodus, with terminal brush of stiff bristles; exopod narrow, arcuate, distally overreaching end of endopodal merus, marginally fringed by long setae; epipod small, partial suture subdividing angular terminal lobe; arthrobranch rudimentary. Third maxilliped (Fig. 2g) without exopod; endopod with long setation on mesial margin, terminal 3 articles also with long setation on extensor margins; length of endopodal merus-ischium exceeding 2 times width; ischium subrectangular, distinctly longer than broad, proximomesial margin rounded, not strongly produced, internal surface with well defined, longitudinally oriented elevation bearing curved row of sharp denticles; merus subtriangular, slightly broader than long; carpus heavy and subtriangular, with setose lobe on flexor margin, internal surface with dense field of fine setae distally; propodus large, subquadrate, height subequal to or exceeding length, internal surface with median field of fine, dense setae; dactylus narrow, slightly arcuate, shorter than height of propodus, terminally with small brush of stiff bristles.

Branchial formula including exopods and epipods as described for first and second maxillipeds above; branchiae limited to single rudimentary arthrobranch on second maxilliped, pair of arthrobranchs on third maxilliped, and pair of arthrobranchs on each of first through fourth pereopods.

First pereopods forming dissimilar chelipeds, major cheliped heavy, massive in adults (Fig. 1b), similar to minor cheliped in juveniles. Major cheliped of adults strongly calcified; ischium slender, superior margin sinuous, inferior (flexor) margin with few widely spaced minute denticles; merus about 1.5 times as long as high, superior margin arcuate, inferior margin lacking distinct enlarged spine, regularly rounded in outline and armed with line of small slightly hooked or distally directed denticles; carpus almost as long as high, relatively shorter and higher in adults than in immature specimens, in larger adults length about ⅚ height and greater than or equal to ⅔ length of palm, superior margin weakly arcuate, forming keel terminated at distal acute corner of article, proximoinferior margin regularly rounded and smooth in outline, low submarginal denticles on internal surface; propodus heavy, length (including fixed finger) in adults distinctly less than twice height, latter greatest proximally, superior margin of palm forming unserrated keel in proximal half, proximal inferior margin with poorly defined smooth keel extending to base of fixed finger, keel lined on internal side by line of submarginal denticles extending onto base of fixed finger; angular, tuberculate prominence at base of gape, below which is rounded excavation in basal, opposable margin of fixed finger; fixed finger in adults with prehensile margin ranging from nearly smooth, with low broad teeth, to serrate; dactylus (movable finger) subequal to or shorter than palm, opposable margin with bilobed subrectangular tooth in proximal half, separated by deep cleft from broad subtriangular tooth distally, terminally with acute hooked tip.

Minor cheliped (Figs. 3a, 5b) well calci-

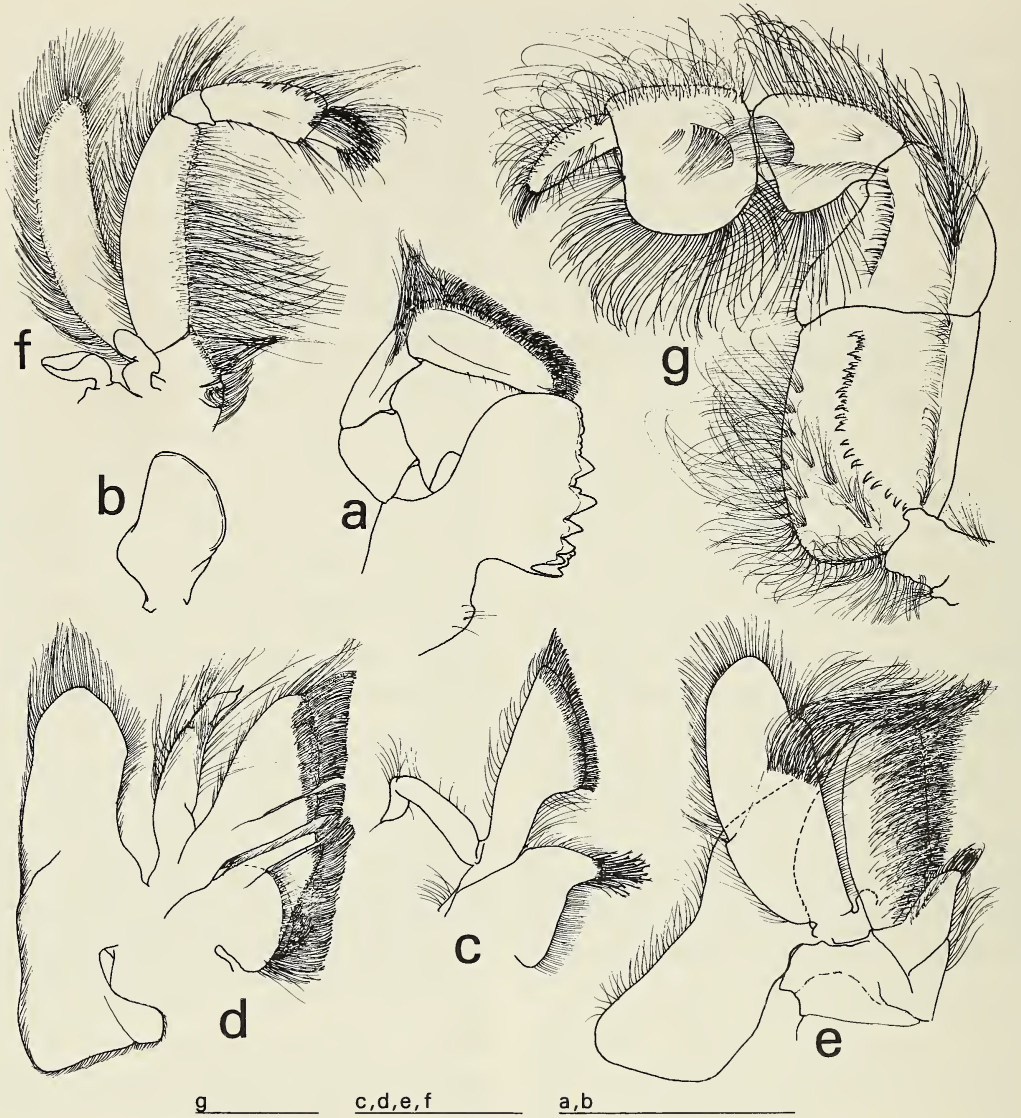

Fig. 2. *Neocallichirus cacahuate,* new species, male holotype (cl 13.2 mm) from Peanut Island, Lake Worth, Florida, USNM 268770, right mouthparts: a, Mandible, external surface; b, Paragnath, external surface; c, First maxilla, external surface; d, Second maxilla, external surface; e, First maxilliped, external surface; F, second maxilliped, external surface; g, Third maxilliped, internal surface. Scale lines indicate 2 mm.

fied but terminally more slender, less massive than major; ischium narrow, unarmed or with at most a few minute denticles on inferior margin, subequal in length to merus; merus elongately ovoid, length less than twice height, inferior margin usually with some minute denticles distally; carpus large, subrectangular, forming most massive article of limb, slightly longer than merus, length slightly exceeding height and markedly exceeding length of palm, height greatest at or just proximal to midlength; chela narrower than and exceeding length of carpus; palm subrectangular, length subequal

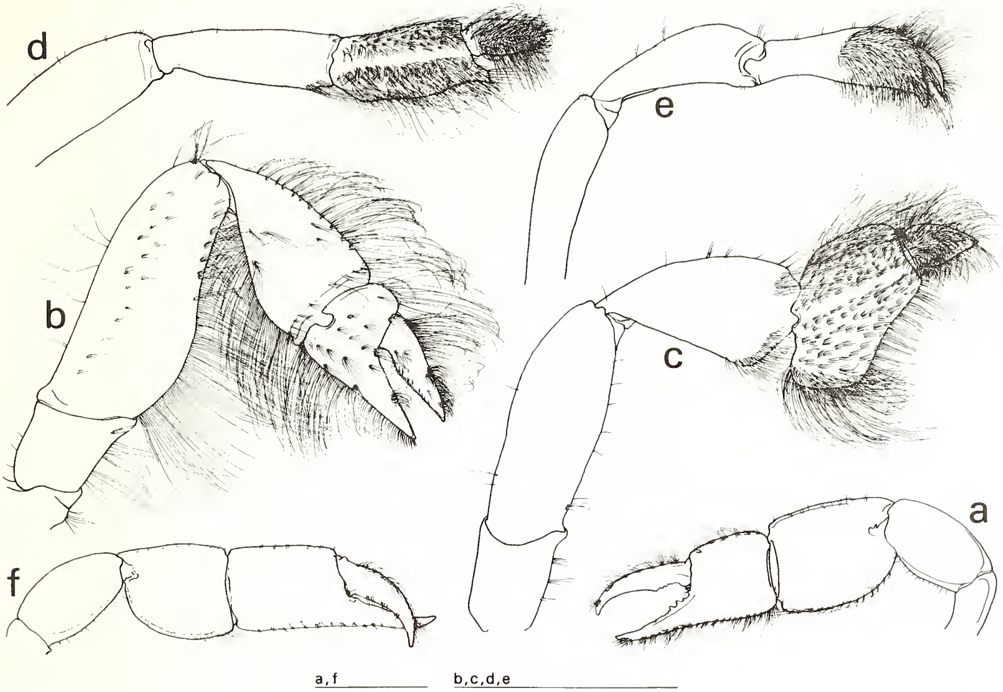

Fig. 3. *Neocallichirus cacahuate,* new species, male holotype (cl 13.2 mm) from Peanut Island, Lake Worth, Florida, USNM 268770: a, Minor cheliped, internal surface; b, Right second pereopod, external surface; c, Right third pereopod, external surface; d, Right fourth pereopod, external surface; e, Right fifth pereopod, external surface. *Neocallichirus grandimana* (Gibbes), immature male (cl 13.2 mm) from just north of St. Lucie Inlet, Florida, USLZ 3554: f, Minor cheliped, internal surface. Scale lines indicate 5 mm.

to height, latter distinctly less than (usually $\leq \frac{4}{5}$) that of carpus; fixed finger subequal in length to palm, opposable margin typically with 3–5 acute teeth proximally, beyond which margin grading from weakly serrate to smooth; gape slightly setose, armed by small denticle on internal side; dactylus (movable finger) in adults consistently exceeding length of palm, opposable margin usually with low, broad tooth and weak serration in proximal half.

Second pereopod (Fig. 3b) chelate, long setae sparsely distributed on inferior margin of ischium, more closely set over most of flexor margin on merus and both margins of carpus, those of superior margin of carpus set in a series of tufts, inferior margin of propodus with similar long setae proximally, progressively reduced in length and stiffened distally, subterminally becoming dense patch of short, stiff bristles; prehensile margins of both fingers corneous, graded from finely micropectinate proximally to smooth distally in both, that of fixed finger obscured by conspicuous tuft of arched bristles on external side near midlength, margins terminated distally in thickened corneous tips of fingers; superior margin of dactylus nearly straight, with long marginal setation proximally, dense patch of short stiff setae and bristles distally; external surface of carpus, propodus and dactylus with scattered patches of short setae.

Third pereopod (Fig. 3c) merus broadest in distal half, length less than 3 times height; carpus broadest distally, length ≤ 2 times height, terminally with patches of long setae overreaching propodus; propodus with proximally-directed lobe of inferior margin not reaching beyond broadest part of carpus, lobe terminally with long distally-directed setae, inferodistal margin with spaced tufts of slightly shorter setae, superior margin with fields of long setae grading to small patterned tufts of lighter, shorter setae on outer face of article; dactylus tear-shaped, densely setose on external surface, terminating in corneous tip hooked toward external side.

Fourth pereopod (Fig. 3d) with merus heavier, longer than carpus; subchelate, inferodistal corner of propodus produced into short fixed finger bearing heavy microserrate setae on external side and short bristles at tip; soft dense setation on outer surface of propodus and dactylus, that of propodus divided into upper and lower fields, densest in lower field where continued onto lower half of internal surface; dactylus terminating in narrow tip hooked toward external side.

Fifth pereopod (Fig. 3e) minutely chelate, opposable surfaces of propodus and minute dactylus excavate, spooned, terminally rounded, forming beak-like chela obscured by dense fields of setation on distal ½ of propodus and superior surface of dactylus; corneous prehensile lip on fixed finger of chela pectinate.

Abdominal somites smooth, glabrous dorsally, with few paired punctae bearing short setae; second tergite posterolaterally with sulcus posterior to which is vertical, crescentic row of setose punctae on low carina, extreme of posterolateral lobe with small tuft of long setae; third through fifth tergites each with small midlateral depression bearing short setae, and broadly triangular depression bearing long soft dense setae on the lateral lobe, position of these depressions more anterior in the more posteriormost tergites; sixth tergite with pattern of small setose punctae and fine marginal setation laterally and distinct transverse, posteriorly-facing groove above telson.

First pleopod of male and female uniramous, composed of 2 articles; in male (Fig. 1c), distal article spatulate, shorter than proximal, subdivided into 2 lobes by weak longitudinal furrow, anterior lobe terminally rounded in mature specimens, posterior lobe terminally acute with tip directed anteriorly; in female (immature, Fig. 5c) both articles narrow and elongate, terminal article with weakly produced shoulder just beyond midlength. Second pleopod of male and female biramous; in male (Fig. 4a), long setation largely restricted to tufts on lateral margin and terminus of exopod, lateral margin of endopod and terminus of appendix masculina; distal lobe of endopod almost as long as appendix masculina, demarcated from remainder of article by weak transverse suture; vestige of appendix masculina marked by small patch of microsetae on mesial margin; in female (Fig. 5d), both rami with long setae, appendix interna narrow and elongate. Third to fifth pleopods (Fig. 4b) forming large, posteriorly cupped fans when coupled at mesial margins of endopods; endopod of each subtriangular, short, stubby appendix interna tightly embedded into mesial margin of endopod.

Telson (Fig. 4c) broader than long, width less than 1.5 times length, subhexagonal, broadest at lateral lobes in anterior half, posteriorly truncate to weakly sinuous, posterolaterally corners broadly rounded, each bearing tuft of long setae; dorsal surface anteromedially elevated, with shallow sulci on lateral lobes to either side and short transverse line of setae to posterior. Uropod with angular, posterolaterally-directed lobe of protopod slightly overreaching anterior margin of endopod; endopod broad, subrectangular, slightly broader than long, posterior margin truncate, nearly straight, dorsal surface with longitudinal carina and small tuft of long setae near posterolateral corner; exopod with anterodorsal plate falling well short of distal endopod margin, distal edge of plate lined with short, thick spiniform setae grading to thinner longer setae of exopod margin; dorsal surface of exopod be-

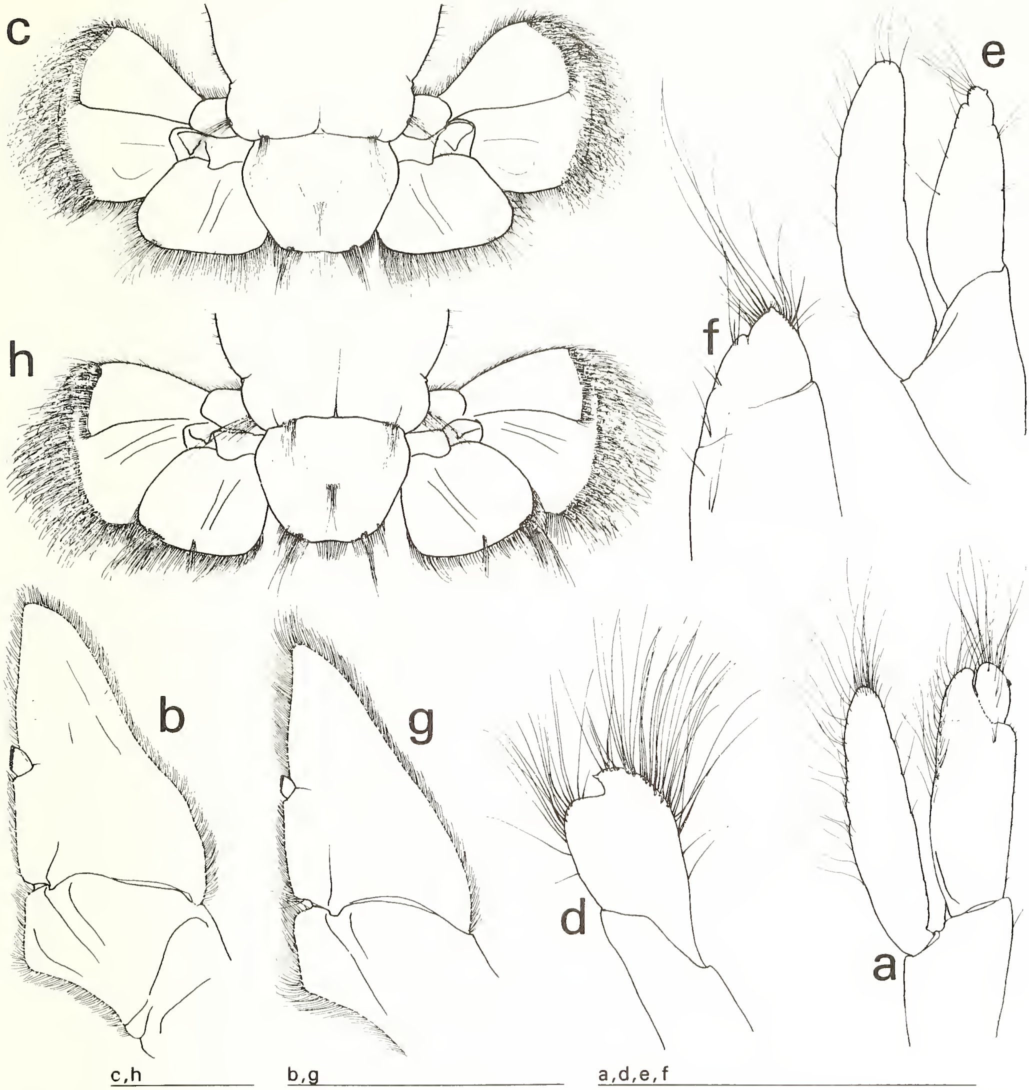

Fig. 4. *Neocallichirus cacahuate,* new species, male holotype (cl 13.2 mm) from Peanut Island, Lake Worth, Florida, USNM 268770: a, Right second pleopod, posterior surface; b, Right third pleopod, anterior surface; c, Telson, uropods, and part of sixth abdominal segment, dorsal surface. *Neocallichirus grandimana* (Gibbes), mature male (cl 27.1 mm) from Bear Cut, Biscayne Bay, Florida, USLZ 3553: d, Right first pleopod, posterolateral surface; f, Right second pleopodal endopod, terminus only, posterior surface. *Neocallichirus grandimana* (Gibbes), immature male (cl 13.2 mm) from just north of St. Lucie Inlet, Florida, USLZ 3554: e, Right second pleopod, posterior surface; g, Left third pleopod, distal endopod and appendix interna, posterior surface; h, Telson, uropods, and part of sixth abdominal segment, dorsal surface. Scale lines indicate 5 mm.

low plate concave, distal margin with dense fringe of setation, fringe diminished and supplemented by row of short spiniform setae on posterior margin.

Size.—Of the four known specimens, three appear to be mature males ranging (after preservation) from cl 9.9 mm to 13.2 mm and tl from 39.4 mm to 51 mm. The single female specimen, cl 7.2 mm and tl 29.8 mm, is apparently immature, given the

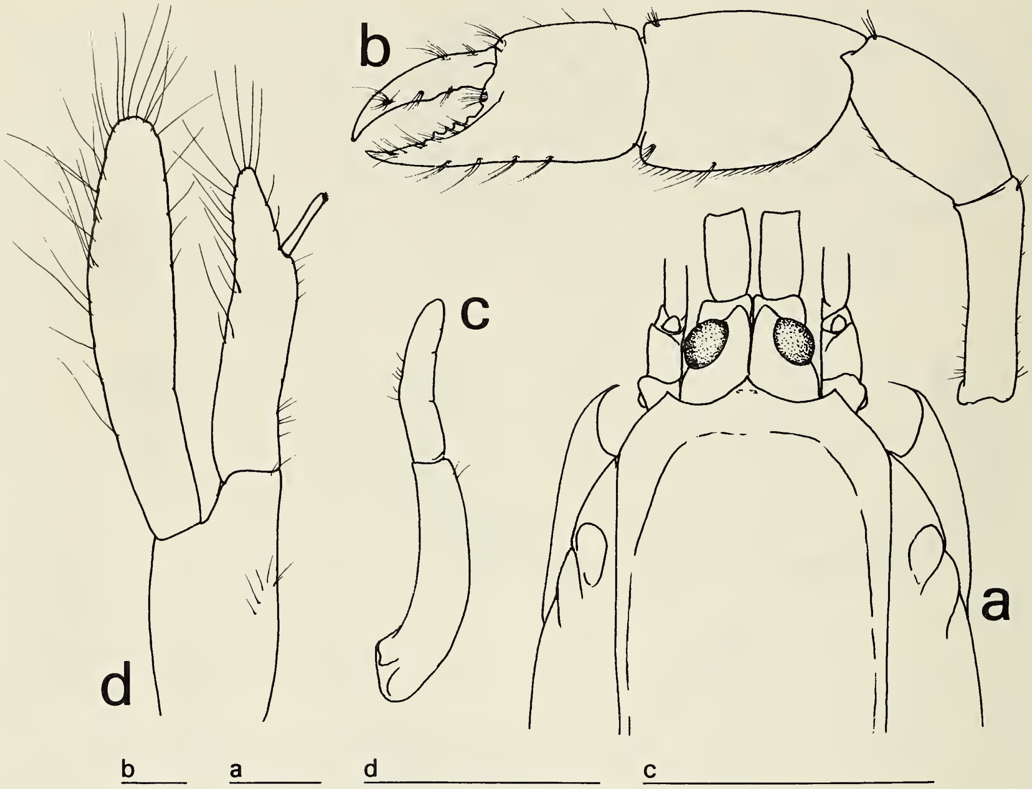

Fig. 5. *Neocallichirus cacahuate,* new species, paratype immature female (cl 7.2 mm) from Peanut Island, Lake Worth, Florida, USNM 268769: a, Carapace front, eyestalks, and basal antennal segments, dorsal view, setae not shown; b, Minor cheliped, external surface; c, First pleopod, posterolateral surface; d, Right second pleopod, posterior surface. Scale lines indicate 1 mm.

limited development of setation in its anterior pleopods.

Color.—Reddish orange, fading quickly to opaque white in alcohol. In life most adult specimens with striking scarlet red to reddish orange highlights on lighter faded orange to cream or translucent white ground color; usually with most vivid scarlet or orange-red patterns on the superior surfaces of the chelae, eyestalks, dorsal oval of carapace, tergites of abdominal segments 2–6, and as a very broad, poorly defined band across telson and uropods; color somewhat less or variably developed on antennae and cardiac region. Light cream to white on inferior surfaces of chelipeds and immediately bordering articulations of pereopodal articles. The reddish coloration is usually distinct from the pinkish-red to rose-violet typical of *N. grandimana.*

Known range and habitat.—Known only from intertidal to shallow subtidal habitats on the northern shores of Peanut Island in Lake Worth, a small marine embayment immediately inside Lake Worth Inlet on the heavily urbanized lower Atlantic coast of Florida, USA. All of the four known specimens of this species were taken with yabby pumps at low tide in sparsely vegetated sand to shelly sand substrates. *Neocallichirus cacahuate* represented a very small percentage of the thalassinids taken from this habitat. Both large and small specimens of *Neocallichirus rathbunae* (Schmitt, 1935) were particularly common in this habitat while *Sergio mericeae* Manning & Felder, 1995, *Callichirus major* (Say, 1818), *N. grandimana,* and *Corallianassa longiventris* (Milne Edwards, 1870) occurred in somewhat lesser abundance. In unvegetated areas on the northern end of the island, especially along the northeastern shoreline near a navigation canal, *Callichirus major* dominated. In the single instance that the burrow shape of a subsequently captured animal was noted, the surface aperture was about 4 mm in diameter and surrounded by a small mound of ejecta slightly darker than the adjacent sand surface.

Etymology.—Derivation of the species name from "*cacahuate,*" the Spanish word for "peanut," recognizes contributions of Mr. Steven C. Rabalais, Supervisor of Vessel Operations and Assistant Director for Physical Facilities of the Louisiana Universities Marine Consortium. Long known to his many friends by the nickname "*Cacahuate*" in Latin America or "Peanut" in the U.S. Gulf states, Mr. Rabalais has contributed substantially to studies of western Atlantic decapod crustaceans through his expert operation of the research vessel R/V *Pelican* and as a volunteer field collector extraordinaire. The name is doubly appropriate in that the type locality for this species is Peanut Island in Lake Worth, Florida.

Remarks.—Like other species of the genus *Neocallichirus, N. cacahuate* can be distinguished from members of the closely related genus *Sergio* on the basis of its relatively longer, posteriorly rounded to truncate telson and its broader, more rectangular uropodal endopods. At the type locality, *N. cacahuate* occurs alongside a commonly encountered reddish colored ghost shrimp of that genus, *Sergio mericeae,* which can be readily distinguished by the aforementioned characters or by the striking shape of the major cheliped in that species (see Manning & Felder 1995). However, *N. cacahuate* also shares its habitat with the more abundant congener *N. rathbunae* and, less commonly, *N. grandimana,* two species that are also commonly reddish to reddish pink in coloration. Fully mature specimens of either of these congeners are conspicuously larger than those of *N. cacahuate* and can be so distinguished outright. Small specimens of *N. rathbunae* can be distinguished on the basis of the uropodal endopod which differs strikingly from that of *N. cacahuate* and *N. grandimana* in that the anterodorsal plate reaches to the distal margin of the endopod. In addition, the lateral frontal spines of the carapace in *N. rathbunae* are almost always each tipped with a sharp conspicuous spinule, while these prominences usually terminate in obtuse lobes or at most sharp corners in *N. cacahuate* or *N. grandimana.*

While subtle variations are evident in the extensive materials of *N. grandimana* that we have examined from the western Atlantic (see also discussion under *Callianassa branneri* by Biffar 1971:666), detailed comparisons between regional subpopulations of this wide-ranging and common form are beyond the scope of the present work. For now, we continue to assign all western Atlantic specimens which (i) lack spinules on the frontal projections of the carapace and (ii) have a short carpus (less than half palm length) on the major cheliped to *N. grandimana* (sensu Manning 1987, Manning & Felder 1991). However, comparative materials of this species used in the present work have been limited to topotypic specimens from Key West, Florida, selected specimens from the Atlantic coast of Florida, and the large male holotype of *Glypturus siguanensis* Boone, 1927 (a subjective junior synonym of *Callianassa grandimana* Gibbes) from Isle of Pines, Cuba.

Differentiation of of fresh material of *N. cacahuate* from live small specimens of the closely related *N. grandimana* can be based upon the more striking coloration of *N. cacahuate,* or can be based on a number of morphological characters. Perhaps most obvious, specimens of *N. grandimana* that are of comparable size to mature specimens of *N. cacahuate* will obviously be immature in secondary sex characters such as the first male pleopods (see Figs. 1c, f, 4d). Also, even though corneas in immature specimens of *N. grandimana* (Fig. 1d) tend to be relatively larger than those in mature specimens, only the very smallest approach the relative size (width consistently >½ eyestalk width) or strongly bulbous shape seen in *N. cacahuate* (Fig. 1a). While corneal width in a small (cl 6.8 mm) topotypic female of *N. grandimana* was about half the eyestalk width, the cornea was not as bulbous as in comparably small specimens of *N. cacahuate* (Fig. 5a) and the major cheliped was clearly distinguishable as typical of *N. grandimana.* The major cheliped in *N. cacahuate* (Fig. 1b) is distinct in its more regularly arcuate, dentate inferior margin of the merus and the much longer carpus than in *N. grandimana* (Fig. 1e), while the minor chela may be distinguished by the larger relative size of the carpus and presence of dentition on opposable margins of the fingers (Fig. 3a), as compared to the minor chela of similar-sized specimens in *N. grandimana* (Fig. 3f). In addition, the mature male first and second pleopods of *N. cacahuate* (Figs. 1c, 4a) differ from both the immature (Figs. 1f, 4e) and mature (Fig. 4d, f) forms of these appendages in *N. grandimana.*

Neocallichirus cacahuate resembles at least two southern Caribbean congeners, *N. lemaitrei* Manning, 1993 and *N. nickellae* Manning, 1993, in reaching mature form at a smaller size than does *N. grandimana* and in having a relatively long carpus on the major chela. However, the major chelae of both these species have a stronger inferior marginal serration on the carpus and propodus which is conspicuously visible in external view. In *N. nickellae,* the broadly sulcate gape at the base of the fixed finger, coniform basal tooth on the opposable margin of the dactylus, and angular inferior margin on the carpus in the major chela, as well as the relative lack of conspicuous teeth on the fingers of the minor chela and the relatively smaller carpus in this appendage, further distinguishes this species from *N. cacahuate.*

However, *N. lemaitrei* appears to be very close to *N. cacahuate* in the shape and dentition of the major chela, as well as in relative proportions of the carpus and propodus of the minor chela. The strong similarity in these features, as well as the similarly bulbous corneas and nearly identical coloration of these species (based on fresh topotypic specimens of *N. lemaitrei*), qualifies *N. lemaitrei* as the congener most similar to *N. cacahuate.* Whereas *N. lemaitrei* matures at smaller size than does *N. grandimana,* it reaches larger size (some with cl ≥ 22 mm) than does *N. cacahuate,* and can be distinguished from the latter species in a number of features related to strength of dentition and amount of setation. In particular, it can be distinguished readily from *N. cacahuate* by its less heavily toothed and more setose gape of the minor chela (Fig. 6a) and by the previously mentioned heavier setation of the inferior margins of the major chela, evident even in small, immature specimens. On the basis of our presently limited sample, the mature males of *N. cacahuate* and *N. lemaitrei* also appear to differ slightly in sculpture of the first pleopods, the anterior lobe of which is angular in *N. lemaitrei* (Fig. 6b), and second pleopods, the appendix masculina of which is relatively broader and bears a larger vestige of the appendix interna in *N. lemaitrei* (Fig. 6c) than in *N. cacahuate* (Fig. 4a).

Another recently reported southern Caribbean form, listed as *Neocallichirus* sp. by Blanco Rambla & Liñero Arana (1994) has proved to be a member of the genus *Sergio* rather than *Neocallichirus.* At the time that their record was published, the name *Sergio* was in press and the differences between *Neocallichirus* and *Sergio,* pointed out by Manning & Lemaitre (1994), were unknown to those authors.

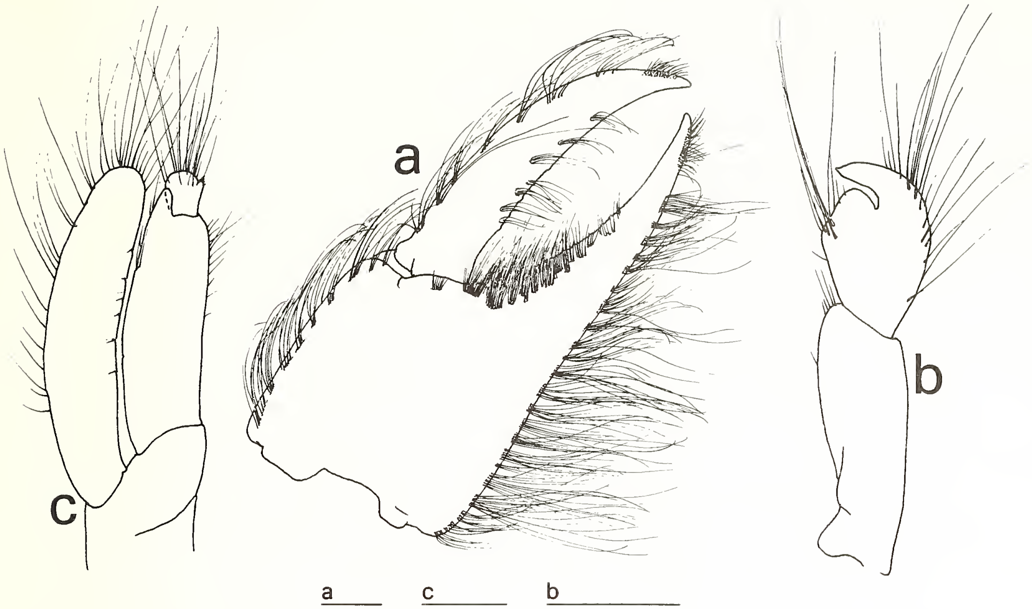

Fig. 6. *Neocallichirus lemaitrei* Manning, male (cl 13.8 mm) from Isla Rosario, Colombia, USLZ 3556. a, Minor chela, internal surface; b, Right first pleopod, posterolateral surface; c, Right second pleopod, posterior surface. Scale lines indicate 1 mm.

The single existing female specimen of *N. cacahuate* is almost certainly immature, given the relatively sparse development of setation in the anterior pleopods, as compared to that in mature females of congeners (see Manning 1993:fig. 3b, d). However, gonopores are clearly evident on the coxae of the third pereopods. While, other than for setation, the second pleopod (Fig. 5d) resembles that of congeners, it is doubtful that articular proportions of this appendage or those of the first pleopod (Fig. 5c) have reached mature form. In the mature female, the terminal article will almost certainly have developed to a larger relative size than seen in this individual and will have developed a more produced shoulder at midlength and much longer and more abundant setation. The more acute frontal prominences on the carapace of this individual, the smallest of either sex collected, may suggest a character typical of immature specimens, perhaps for either sex. As the female specimen is missing the major cheliped, possible sexual dimorphism in this appendage cannot be evaluated.

Acknowledgments

We sincerely thank M. E. Rice, Director of the Smithsonian Marine Station at Link Port, who facilitated access to collecting sites and laboratory facilities at Fort Pierce, Florida. Among many individuals who assisted with our field collections and laboratory observations, we especially thank J. M. Felder, R. D. Felder, W. D. Lee, R. Lemaitre, E. A. Lazo-Wasem, L. K. Manning, P. M. Mikkelsen, S. F. Nates, S. Petry and P. Rothman. We also thank Lilly King Manning for preparation of numerous comparative study sketches reviewed during our preparation of the present paper. This study was supported through an ongoing program of Smithsonian Marine Station project grants to R. B. Manning and D. L. Felder. Partial support was also provided to D. L. Felder through U.S. Minerals Management

Service Cooperative Agreement 14-35-0001-30470, U.S. Fish and Wildlife Service Cooperative Agreement 14-16-0009-89-963, Task Order No. 6, and a small grant from the Coypu Foundation. This is contribution No. 372 for the Smithsonian Marine Station and contribution No. 49 for the USL Laboratory for Crustacean Research.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(3):491–495. 1995.

Olavius nicolae, a new gutless marine tubificid species (Oligochaeta) from Belize

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Abstract.—*Olavius nicolae,* a new species from shallow water sediments at Carrie Bow Cay, on the barrier reef off Belize in Central America, is described. It belongs to an apomorphic group within the gutless genus *Olavius* Erséus, 1984, characterized by small, oval atria, large copulatory sacs, and dorsal spermathecae (the latter located in the middle of segment X). It differs from the closely related, Hawaiian species, *O. parapellucidus* Erséus & Davis, 1989, by its more slender body form and longer clitellum, its more numerous somatic setae, and the more dorsal position of its spermathecal pores.

The barrier reef off Belize in Central America (Caribbean Sea) provides suitable habitats for several species of gutless Tubificidae within the genera *Inanidrilus* Erséus, 1979, and *Olavius* Erséus, 1984 (Erséus 1990, Diaz & Erséus 1994). The Smithsonian Institution's Carrie Bow Cay Field Laboratory in Belize was therefore chosen as a site for the collection of material of various gutless taxa, as part of an ongoing research project on evolutionary and biogeographical aspects of the symbiosis of gutless Tubificidae with sulphur oxidizing bacteria (N. Dubilier, C. Erséus and O. Giere, principal investigators; see Giere et al. 1995). While at Carrie Bow, one previously unknown species of *Olavius* was found by the present authors. This species is described herein.

Tubificid worms were sorted live from sieved organic material extracted from sediment samples collected in shallow water on the reef platform surrounding Carrie Bow Cay. Specimens to be used for light microscopy examination were fixed in Bouin's fluid overnight, preserved in 70% ethanol for some weeks, and then stained in (alcoholic) paracarmine, dehydrated in an alcohol series and mounted whole in Canada balsam. For transmission microscopy examination of body wall and symbiotic bacteria, mid-body or posterior fragments of a few worms were fixed in Trump's fixative (McDowell & Trump 1976), buffered with cacodylate. After embedding (Spurr's resin) ultrathin sections were mounted on copper grids, contrasted in aqueous uranyl acetate and lead citrate and inspected in a ZEISS EM 902A.

The type specimens are deposited in the United States Museum of Natural History (USNM), Smithsonian Institution, in Washington, D.C., and the Swedish Museum of Natural History (SMNH), in Stockholm.

Olavius nicolae, new species
Figs. 1–2

Olavius n. sp.; Giere et al. 1995:table 1.

Holotype.—USNM 171048, whole-mounted specimen.

Type locality.—Immediately E of N tip of Carrie Bow Cay (16°48′N, 88°05′W), bar-

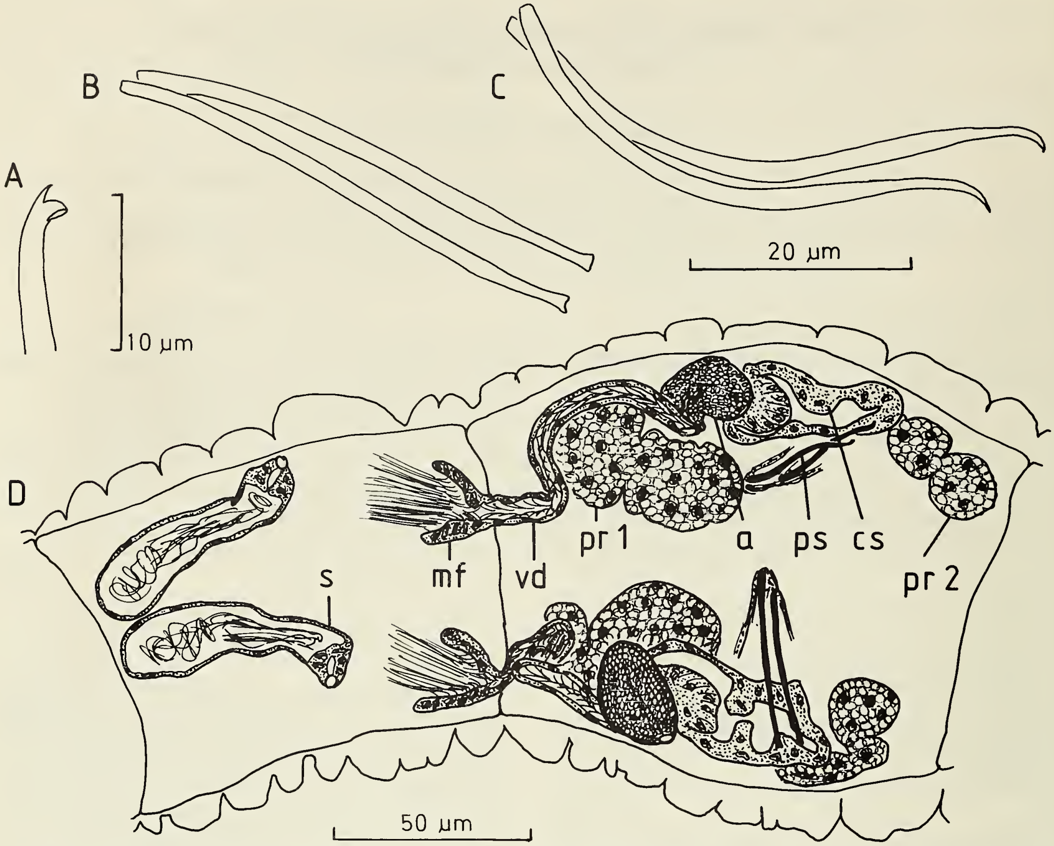

Fig. 1. *Olavius nicolae,* new species. A, Somatic seta; B, penial setae of one specimen; C, penial setae of another specimen; D, horizontal view of genitalia in segments X–XI. Abbreviations: a, atrium; cs, copulatory sac; mf, male funnel, pr1, anterior prostate gland; pr2, posterior prostate gland; ps, penial seta; s, spermathecae; vd, vas deferens.

rier reef of Belize, Central America, inner end of *Thalassia* bed (about 5 m from beach), barely subtidal, fine to medium, heterogeneous sand; 6 March 1993.

Paratypes.—USNM 171049-171051, three specimens, and SMNH Type coll. 4676-4682, seven specimens; all wholemounted, from type locality.

Description.—Length of (only) three complete specimens, 4.6–5.0 mm, 35–38 segments. Width at segment XI, 0.09–0.19 mm; but worms much narrower in other parts of body, at posterior end (of complete specimens) only about 0.04 mm wide. Prostomium generally elongate, pointed triangular. Secondary annulation of body wall variable, not always distinct, with 5–8 annuli per segment in postclitellar part of body; in some specimens irregular, large annuli giving worm a "knotty" appearance. Clitellum extending over ⅔X–XII plus anterior margin of segment XIII. Somatic setae (Fig. 1A) bifid, with upper tooth shorter and much thinner than lower, and with subdental ligament. Bifid setae 21–33 μm long, about 1–1.5 μm thick, three or four per bundle anteriorly, two or three per bundle in postclitellar segments. Penial setae (Fig. 1B–C, D) slender, two per bundle, ventrally in segment XI, 38–56 μm long, about 2 μm thick. In front view, penial setae appearing straight, with chisel-shaped tips (Fig. 1B); in side

Fig. 2. *Olavius nicolae,* new species, TEM micrograph. Cross-section through dermal-muscular layer with numerous bacteria (ba) between cuticle and epidermal tissue (ep); bc, coelomic body cavity; mu, longitudinal musculature.

view, penial setae sigmoid, with tips appearing sharply single-pointed and very thin (Fig. 1C). Penial setae tightly parallel within bundle, either obliquely directed towards posterior, sometimes even approaching a horizontal position in segment (a withdrawn position), or more or less erect in segment, i.e., perpendicular to long axis of worm (a protruded position). Male pores paired, in line with ventral setae, posterior to middle of segment XI. Spermathecal pores paired, in line with dorsal setae, in middle of segment X.

Alimentary canal absent. Body wall with numerous subcuticular bacteria (Fig. 2; see Remarks). Male genitalia (Fig. 1D) paired. Vas deferens non-muscular, ciliated, 6–8 μm wide, much longer than atrium, entering apical end of latter. Atrium oval, only 26–30 μm long, 16–19 μm wide, with very thin outer lining and granulated inner epithelium (internal ciliation probably present, but not seen). Atrium opening into inner end of complex copulatory sac. Sac with folded walls of varying thickness, generally with a distinct papilla near entrance of atrium. Sac everted in a few specimens. Anterior prostate gland larger than posterior one, located anterior to atrium; attachment with atrium, however, not seen. Posterior prostate gland located posterior to copulatory sac, attached to atrium by long stalk. Spermathecae (Fig. 1D) slender, generally club-shaped, 60–75 μm long, consisting of very short ducts, and thin-walled ampullae; latter 15–28 μm wide, with loose masses of, or somewhat bundled, sperm. Spermathecal ampullae generally directed towards the anterior.

Etymology.—Named for Dr. Nicole Dubilier (Biolabs, Harvard University, Cambridge, MA), friend and collaborator in our joint symbiosis project, who participated in the collection of gutless Tubificidae at Carrie Bow Cay.

Remarks.—The subcuticular bacteria (Fig. 2) are of the same morphotype and arrangement as first described for *Inanidrilus leukodermatus* (Giere, 1979) by Giere (1981), and as found also in other related species (Giere et al. 1995, for details).

Distribution and habitat.—Known only from Belize. Barely subtidal heterogeneous sand associated with seagrass. At the type locality, it co-occurs with other gutless taxa: *Inanidrilus reginae* Erséus, 1990, *Olavius* (*O.*) *tantulus* Erséus, 1984, and *O. imperfectus* Erséus, 1984.

Discussion

Olavius nicolae belongs to a group of small species within *Olavius,* all characterized by (1) the location of the spermathecal pores in the middle, rather than the anterior, of segment X, (2) the dorsal, rather than ventral or lateral, location of the same pores, and (3) the very small atria, opening at the inner end of large, convoluted copulatory sacs. Other taxa in this group are *O. tenuissimus* (Erséus, 1979), *O. cornuatus* Davis, 1984, *O. pellucidus* Erséus, 1984, *O. macer* Erséus, 1984, *O. bullatus* Finogenova, 1986, *O. parapellucidus* Erséus & Davis, 1989, *O. finitimus* Erséus, 1990, *O. tannerensis* Erséus, 1991, and *O. rallus* Erséus, 1991, some of which are from the Atlantic, others from the Pacific Ocean.

The new species appears most closely related to *O. parapellucidus,* only known from Hawaii. This species has penial setae, two per bundle, with chisel-shaped tips (Erséus & Davis 1989), almost identical to those of *O. nicolae.* A number of differences are noted, however. *Olavius nicolae* is very slender, with the mid-body and posterior parts considerably narrower than clitellar region, whereas *O. parapellucidus* is more or less evenly wide throughout body (unpublished observation on material in CE collection). Moreover, in *O. parapelludicus* the clitellum covers most of segment XII, but never extends into XIII as in the present species. The somatic setae (about 2 μm thick in *O. parapellucidus*) are more numerous in *O. nicolae* (setae maximally three per bundle anteriorly, two per bundle posteriorly, in *O. parapellucidus*). Finally, the spermathecal pores are in the lines of the dorsal setae in *O. nicolae,* but between these lines and the lateral lines in *O. parapellucidus.*

With the addition of *O. nicolae,* a total of 60 species of marine Tubificidae are known from the barrier reef off Belize (cf. Erséus 1990).

Acknowledgments

We are grateful to Dr. Nicole Dubilier (Harvard University) for cooperation in the gutless tubificid project; to Ms. Barbro Löfnertz (University of Göteborg) and Ms. Christine Hammar (Swedish Museum of Natural History), for technical assistance; to the Smithsonian Institution's Caribbean Coral Reef Ecosystems Program (CCRE), the Swedish Natural Science Research Council, and the Deutsche Forschungsgemeinschaft (Gi 100/14-1), for financial support. This is CCRE Contribution No. 461 from the Carrie Bow Cay Field Laboratory.

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108(3):496–501. 1995.

Pionosyllis maxima Monro, 1930, *P. anops* Hartman, 1953, and *P. epipharynx* Hartman, 1953, redescribed as *Eusyllis maxima* (Monro, 1930), a new combination (Polychaeta: Syllidae: Eusyllinae)

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Abstract.—Three Antarctic species of *Pionosyllis* Malmgren, 1867 (Polychaeta: Syllidae: Eusyllinae) including *P. maxima* Monro, 1930; *P. anops* Hartman, 1953, and *P. epipharynx* Hartman, 1953, are synonymous. They are redescribed and referred to *Eusyllis maxima* (Monro, 1930), new combination, based on morphological characters, most notably the presence of an incomplete crown of denticles on the opening of the pharynx.

We have recently begun a revision of the genus *Pionosyllis* Malmgren, 1867, and are currently examining all available types to redescribe poorly known species (Jiménez et al. 1994). Examination of *P. maxima* Monro, 1930, *P. anops* Hartman, 1953, and *P. epipharynx* Hartman, 1953, types from South Georgia reveals that they have identical parapodia, aciculae, compound setae and characteristic pharynges. All species are considered to be synonymous, and are referred below to *Eusyllis* Malmgren, 1867, because the rim of eversible pharynx is denticulated. *Pionosyllis epipharynx* and *P. anops* are considered the junior synonyms of *P. maxima:* the latter is redescribed as *Eusyllis maxima* (Monro, 1930) new combination.

All the material examined is preserved specimens or fragments provided by The Natural History Museum (BMNH), London, and the Swedish Museum of Natural History (SMNH), Stockholm. The origins of these specimens are detailed under material examined.

The specimens were examined using a stereomicroscope and a compound microscope provided with differential interference contrast optics (Nomarsky). Drawings were made by means of a camera lucida drawing tube, using the stereomicroscope for the complete specimens and the compound microscope for the parapodia and setae. Body width measurements were taken across the proventriculus, and exclude parapodia or cirri; body length measurements exclude antennae, palps and anal cirri.

Taxonomy

Family Syllidae Grube, 1850
Subfamily Eusyllinae Rioja, 1925
Genus *Eusyllis* Malmgren, 1867
Eusyllis maxima (Monro, 1930),
new combination
Figs. 1, 2

Pionosyllis maxima Monro, 1930: 92, fig. 29; Hartman 1964: 87, pl. 27, figs. 3–5; Hartmann-Schröder & Rosenfeldt 1988: 39.

Pionosyllis anops Hartman, 1953: 24, fig. 6 a–c; 1964: 85, pl. 26, figs. 5–6.

Pionosyllis epipharynx Hartman, 1953: 23, figs. 3–4; 1964: 87, pl. 27, figs. 3–5; 1967: 58.

Material examined.—South Georgia: 2.7 miles S, 85°E of Jason Light, 238–270 m, grey mud, st. 45, 6 April 1926 (3 specimens, syntypes of *P. maxima,* BMNH 1930.10.8.319–20); Swedish Antarctic Expedition 1901-1903, Cumberland Bay, 252–310 m, grey mud with few stones, st. 34 (syntypes of *P. epipharynx,* SMNH 611, 7 spec. and SMNH 622, 2 spec.); mouth of Westfjord, 54°15′S, 36°25′W, 250 m, st. 18 (as *P. epipharynx,* SMNH 3050, 1 spec.); May Bay, intertidal algae (syntypes of *P. anops,* SMNH 607, 2 spec. and as *P. epipharynx,* SMNH 3045, 1 ant. end); Grytviken, algae (as *P. epipharynx,* SMNH 3044, 1 spec.); Antarctic Bay, 54°12′S, 36°50′W, 250 m, stones, st. 20 (as *P. epipharynx,* SMNH 3032, 3 ant. ends). All examined specimens were fragmented, except SMNH 607.

Description.—Body long, thick, massive, opaque, subcylindrical anteriorly, arched dorsally, flattened ventrally, with well defined segments (Fig. 1A, B). Only one complete specimen: 9.5 mm long, 0.8 mm wide with 52 setigers (*P. anops,* SMNH 607); largest anterior end fragment 15 mm long with 50 setigers. Dorsum with a broad, transverse reddish brown band on anterior part of each segment surrounded by a narrow pale area posteriorly and laterally, giving an overall impression of alternating dark and light transverse stripes (Fig. 1A), sometimes faded and without color in several specimens. Prostomium slightly wider than long, occipital cleft small, usually covered by dorsal flap of first setiger; four lensed eyes in almost rectangular arrangement, anterior pair slightly larger than posterior one. Median antenna arising from middle of prostomium; lateral antennae arising anterior to anterior pair of eyes, somewhat shorter than median antenna. Antennae cylindrical, smooth generally missing or broken. Palps broad, fused basally, divergent, as long as prostomium (Fig. 1A, B). Peristomial ring strongly reduced dorsally, covered by flap from first setiger; dorsal tentacular cirri somewhat longer than body width, ventral tentacular cirri ⅔ shorter. Antennae, tentacular and dorsal cirri similar in shape, cylindrical, ending in conical tip (Fig. 1C), sometimes coiled over dorsum (Fig. 1A), slender, smooth, somewhat wrinkled distally. Dorsal cirri about two times longer than body width, alternating with shorter cirri, about as long as body width (Fig. 1A) arising from massive cirrophores. Ventral cirri thick, rounded not extending beyond parapodial lobes. Parapodial lobes with a postsetal papilla and a smaller presetal papilla (Fig. 1C, D). Compound setae heterogomph falcigers, numerous, 80–100 per anterior parapodia, progressively decreasing to about ten posteriorly; distal superior surface of shafts spinous, with three or four rows of spines (Fig. 2B, E). Compound setae of anterior parapodia (Fig. 2B) with marked dorso-ventral gradation in shape; dorsal blades bidentate, distal tooth falcate and increasing in size ventrally; ventral blades unidentate, distal tooth with an inconspicuous furrow on the edge; blades about 38 μm dorsally, 24 μm ventrally. Posterior setigers provided only with unidentate blades (Fig. 2E), distally curved, falcate; blades on posterior setigers 28 μm dorsally, 20 μm ventrally; spines on edge of blades short, upwardly directed. Anterior parapodia each with two or three aciculae, slightly curved distally, with blunt tips (Fig. 2C); posterior parapodia each with one or two aciculae of the same type (Fig. 2F). Solitary dorsal simple seta present from setiger 39 (only found in *P. anops,* SMNH 607), indistinctly bidentate, slender, somewhat curved, finely serrated distally on inferior cutting surface (Fig. 2D). Ventral simple setae not seen. Notosetae and notoaciculae present from setiger 19. Pygidium with paired ventrolateral anal cirri, smooth as long as the last five segments. Pharynx extending through five to ten setigers, with a distal circlet of ten soft papillae surrounding opening and an incomplete crown of about 28 chitinous denticles on the rim; anterior pharyngeal tooth conical with enlarged base (Fig. 2A). Proventriculus barrel-shaped, extending

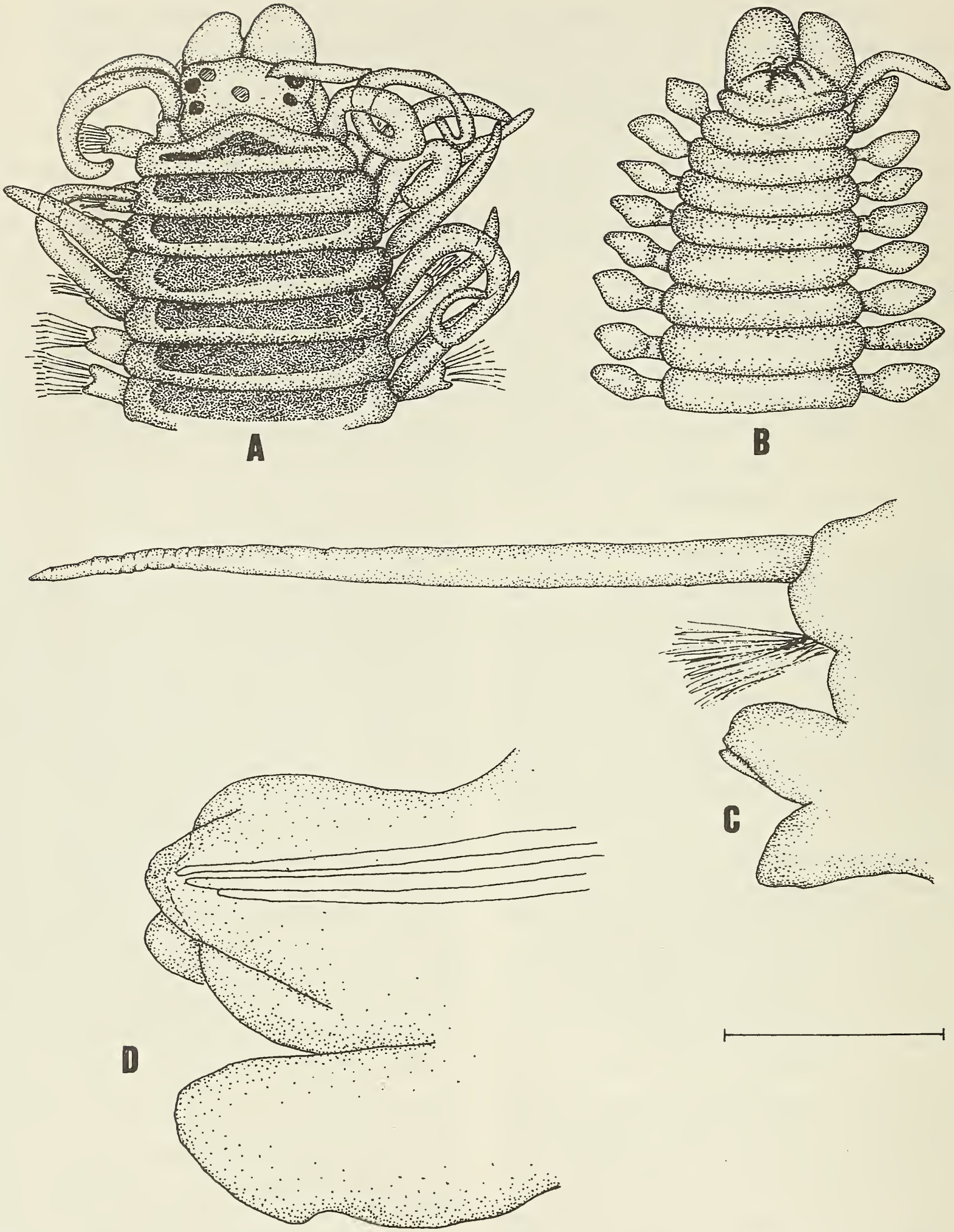

Fig. 1. *Eusyllis maxima* (Monro, 1930) n. comb.: A. anterior end, dorsal view, B. anterior end, ventral view (A, B: *P. maxima,* BMNH 1930.10.8.319–20), C. midbody parapodium, posterior view showing notosetae (neurosetae not drawn) (*P. epipharynx,* SMNH 3044), D. anterior parapodium, posterior view (*P. maxima,* BMNH 1930.10.8.319–20). Scale: A, B: 0.6 mm; C: 0.25 mm; D: 0.2 mm.

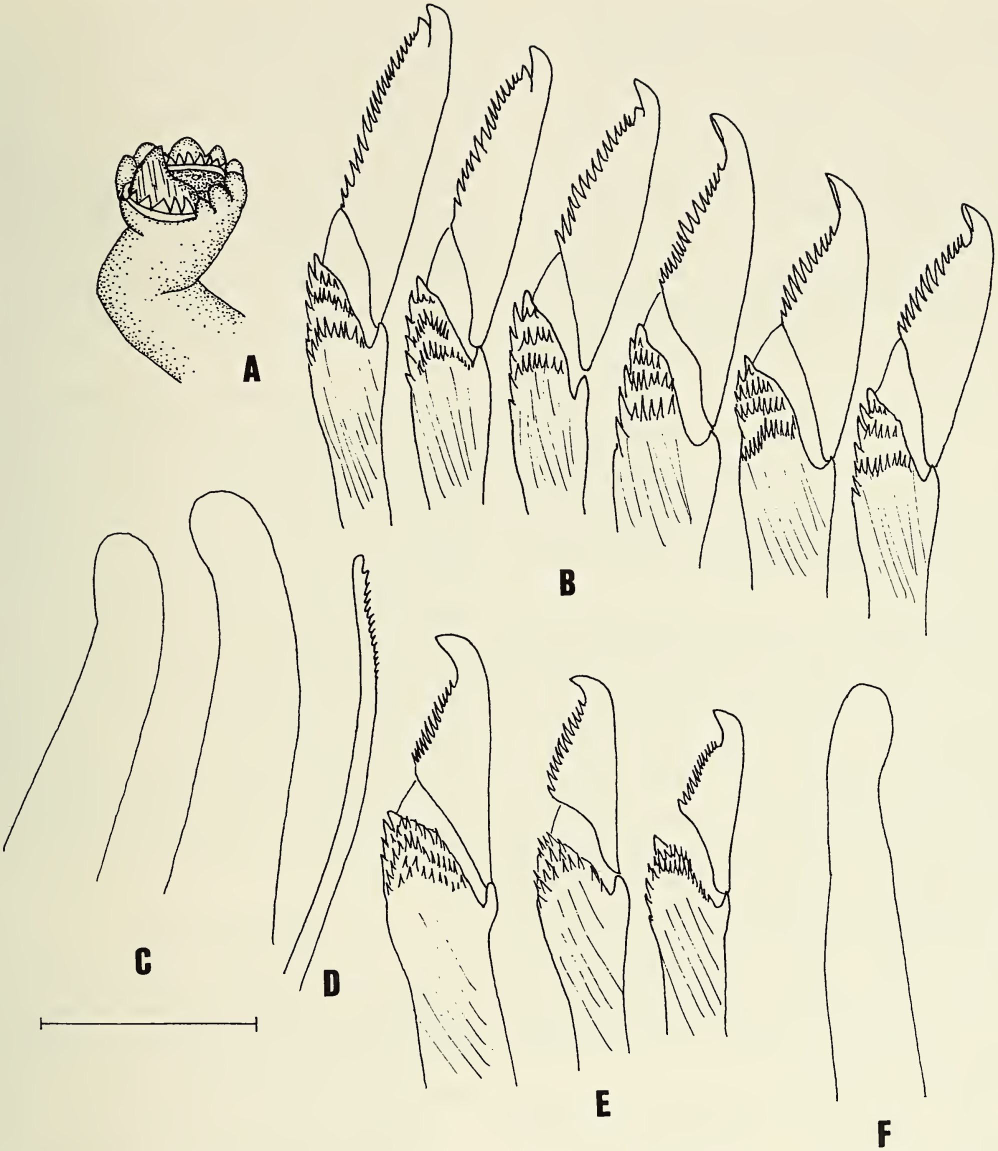

Fig. 2. *Eusyllis maxima* (Monro, 1930) n. comb.: A. pharynx (*P. epipharynx*, SMNH 611), B. dorsal, median and ventral compound setae, anterior parapodium, C. aciculae, anterior parapodium (B, C: *P. maxima*, BMNH 1930.10.8.319–20), D. dorsal simple seta (*P. anops*, SMNH 607), E. dorsal, median and ventral compound setae, posterior parapodium, F. acicula, posterior parapodium (E, F: *P. maxima*, BMNH 1930.10.8.319–20). Scale: A: 0.8 mm; B–F:20 μm.

through four to ten setigers, with about 120 muscle cell rows.

Type locality.—East of Jason Light, South Georgia, 238–270 m.

Distribution.—South Georgia: East of Jason Light, May Bay, Cumberland Bay, and nearby localities; Antarctic; Southern Argentina.

Ecology.—Intertidal with algae to 900 m depth (Hartmann-Schröder & Rosenfeldt 1988, as *P. maxima*) in grey mud.

Remarks.—*Pionosyllis maxima, P. epi-*

pharynx and *P. anops* have identical parapodia, aciculae and compound setae, and were described from South Georgia. These three species were described as having pharyngeal armature composed by a solitary tooth; however, a careful examination of the opening of the pharynx on specimens from each the three species, shows an incomplete crown of chitinous denticles surrounded by a crown of ten soft, thick papillae that is difficult to see. For this reason, we consider these three species to be synonymous and transfer them to the genus *Eusyllis. Eusyllis* is characterized by having smooth to irregularly wrinkled antennae and dorsal cirri, and an incomplete crown of denticles on the anterior rim of the pharynx together with a pharyngeal tooth (Malmgren 1867, Fauvel 1923).

Hartman (1953) described the pharynx of *P. epipharynx* having a middorsal process and a crown of 23 papillae; this is a misinterpretation of the pharynx. Her figure 4B shows the ten soft papillae and the pharyngeal tooth, which is much larger than that of the remaining species of the genus, and her figure 4A shows the pharyngeal tooth and the crown of chitinous denticles, which she describes as papillae. In the same paper she describes a smaller specimen of the same species as *P. anops*; the only difference was that the last species lacks eyes which is not a good character because these sometimes disappear in alcohol.

Most species of *Eusyllis* have been described as having compound setae with bidentate blades, but *E. maxima* has compound setae falcate and unidentate, except the dorsalmost setae of anterior parapodia; *E. maxima* is close both to *E. kupfferi* Langerhans, 1879 (Langerhans 1879, San Martín 1990) from Madeira, Cuba and Canary Islands and *E. transecta* Hartman, 1966 (Hartman 1969) from California, in having a large pharyngeal tooth and unidentate compound setae. However, these two species are much smaller. Hartman (1953) reported the maximum size for *P. epipharynx* 41 mm long, 2.2 mm wide for more 75 setigers; *E. transecta* has 6.1 mm long for about 46 setigers and *E. kupfferi* 4.5 mm long for 35 setigers and have different colour pattern; moreover, they have unidentate dorsal simple seta and the shafts of the compound setae are smooth or with few, short spines; furthermore *E. transecta* has dorsal cirri weakly wrinkled.

Acknowledgments

We wish to express our gratitude to Dr. L. Sandberg, Swedish Museum of Natural History (Stockholm), Mr. A. Muir and Ms. M. Lowe, The Natural History Museum (London), who have lent us the material required in our study. Dr. M. E. Petersen, revised the manuscript and gave us very valuable advice. The comments of two anonymous referees greatly improved the quality of the paper. This paper has been supported by the project CICYT (Comisión Interministerial de Ciencia y Tecnología) ANT 93-0996: "Estudios de la fauna y flora bentónica de los fondos de la zona Sur de la Isla Livingston (Shetland del Sur, Antártida)."

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(3):502–507. 1995.

A new freshwater snail from the Coosa River, Alabama (Gastropoda: Prosobranchia: Hydrobiidae)

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Abstract.—*Pyrgulopsis hershleri,* a new species, is described from the Coosa River, Alabama. It is closely related to three species from the Tennessee River system of northern Alabama. It is distinguished by characteristics of the shell and soft anatomy. The new species was incorrectly identified in earlier literature as *Amnicola olivacea* Pilsbry, 1895 (=*Pyrgulopsis olivacea*).

The hydrobiid genus *Pyrgulopsis* Call & Pilsbry, 1886 includes 66 described and many undescribed species of freshwater snails that are confined to temperate North America (Hershler 1994). Earlier Thompson (1977) reviewed eight eastern North American species under the genus name *Marstonia* Baker, 1926, which Hershler & Thompson (1987) later relegated to junior synonymy of *Pyrgulopsis.* The eastern species form a distinct clade within *Pyrgulopsis* distinguished by characteristics of apical whorl sculpture, operculum indentation, orientation of the terminal lobe on the penis, and aspects of the oviduct coil and the bursa copulatrix duct (Hershler 1994:81). Thompson (1977) noted the existence of an undescribed species in the Coosa River, Alabama, but the material available at the time was insufficient for taxonomic treatment. Recent field studies on the ecology of an endangered snail, *Tulotoma magnifica* (Conrad, 1838) provided the opportunity to collect other mollusks from a limited section of the Coosa River near Wetumpka, Alabama. The undescribed *Pyrgulopsis* was found to be common in this area. Its description is as follows.

Pyrgulopsis hershleri, new species
Vernacular name: Coosa Pyrg

Diagnosis.—A medium-sized species of *Pyrgulopsis* that is about 2.7–2.9 mm long with an elongate-conical shell consisting of about 4.5 strongly arched whorls. The shell is thin and fragile, and lacks a noticeable callus within the aperture. The verge has a square-shaped oblique apical lobe, thereby relating it to a group of species recorded from the Tennessee River system in Alabama (Fig 1). This group includes *Pyrgulopsis argus* (Thompson, 1977), *P. ogmorhaphe* (Thompson, 1977) and possibly *P. olivaceus* (Pilsbry, 1895). The new species is unique within this group by having a pigmented penis filament.

Shell (Figs. 2, 3A–C).—Shell thin, transparent when live; small, about 2.7–2.9 mm long (Table 1); light gray in color, surface glossy when fresh; elongate-conical in shape, 0.62–0.70 times as wide as long; spire slightly convex in outline, equal to or slightly longer than height of aperture, about 0.50–0.58 times length of the shell. Whorls 4.5–4.7; strongly arched but tending to be flattened along the periphery; suture deeply impressed; apical whorl 0.23–0.24 mm in diameter perpendicular to initial suture. Microsculpture on first half of the apical whorl coarsely pitted. Surface of shell smooth; microsculpture consisting of very fine irregular incremental striations and fine sparse spiral striations. Umbilicus narrowly perforate. Aperture slightly oblique, prosocline, lying at an angle of 16–20° to axis of shell in lateral profile; tending to be rhomboid in shape in

Fig. 1. The Coosa River at the type locality of *Pyrgulopsis hershleri,* new species.

most specimens, about 0.81–0.90 times as high as wide; posterior corner bluntly angulate; interior with a thin internal callus along outer and basal margin. Peristome complete across parietal wall; outer lip tending to be flattened compared to contour of earlier whorls; outer lip weakly arched forward in lateral profile. Measurements for the holotype and selected paratype are given in Table 1.

Operculum (Fig. 3D).—Broadly ovate in shape; upper columellar edge slightly indented; paucispiral, consisting of about 2.5 rapidly expanding whorls, nucleus subcentric. Attachment scar very thin and broad, about half the length of the operculum, extending through nucleus; ventral callus of scar weak or absent.

Male (Fig. 3E).—Base of penis compressed and nearly uniform in width. Penis with an enlarged oblique apical lobe that usually has a small terminal gland on its tip. Occasional specimens lack the terminal gland. Other glands are absent elsewhere on

Table 1.—*Pyrgulopsis hershleri,* new species. Measurements in mm based on 13 adult paratypes and the holotype. SL = standard length, SW = standard width, ApH = aperture height, ApW = aperture width, Wh = whorls.

	SL	SW	ApH	ApW	Wh	SW/SL	ApH/SL	ApW/ApL
$\bar{X}$	2.7	1.8	1.2	1.1	4.6	0.66	0.45	0.85
S^2	0.12	0.07	0.06	0.06	0.11	0.03	0.04	0.04
min.	2.5	1.7	1.1	0.9	4.5	0.61	0.42	0.79
max.	2.9	1.9	1.4	1.2	4.7	0.71	0.50	0.90
holotype	2.8	1.8	1.2	1.1	4.5	0.64	0.44	0.85

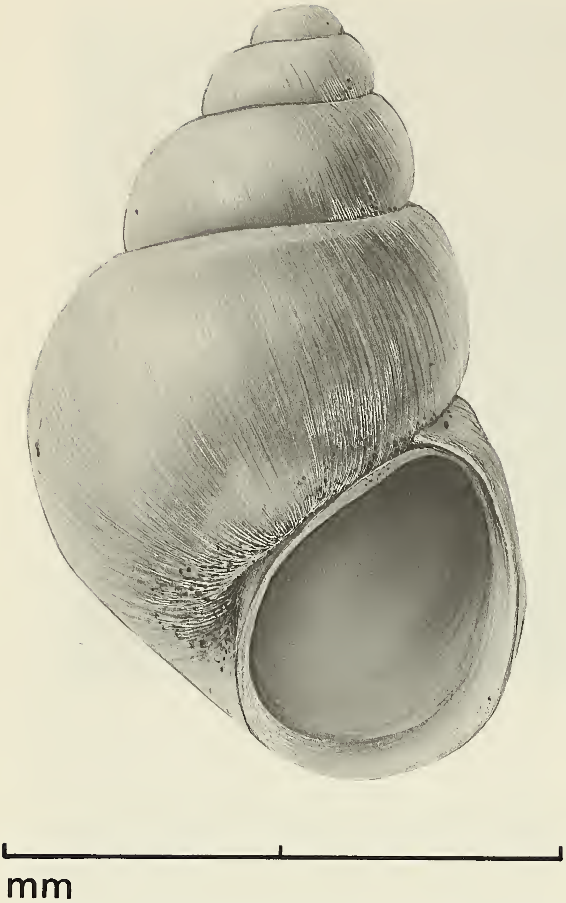

Fig. 2. *Pyrgulopsis hershleri,* new species. Holotype (UF 165788).

surface of penis. Penis filament moderately slender, extending beyond the apical lobe, densely pigmented with melanophores.

Type locality.—Alabama, Elmore County, Coosa River, braided island area above Moccasin Shoals, about 2.2 miles downstream from the Jordan Hydroelectric Dam; T 18 N, R 18 E. Holotype: UF 165788; collected July 24, 1990 by Fred G. Thompson and Malcolm Pierson. Paratype: UF 165789 (9), UF 174347 (30), USNM 860563 (8); UF 165790 (5 in alcohol), same data as the holotype. Corn Creek Shoals, ca 7.0 mi. NW of Wetumpka UF 230595 (22), UF 230735 (10).

The river at the type locality consists of numerous shoals and shallow intermittent pools overlying a substrata of granite-schist outcrops, boulders and gravel. The river is braided with small islands and rock reefs (Fig. 1). This section of the river fluctuates between shallow gentle flow and violent floods that occasionally rise as much as 35 feet above normal water level. Normally the river fluctuates by less than a meter on a daily cycle because of regulated discharge from the Jordan Hydroelectric Dam upstream, but heavy rains may raise the water level to torrential levels that can scour and reorganize the river bed. *Pyrgulopsis hershleri* was found only on rootlets of the bald cypress, *Taxodium disticum,* growing along the edges of quiet shallow pools. Other species of aquatic angiosperms, algae mats and various types of substrata were screened for specimens, but without success.

Distribution.—Specimens are available from two sections in the Coosa River. One lot (UMMZ 161894), contains two specimens from Etowah County, without more exact information. The second section from which specimens are known is the short segment of the river between Jordan Dam and Wetumpka. This portion of river contains numerous intermittent shoals distributed over a distance of about seven miles. This is virtually the only section of the Coosa River that remains in a nearly original state. The rest of the river above and below this section is highly modified by impoundments. The microhabitat from which *P. hershleri* was collected suggests that the species may be present in other sections of the river where there are bald cypress trees along the river edge. Available survey data is insufficient to address this question. Recommendations concerning the conservation status of the snail are not practical until a more intensive search is made elsewhere in the Coosa River. *Pyrgulopsis hershleri* is the only species of the genus known from the Alabama River system.

Remarks.—A popular misconception in

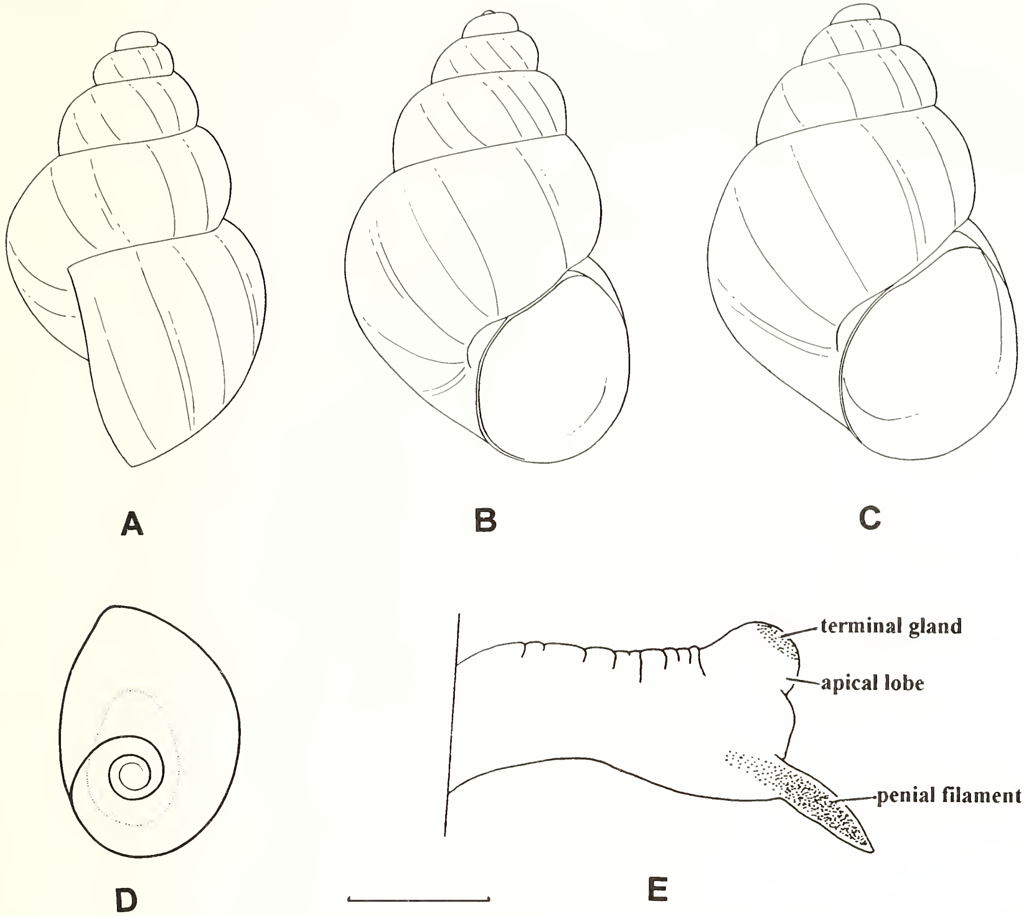

Fig. 3. *Pyrgulopsis hershleri,* new species. A, lateral view of holotype; B–C, paratypes; D, operculum; E, penis. Scale bar = 1 mm for Figs. A–D, 0.75 mm for Fig. E.

malacology is that the freshwater molluscan faunas of the Alabama River system and its principal tributary, the Coosa River, are well known. This misconception is based primarily on the numerous works by Calvin Goodrich who wrote extensively on the Pleuroceridae as well as other prosobranchs (e.g., 1936, 1941, 1944a, 1944b). His studies on the Pleuroceridae are marred by omission of data concerning distributions, taxonomy and the unresolved status of the numerous names that he placed in synonymies. His treatments of other families include many species that are suspect of misidentification. Indeed the systematic status of virtually every species of gastropod recorded from the Coosa requires reexamination. This paper concerns one such species.

Goodrich (1944a:6–10) discussed various hydrobiid gastropods from the Coosa River system, including five species of *Amnicola.* Specimens of the first species, *Amnicola limosa* (Say, 1817) remain as Goodrich assigned them by virtue of the fact that the systematics of the *limosa* species-group are in critical need of review. A different assignment to species could not be made at present. Certainly they are a species of *Amnicola.* The names of two other species recorded by Goodrich, *A. sanctijohannis* Pilsbry, 1899 and *A. augustina* Pilsbry, 1904, are synonyms of *Cincinnatia floridana* (Frauenfeld, 1863), a species endemic to the Florida peninsula. The specimens upon which Goodrich based his records as well as those for "*A.*" *floridana* from the Coosa River have been shown to be incorrectly identified (Thompson 1968:123). Specimens of another species were identified by Goodrich as *Amnicola olivacea* Pilsbry, 1895 (=*Pyrgulopsis olivacea*), which until then was known only from a spring in the Tennessee River system at Huntsville, Alabama. Thompson (1977:123) showed that these also were misidentified. They represent the new species that is the subject of this paper.

Pyrgulopsis hershleri is a small, thin-shelled species with a simple conical shell that has 4.5 or fewer whorls. Its size, shell-shape and aperture-shape distinguish it from other eastern North American *Pyrgulopsis.* Anatomical features are rather monotonously similar among the eastern species compared to western congeners (Hershler 1994). Variation in penial morphology offers some useful comparisons. Penial morphology of *Pyrgulopsis hershleri* is most similar to that of two species from the Tennessee River system, *P. argus* (Thompson, 1977) and *P. ogmorhaphe* (Thompson, 1977). These species are alike by having a well developed oblique apical lobe on the distal left margin of the penis. The right margin of the penis ends with a slender short penis filament. The lobe has a single small terminal apocrine gland. Other glands are absent on the lobe and penis. *Pyrgulopsis hershleri* differs from *P. argus* and *P. ogmorhaphe* by having a pigmented penis filament. The filament is unmarked in the other two species. It differs further from these two species by its smaller size and thinner shell, as well as by shell shape. The adult shell of *Pyrgulopsis ogmorhaphe* is about 4.0–5.1 mm long with about 5.2–5.8 whorls. It is elongate conical-terrete in shape, and it has a more broadly ovate aperture. Juvenile shells are thin and transparent as in *P. hershleri,* but the shell becomes slightly thicker in adults. Like *P. hershleri* the shell is relatively fragile, it does not develop a strong callus on the inner margin of the outer lip, and the outer lip is nearly straight when viewed in latyeral profile. The adult shell of *Pyrgulopsis argus* is about 3.2–3.9 mm long with about 4.6–5.4 whorls. It is ovate-conical in shape with a narrow conical spire. The shell is thick and opaque, and the aperture has a heavy callus ridge along the outer lip. In addition the middle of the outer lip is strongly arched forward as viewed in lateral profile (Thompson, 1977: Fig. 1 B, Fig. 6 B). The shell of *P. hershleri* is similar in shape to that of *P. olivacea* (Pilsbry, 1895). *Pyrgulopsis olivacea* is a much larger species, being 3.9–4.5 mm long; it has 5.0–5.4 whorls, and the inner lip of the peristome is incomplete across the parietal margin. It remains unknown anatomically, and it may be extinct (Thompson 1977:122–124).

Etymology.—I take pleasure in naming this species after Robert Hershler in recognition of his numerous contributions to malacology.

Acknowledgments

This species was rediscovered during the course of an ecology study of the endangered viviparid snail, *Tulotoma magnifica,* a project sponsored by the Alabama Power Company (APC). Assistance in the field was provided by Malcolm Pierson (APC) and Steven P. Christman (Florida Museum of Natural History). The photograph of the Coosa River (Fig. 1) was provided by Malcolm Pierson (Alabama Power Company). The illustration comprising Fig. 2 was rendered by Barbara Harmon, Scientific Illustrator, Florida Museum of Natural History. I am grateful to Kurt Auffenberg and Elizabeth L. Raiser for assistance in the preparation of this paper.

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The genus *Laxus* Cobb, 1894 (Stilbonematinae: Nematoda): Description of two new species with ectosymbiotic chemoautotrophic bacteria

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Abstract.—Two new species of free-living marine nematodes belonging to the genus *Laxus* Cobb, 1894, *L. oneistus* and *L. cosmopolitus,* are described from shallow subtidal sands in the Belize Barrier Reef and the Adriatic Sea. Both species are covered by ectosymbiotic chemoautotrophic sulfur-oxidizing bacteria. The genus *Laxus* is redefined and *Catanema cobbi* Inglis, 1967 transferred to this genus. For *L. oneistus,* biometrical data for juvenile stages are given.

The Stilbonematinae are a subfamily within the family Desmodoridae (order Desmodorida), characterized by an obligate ectosymbiosis with sulfur-oxidizing chemolithoautotrophic bacteria covering their cuticle in a manner that is characteristic for the genus, and even the species (Ott et al. 1991, Polz et al. 1992). The complex glandular sense organ described by Nebelsick et al. (1992) has so far been found only in the Stilbonematinae and is absent in species of other genera within the Desmodoridae, such as *Acanthopharynx* Marion, 1870, *Desmodora* DeMan, 1889 and *Spirinia* Gerlach, 1963 (M. Bauer-Nebelsick, pers. comm.). This is the only morphological autapomorphic character so far known to indicate the monophyly of this taxon. Otherwise, only a few common features unite the group, most of them being negative characters, such as the lack of a buccal armature.

The high variability regarding a number of taxonomically important characters, such as the amphid or the structure of cuticular reinforcement of the anterior end ("cephalic capsule," see Urbancik 1994) complicates assessment of the relationship of the Stilbonematinae with other subfamilies of the desmodorids and between the various known genera. It is, therefore, difficult to decide whether some characters have developed or have been modified (reduced) independently more than once. There is, for example, a tendency towards the development of an enlarged muscular portion at the anterior end of the pharynx, which in the genera *Robbea* Gerlach, 1956 and *Catanema* Cobb, 1920 is highly developed and found in all species, whereas in other genera (*Leptonemella* Cobb, 1920; *Eubostrichus* Greeff, 1869) it is only apparent in a few species. The reduction of the fovea of the amphid from the usual spiral shape to just a porus from which the corpus gelatum usually protrudes seems to have occurred independently at least three times (in the genera *Leptonemella, Stilbonema* Cobb, 1920 and *Catanema*).

In addition, the type species of several genera (e.g., *Laxus, Catanema, Leptonemella, Eubostrichus*) are either inadequately described or have features that are the exception rather than the rule in the subsequently described members of the genus. Liberal synonymization has contributed the rest of the problems.

During studies of the ecology and ecophysiology of the symbiosis (Ott & Novak 1989, Schiemer et al. 1990, Ott et al. 1991) using material from the Caribbean and the

Mediterranean Sea, a number of species new to science have been used and have been designated preliminary names. These animals, designated "sp. 1" or "sp. 2," need to be described and formally named. In addition, collections have been made by the authors in various other locations. Two species from these collections belong—in our opinion—to the genus *Laxus,* which was described by Cobb (1894) from specimens coming from sand in the Bay of Naples (*L. contortus*) and Port Jackson, New South Wales (*L. longus*). Although subsequent authors (Gerlach 1963a, Wieser & Hopper 1967, Hopper & Cefalu 1973) have classified this genus as doubtful, we have reasons to believe that we can assign our animals to Cobb's genus and can attempt a redefinition of this taxon.

Material and Methods

Sediment was collected in buckets by hand and the animals extracted by shaking aliquots of sediment in seawater and decanting the supernatant through a 63-μm screen. In some cases a $MgCl_2$ solution isotonic to seawater was used as an anaesthetic. Quantitative samples were taken with cores having an internal diameter of 3.5 cm down to a depth of 10 cm.

For light microscopy the animals were fixed in 4% formaldehyde, transferred in glycerol:water 1:9 and slowly evaporated before mounting in pure glycerol on microscopic slides. Drawings and measurements were made on a Reichert Diavar, Reichert Polyvar or Leitz Diaplan, all equipped with a camera lucida. Nomarski interference contrast photos were made on the Reichert Polyvar.

For scanning electron microscopy (SEM) specimens were fixed in 2.5% glutaraldehyde in 0.1M sodium cacodylate buffer (pH 7.2) isotonic to sea water and postfixed in 2% OsO_4 over night. After dehydration in a graded ethanol series they were critical point dried, coated with gold and examined with a JEOL JSM-35 CF.

Semithin sections were cut on a Reichert Ultracut from specimens fixed for transmission electron microscopy (TEM) according to Eisenman & Alfert (1982) and embedded in Spurr epoxy resin, stained with toluidin blue and photographed on a Reichert Polyvar.

Type material has been deposited in the Natural History Museum Vienna, Evertebrata Varia Collection (NHMW-EV).

Laxus oneistus, new species

Figs. 1–4, Table 1

Catanema sp. in Ott & Novak 1989, Schiemer et al. 1990, Polz et al. 1992, Ott et al. 1991, Nebelsick et al. 1992.

Holotype: male, NHMW-EV Nr.3406
L = 8.82 mm $a = 193$ $b = 77$ $c = 130$
Allotype: female, NHMW-EV Nr.3407
L = 8.40 mm $a = 168$ $b = 75$ $c = 130$
Paratypes: male, NHMW-EV Nr.3408
L = 6.89 mm $a = 156$ $b = 58$ $c = 99$
male, NHMW-EV Nr.3409
L = 9.94 mm $a = 202$ $b = 76$ $c = 99$
male, NHMW-EV Nr.3410
L = 10.25 mm $a = 195$ $b = 78$ $c = 144$
male, NHMW-EV Nr.3411
L = 9.50 mm $a = 181$ $b = 81$ $c = 140$
female, NHMW-EV Nr.3412
L = 9.79 mm $a = 222$ $b = 73$ $c = 122$
female, NHMW-EV Nr.3413
L = 8.91 mm $a = 175$ $b = 79$ $c = 117$
female, NHMW-EV Nr.3414
L = 9.83 mm $a = 200$ $b = 77$ $c = 145$

Etymology.—from the greek *oneistos,* meaning "most useful," because of its value as an experimental animal during ecological and ecophysiological studies.

Type locality.—Carrie Bow Cay, Belize, Caribbean Sea; coarse, poorly-sorted, coralline sand at the northern tip of the island; 0.2 to 0.5 m depth.

Extremely slender worms, with a cylin-

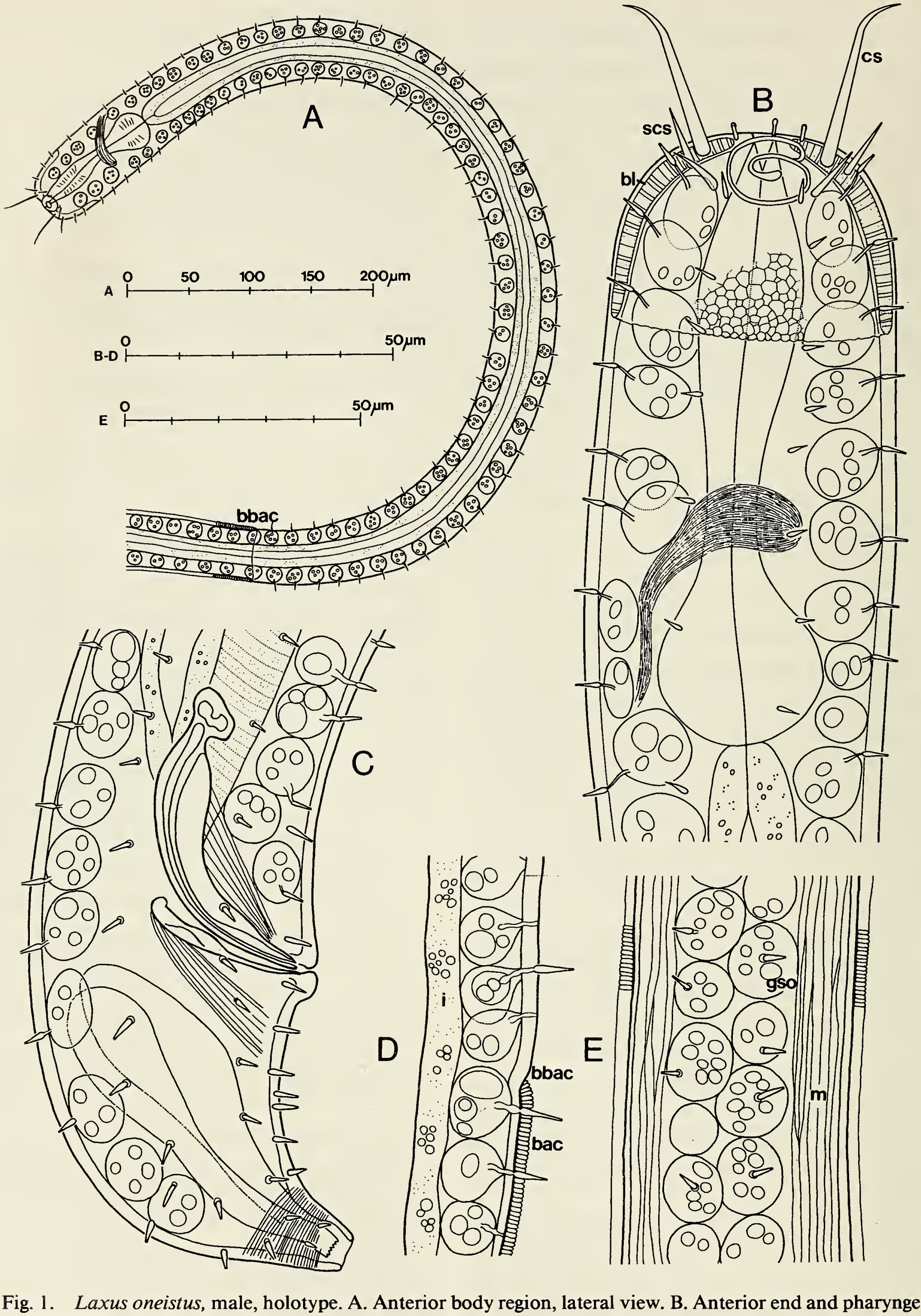

Fig. 1. *Laxus oneistus,* male, holotype. A. Anterior body region, lateral view. B. Anterior end and pharyngeal region. C. Posterior end with spicular apparatus and tail containing caudal glands. D. Beginning of bacterial coat showing reduction of body diameter. E. Midbody region showing longitudinal muscles and two sublateral rows of glandular sensory organs. A–E, lateral views. Abbreviations:am, amphid; bac, ectosymbiotic bacteria;

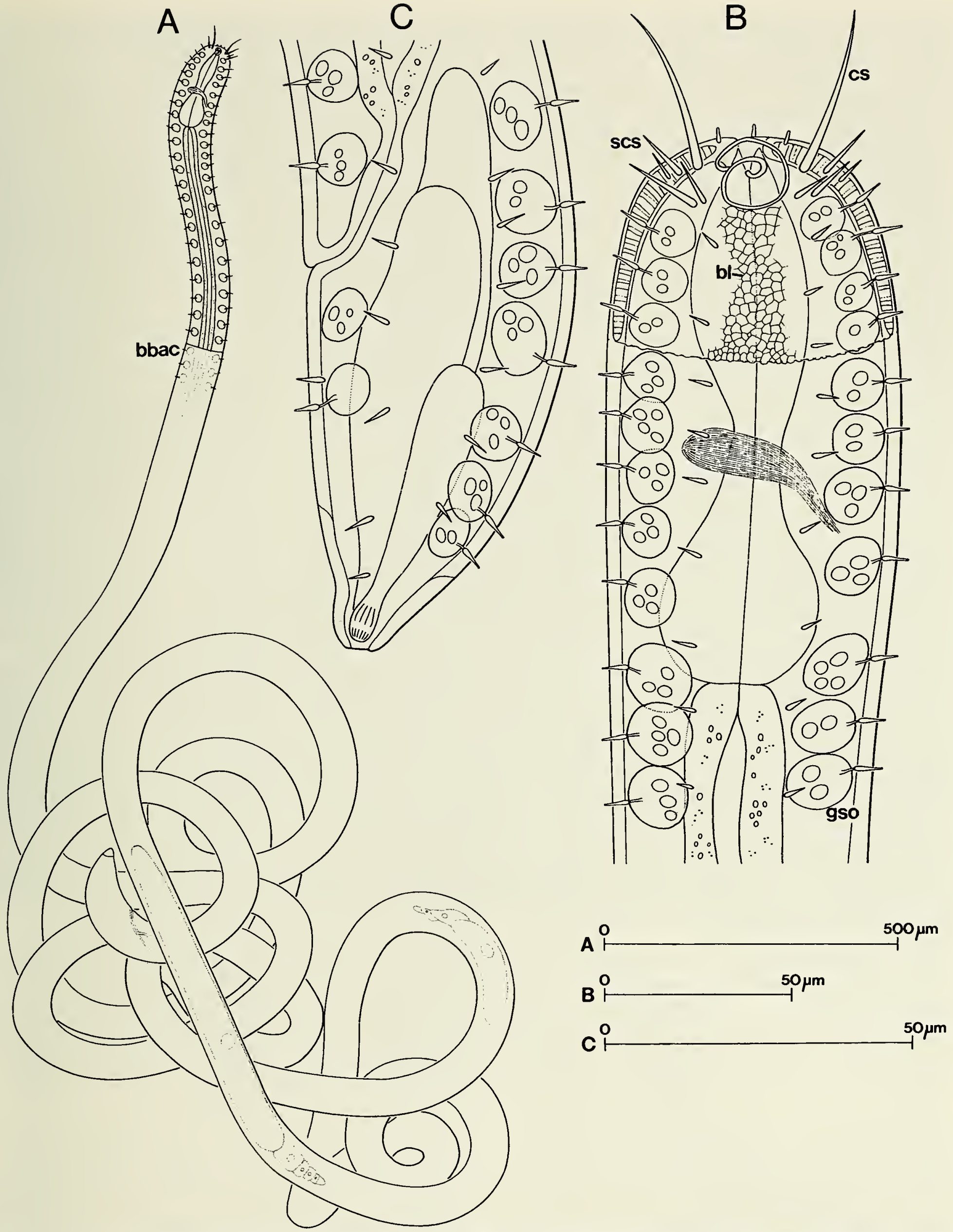

Fig. 2. *Laxus oneistus,* female, allotype. A. Total view. B. Anterior end and pharyngeal region. C. Tail. A–C, lateral views. (For abbrevations see Fig. 1.)

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bbac, begin of bacterial coat; bl, block layer; ca, cardia; cg, corpus gelatum; cgso, concentration of gso; cs, cephalic sensillae; cut, cuticula; de, ductus ejaculatorius: fa, fovea amphidialis; fp, fingerprint region; gr, granules of gso; gso, glandular sense organ; gu, gubernaculum; i, intestine; m, longitudinal muscles; nr, nerve ring; ov, egg; ovr, ovary; re, rectum; rs, receptaculum seminis; scs, subcephalic setae; sp, spiculum; ss, somatic setae; te, testis; ut, uterus; vu, vulva.

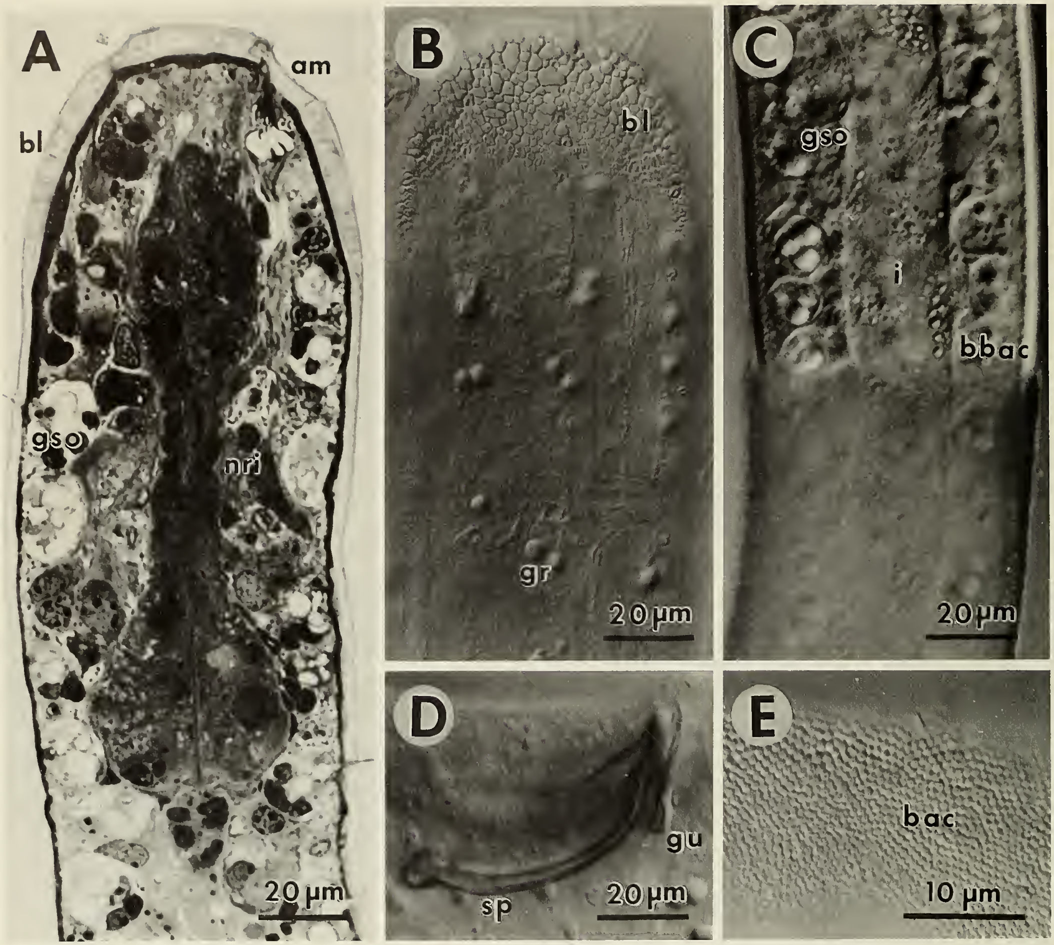

Fig. 3. *Laxus oneistus.* A. Anterior end and pharyngeal region showing the block layer of the cephalic capsule, the tripartite pharynx and several glandular sensory organs. Light microphotograph of a semithin section stained with toluidin blue. B–E. Nomarski interference contrast microphotographs of whole-mounts in glycerol. B. Anterior end showing cephalic capsule with block layers and granules in glandular sense organs. C. Beginning of bacterial coat. D. Spicular apparatus. E. Surface view of bacterial coat. (For abbrevations see Fig. 1.)

drical body. Body covered with radially arranged, rod-shaped bacteria (2.1 × 0.6 μm) except for the anterior region (Figs. 1A, 2A, 3C, E, 4F, G) which appears clear. Bacteria-covered remainder of the body white in incident and dark in transmitted light. Bacteria-free portion is 1010–1090 μm (8–9 times the pharynx length) in males, but only 340–500 μm (3–3.6 times the pharynx length) in females (Fig. 2A). Anterior region containing pharynx slightly swollen (Figs. 1A, B, 2A, B), maximum body diameter at

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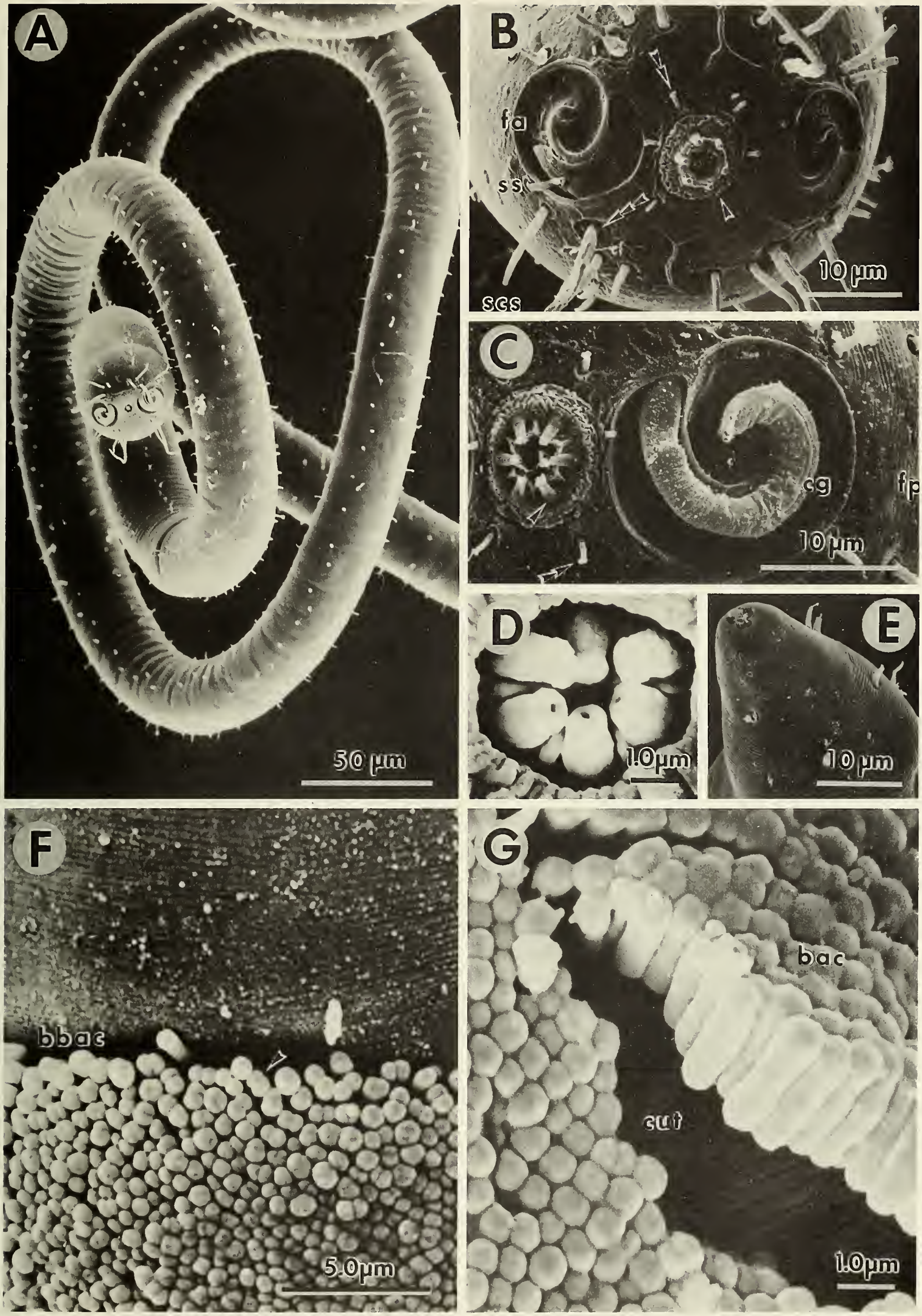
Fig. 4. *Laxus oneistus.* SEM photographs. A. Anterior body region with bacterial coat removed showing rows of somatic setae. B. *En-face* view of anterior end showing the three circles of cephalic sensillae (6 + 6 + 4), 8 subcephalic setae, the first circle of 8 somatic setae and the amphids. The mouth opening protrudes slightly



exposing the first circle of cephalic sensillae. C. *En-face* view of amphid with corpus gelatum surrounded by cuticular "fingerprint region." D. Close-up of first circle of cephalic sensillae showing terminal pores. E. Tip of tail with openings of caudal glands. F. Transition between bacteria-free and bacteria-coated region. G. Rod-shaped bacteria on cuticle. (For abbrevations see Fig. 1.)

Table 1.—Biometrical data for selected characters of the type specimens in *Laxus oneistus* ($n = 10$) and *L. cosmopolitus* ($n = 8$). All measurements are in μm.

Character	*L. oneistus*	*L. cosmopolitus*
Diameter at end of cc.	52.5–66.1	42.4–49.2
Mid-body diameter	44.1–52.5	49.2–55.9
Diameter at anus	50.1–61.0	42.4–56.1
Amphid width	13.6–20.3	11.9–15.3
Amphid (cbd)	27.1–42.4	35.6–37.3
Nerve ring (dfae)	66.1–83.1	84.8–110.2
Nerve ring (cbd)	52.5–69.5	47.5–59.3
Pharynx length	112.0–134.0	141.0–168.0
Bulbus width	28.8–40.7	28.8–32.2
Bulbus (cbd)	52.5–67.8	47.5–54.2
Vulva (dfae)	4290.0–4450.0	3644–5847.0
Vulva (% body length)	51.5–56.0	60.3–72.3
Spiculum length	67.8–89.8	67.8–84.8
Gubernaculum length	32.2–35.6	35.6–50.9
Tail length	64.4–79.7	84.8–113.0

dfae = distance from anterior end.
cbd = corresponding body diameter.

level of nerve ring. Body diameter is practically constant from a short distance posterior to end of pharynx all the way to the anus. This midbody diameter has been used to calculate *a*. Tail is conical, 1.4–1.5 anal diameters long in both sexes, curved ventrally in males (Fig. 1C), nearly straight in females (Fig. 2C).

Cuticle faintly annulated (Figs. 1C, 4E, F, G); annuli 0.25 μm wide. Annulation in the head region irregular forming a characteristic "fingerprint" pattern (Fig. 4C). Cephalic capsule consisting of a special layer of blocks of a homogeneous material, giving the anterior end a reticulated appearance if one focusses slightly below the surface (Figs. 1B, 2B, 3A, B). Tip of tail free of annulations and caudal glands open terminally through a complicated pore complex (Fig. 4E, see also Nebelsick et al. 1992: fig. 2). Cuticle 3 μm thick in bacteria-free body region. Cuticle thins at the beginning of bacterial coat and body diameter becomes smaller to an extent that the bacterial coat does not increase the overall thickness of the animal (Figs. 1D, 4F). Eight rows (four sublateral, four submedian) of somatic setae (5 μm long) in anterior body region (Figs. 1B, 2B) are outlets of glandular sense organs (*gso,* Nebelsick et al. 1992) which lie in double rows in lateral (Fig. 1E), dorsal, and ventral positions. Posterior to end of pharynx ventral and dorsal double rows of *gso* merge gradually into a single row each. Consequently only six rows of setae (four sublateral, one mediodorsal and one medioventral) and *gso* are present over most of the body. Near posterior end the submedian rows become distinct from each other again (Fig. 1C). Cephalic sensillae consist of a circle of six blunt papillae with apical openings surrounding the mouth opening (Fig. 4B, C), often appearing retracted and not visible from the outside except in *en-face* view (Fig. 4D). Second circle formed by six short setae (2.2 μm) with swollen tips, the third by four long, conical setae (32–35 μm). A circle of eight subcephalic setae, 10–13 μm long, apparently not connected to glandular sensory organs is flanked by first circle of regular somatic setae. Two or three more circles of eight setae

Table 2.—*Laxus oneistus.* Distribution of males, females and juveniles in 10 cores.

Core #	Males	Females	Juveniles
1	10	17	6
2	19	24	3
3	1	2	7
4	5	4	4
5	27	26	30
6	6	7	5
7	38	28	6
8	7	6	2
9	1	7	19
10	—	1	4
Total	114	122	86

situated on the reinforced cuticle of the head. Amphids close to the anterior end consisting of a simple ventrally wound spiral.

Buccal cavity small and tubular, tri-partite pharynx consisting of a distinctly swollen corpus occupying almost the anterior half, twice as wide as the isthmus, and a round terminal bulb leading into intestine without cardia (Figs. 1B, 2B, 3A). Isthmus and bulb occupy approximately 30 and 24% of pharynx length, respectively. Nerve ring encircling isthmus approximately at two-thirds of the length of the pharynx. No ventral gland or excretory pore seen.

Single testis in males at 39–46% of body length. Spicula cephalate proximally, arcuate, with a velum (Figs. 1C, 3D), about one anal diameter long (chord) or up to 1.3 anal diameters (arch). Gubernaculum simple, with a dorsally directed apophysis. Ovaries paired, symmetrical, antidromous reflexed, uteri containing extremely long (up to 620 μm) ova. Vulva at 51–56% of body length.

Diagnosis.—Characters of the genus; corpus occupying anterior 46% of the pharynx, twice as wide as the isthmus, bulbus 24% of pharynx length; subcephalic setae ca. 40% of the length of the cephalic setae; annulation very faint; coat of bacterial symbionts begins at a distinct level several hundred microns behind the anterior end.

Biometry of developmental stages.—Ten

Table 3.—*Laxus oneistus.* Biometrical data for juvenile stages (j) 1 + 2, 3 and 4, males, females and pooled adults from the cores (only 61 adults included).

Stage	*n*	Length			a			b			c		
		Mean	*SD*	Range	Mean	*SD*	Range	Mean	*SD*	Range	Mean	*SD*	Range
j 1 +2	39	1.93	0.55	1.08–2.92	51.2	13.1	29.8–88.0	22.1	5.7	13.9–35.6	29.8	6.9	13.6–44.3
j 3	27	3.75	0.55	3.05–4.91	86.8	15.8	68.0–135.0	37.1	6.6	26.6–49.3	53.6	9.2	37.2–71.0
j 4	20	5.81	0.50	5.09–6.86	124.0	16.2	93.7–154.1	54.4	5.7	44.1–64.4	78.6	16.8	46.8–109.4
Males	21	6.86	0.90	5.36–8.71	134.3	18.1	101.6–161.1	61.7	9.3	42.4–75.9	93.0	12.8	75.8–125.3
Females	40	7.19	1.06	5.18–9.36	130.9	22.2	91.9–176.4	66.6	14.2	36.4–99.0	94.0	19.2	56.0–132.8
Adults	61	7.08	1.02	5.18–9.36	132.0	20.9	91.9–176.4	64.8	12.7	36.4–99.0	93.7	17.2	56.0–132.8

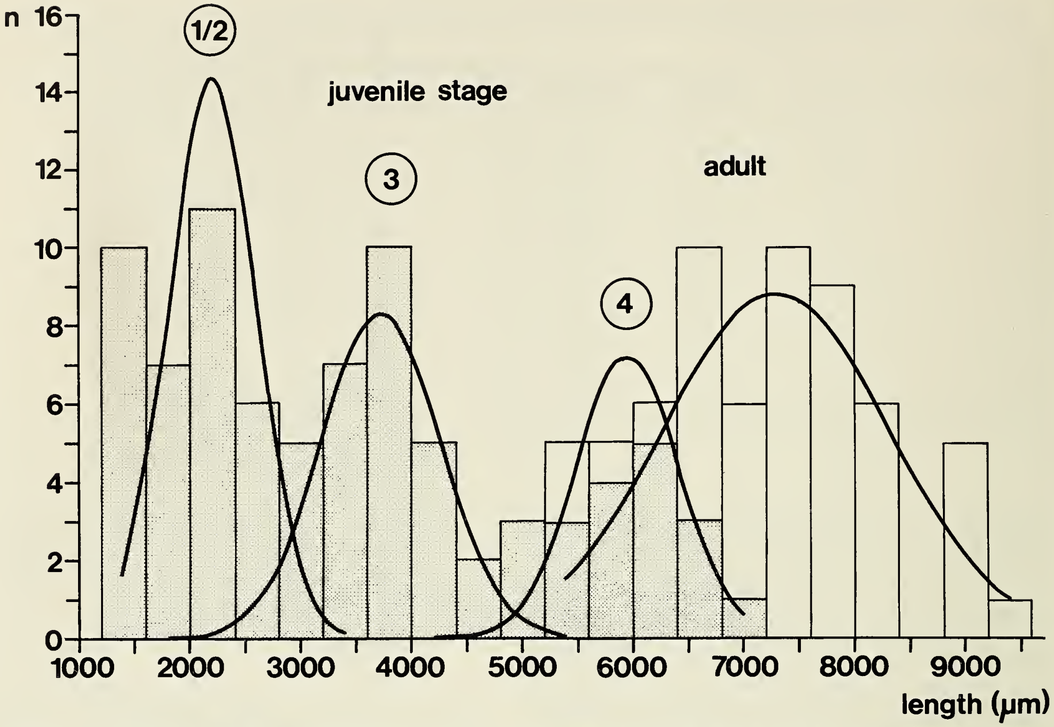


Fig. 5. *Laxus oneistus.* Size-frequency plot of juveniles (shaded) and adults (white). Separation of juvenile stages 1/2, 3 and 4 by fitting normal distributions using Bhattacharaya's method (Elefan).

quantitative cores taken in 1991 contained a total of 322 specimens, 236 of which were adults (114 males, 122 females) (Table 2). The 86 juveniles ranged in size from 1.1 mm to 6.9 mm (Table 3). A size frequency plot (Fig. 5) revealed four modes among the juveniles. Bhattacharaya's method for separating frequency distributions, however, gave only three normal distributions. We interpret these as the pooled stages 1 and 2, stage 3 and stage 4 juveniles. The stage 4 juveniles length distribution strongly overlaps with that of the adults. The statistical method used was unable to separate stage 4 juveniles by length from the adults, which were identified by the presence of fully developed gonads and treated separately.

Plotting *a* (body length divided by maximum body width) against length (Fig. 6) shows that juveniles become progressively more slender during growth. With the adult molt the worms become stouter, especially the females due to the development of the gonads. The midbody region elongates more strongly during growth than either the pharynx and the tail as is evident from plots of *b* (body length divided by pharynx length) or *c* (body length divided by tail length) against body length (Figs. 7, 8). The index c shows little correlation to body size in adult males probably due to different degrees of curvature of the tail.

Remarks.—Laxus oneistus is extremely common in subtidal coarse sands in the Belize Barrier Reef system, from just below the waterline to at least 7 m depth. It inhabits the deeper, microxic to anoxic sediment layers. By migration through the chemocline it exposes its symbiontic bacteria alternately to sulfide and oxygen. The

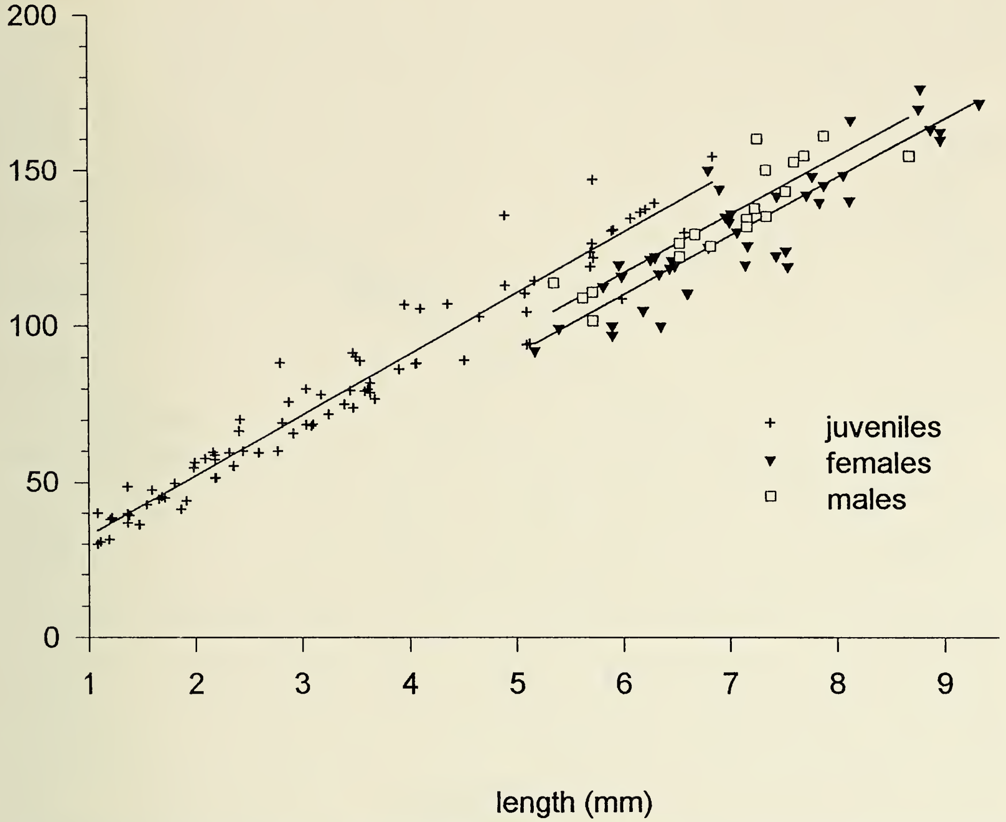


Fig. 6. *Laxus oneistus.* Biometry of development: Relationship between body length and ratio *a* (body length/maximum body width). Linear regression.

chemoautotrophic bacteria constitute probably the main bulk of the food for these worms (for details of the biology see Ott and Novak, 1989 and Ott et al., 1991). When extracted from the sediment it tends to curl up its body except for the anteriormost part (Fig. 2A). It is very thigmotactic and in dishes forms tightly knotted aggregations with conspecifics or other long nematodes from which only the anterior parts protrude executing elegant undulating movements.

Laxus cosmopolitus, new species

Synonym.—"undescribed genus from the Adriatic Sea" in Ott et al. 1991, "undescribed genus from the Mediterranean" in Polz et al. 1992, *Eubostrichus exilis* (Cobb, 1920) in Gerlach 1963a, probably *E. exilis* (Cobb, 1920) in Gerlach 1964

Holotype: male, NHMW-EV Nr.3415
L = 6.53 mm *a* = 133 *b* = 46 c = 59
Allotype: female, NHMW-EV Nr.3416
L = 7.71 mm *a* = 138 *b* = 45 *c* = 76
Paratypes: male, NHMW-EV Nr.3417
L = 6.01 mm *a* = 115 *b* = 42 *c* = 57
male, NHMW-EV Nr.3418
L = 6.99 mm *a* = 128 *b* = 45 *c* = 83
female, NHMW-EV Nr.3419
L = 7.29 mm *a* = 148 *b* = 48 *c* = 66
female, NHMW-EV Nr.3420
L = 6.22 mm *a* = 122 *b* = 42 *c* = 73
female, NHMW-EV Nr.3421

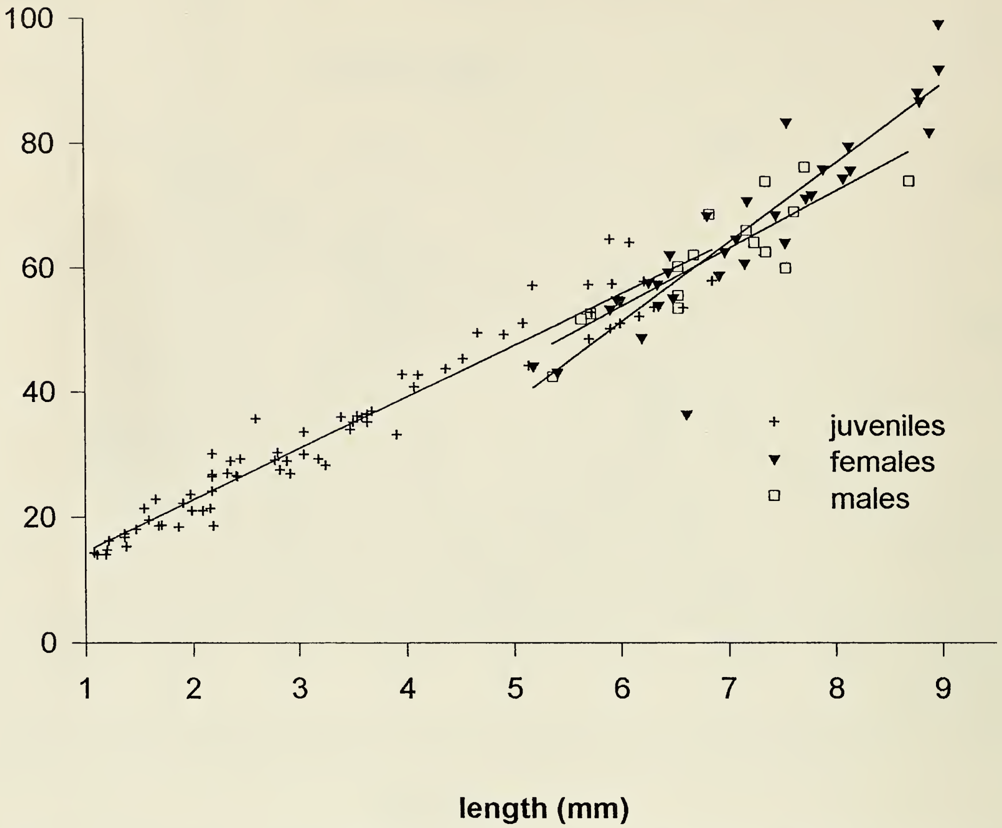


Fig. 7. *Laxus oneistus.* Biometry of development: Relationship between body length and ratio *b* (body length/pharynx length). Linear regression.

L = 7.97 mm a = 164 b = 42 c = 83
female, NHMW-EV Nr.3422
L = 9.07 mm a = 178 b = 61 c = 80

Etymology.—from the greek *kosmopolites,* meaning "citizen of the world," because of its wide distribution.

Type locality.—Bay of Vestar south of Rovinj, Croatia, Adriatic Sea, Mediterranean; moderately well sorted coarse calcareous sand in 3–4 m depth.

Cylindrical, long, robust worms (Figs. 9A, 10A), body completely covered by radially arranged rod shaped bacteria (1.8 × 0.7 μm) except for head and tip of tail (Figs. 9B, C, 10B, C, 11C–F, 12A, D), bacteria appearing white in incident and dark in transmitted light.

Cuticle distinctly annulated; annuli 1.3 μm wide; anterior end with "fingerprint"-pattern and cephalic capsule composed of a block layer similar but coarser than in the foregoing species. Eight rows of somatic setae (5 μm long) distinct in cervical region. After end of pharynx the two subventral and the two subdorsal rows merge as in the foregoing species. Males with a region of especially dense and large glandular sense organs (*gso*) ventrally starting at level of the end of pharynx extending 1.27 mm posteriad (Figs. 9A, 11A), a similar region of dense *gso* (0.9 mm long) in front of the cloaca (Fig. 9A). In females the *gso* denser in vulvar region than in remainder of body (Fig. 10D).

Arrangement of cephalic sensillae is similar to that in *L. oneistus.* First circle of six

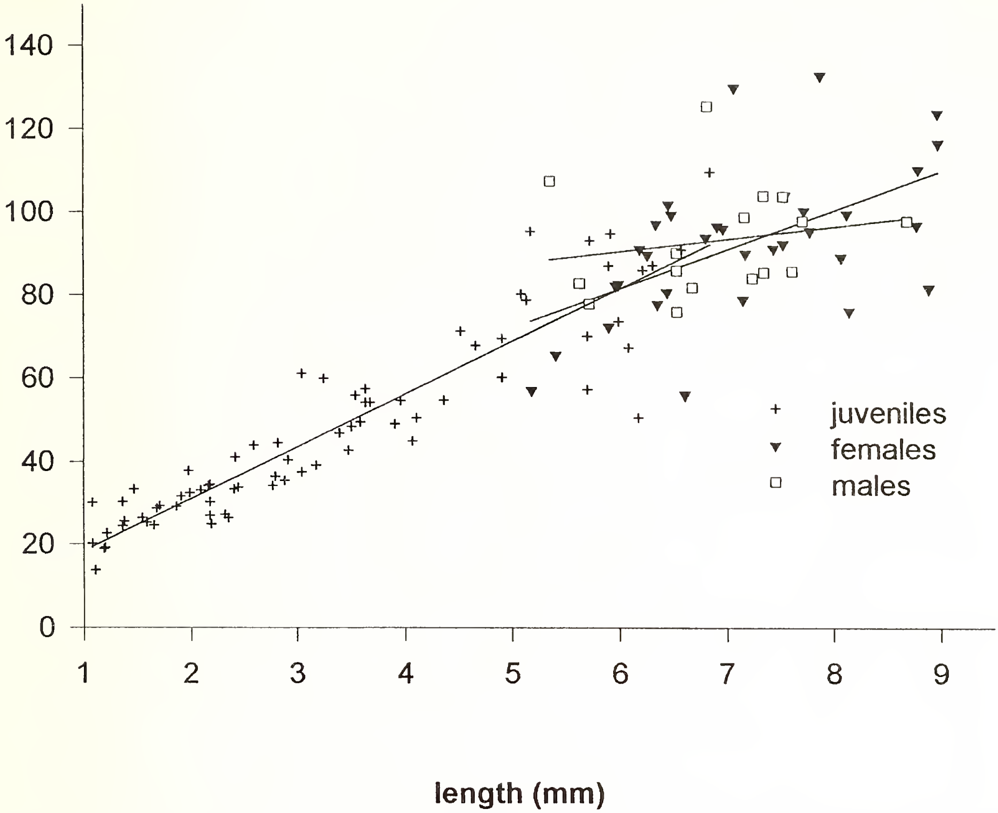


Fig. 8. *Laxus oneistus.* Biometry of development: Relationship between body length and ratio *c* (body length/tail length). Linear regression.

blunt papillae is in most cases retracted into mouth, second circle again consisting of six short setae with swollen ends (Figs. 12A, B). Four setae of the third circle 26–29 μm long. Eight subcephalic setae only slightly longer (7–8 μm) than setae of following three circles situated on cephalic capsule. Amphids ventrally wound spirals with 1.5 turns and deeply incised fovea (Fig. 12B).

Pharynx only slightly swollen in anterior half, forming a corpus 30–50% wider than isthmus, terminating in a round to pyriform bulb. Small cardium projects into intestine. Nerve ring encircling the isthmus. No excretory system seen.

Single testis in males begins at 38% of body length. Spicula 1.2 (chord) or 1.4–1.6 (arch) anal body diameters long, cephalate proximally, with a velum. Gubernaculum, with dorsally directed apophysis. Female gonads paired, ovaries symmetrical antidromous reflexed. Distinct *receptacula seminalis* visible at junction of ovaries and uteri. Vulva at 60–72% body length.

In addition to the type locality, *L. cosmopolitus* was also found near the Island of Tubya Al-Bauda, Bay of Safaga (Egypt, Red Sea) and at Biyadoo (Maldive Islands, Indian Ocean). The animals from these localities agree in most characters with the Mediterranean specimens. There are, however, a few consistent differences. With 6 to 9 mm body length ($\bar{X} = 7.22 \pm 1.0$ mm, $n = 8$) the specimens from Rovinj are significantly larger than those from Safaga (4.6–7.4 mm, $\bar{X} = 5.94 \pm 0.9$ mm, $n = 10$) and

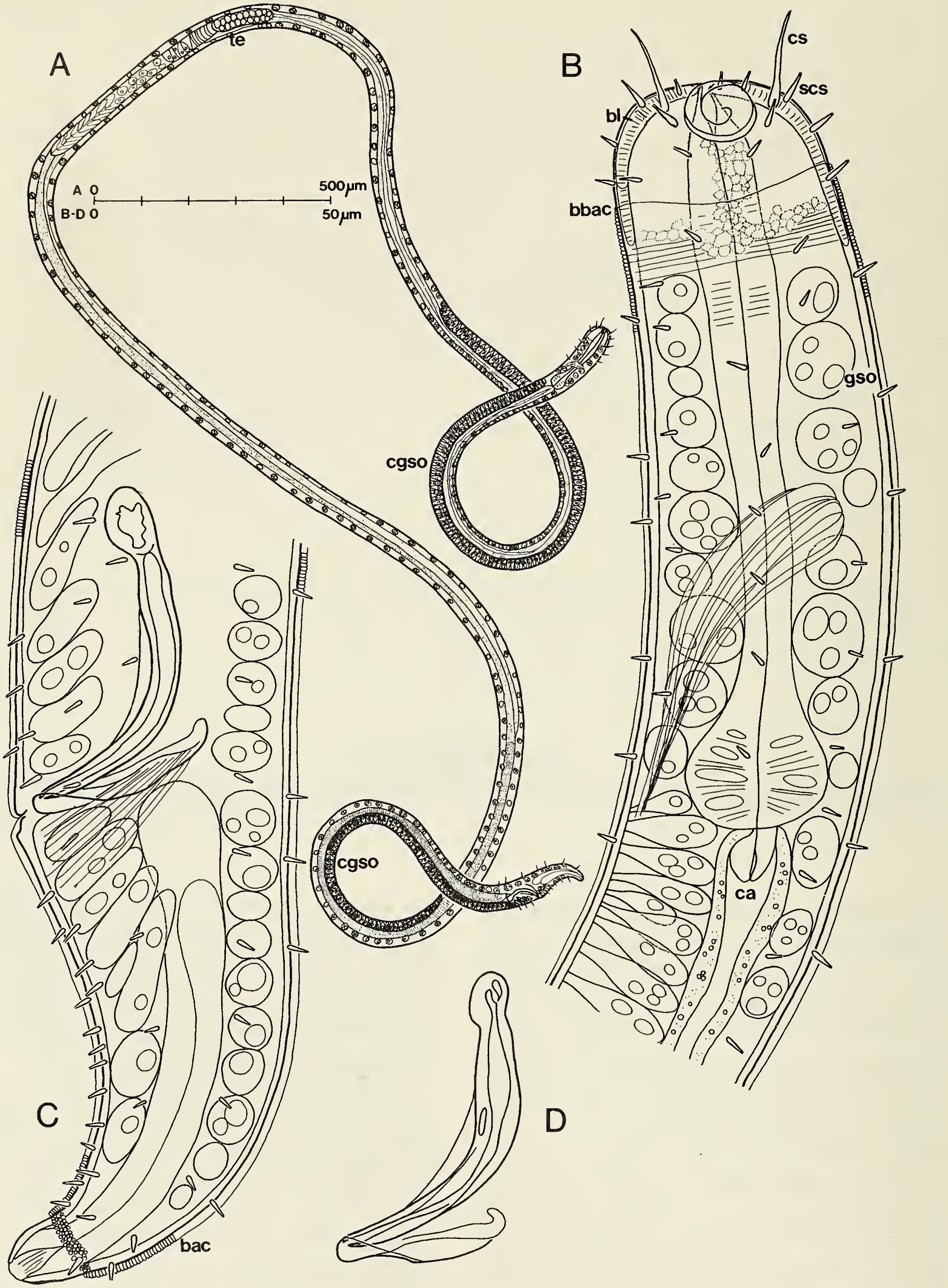


Fig. 9. A–C. *Laxus cosmopolitus,* male, holotype. A. Total view showing concentrations of *gso* ventrally in postpharyngeal and preanal region. B. Anterior end and pharyngeal region, showing cephalic capsule and pharynx. C. Posterior end with spicular apparatus and tail with caudal glands. D. Male, paratype. Spicular apparatus. A–D, lateral views. (For abbrevations see Fig. 1.)

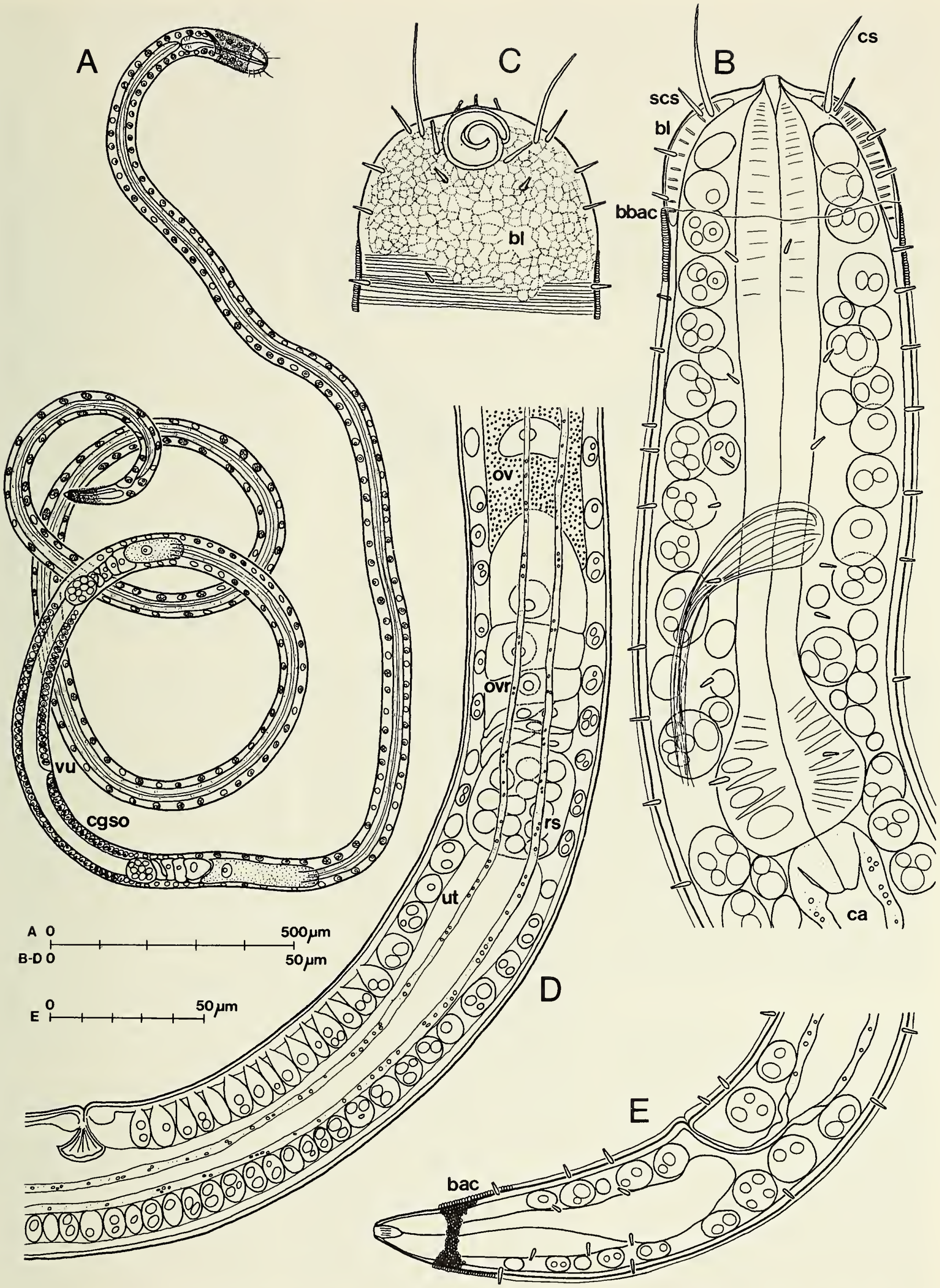


Fig. 10. *Laxus cosmopolitus,* female, allotype. A. Total view. B. Anterior end and pharyngeal region, optical section. C. Head, surface view showing amphid and honeycomb pattern of block layer. D. Vulvar region and part of anterior ovary. E. Tail with caudal glands. A–E, lateral views. (For abbrevations see Fig. 1.)

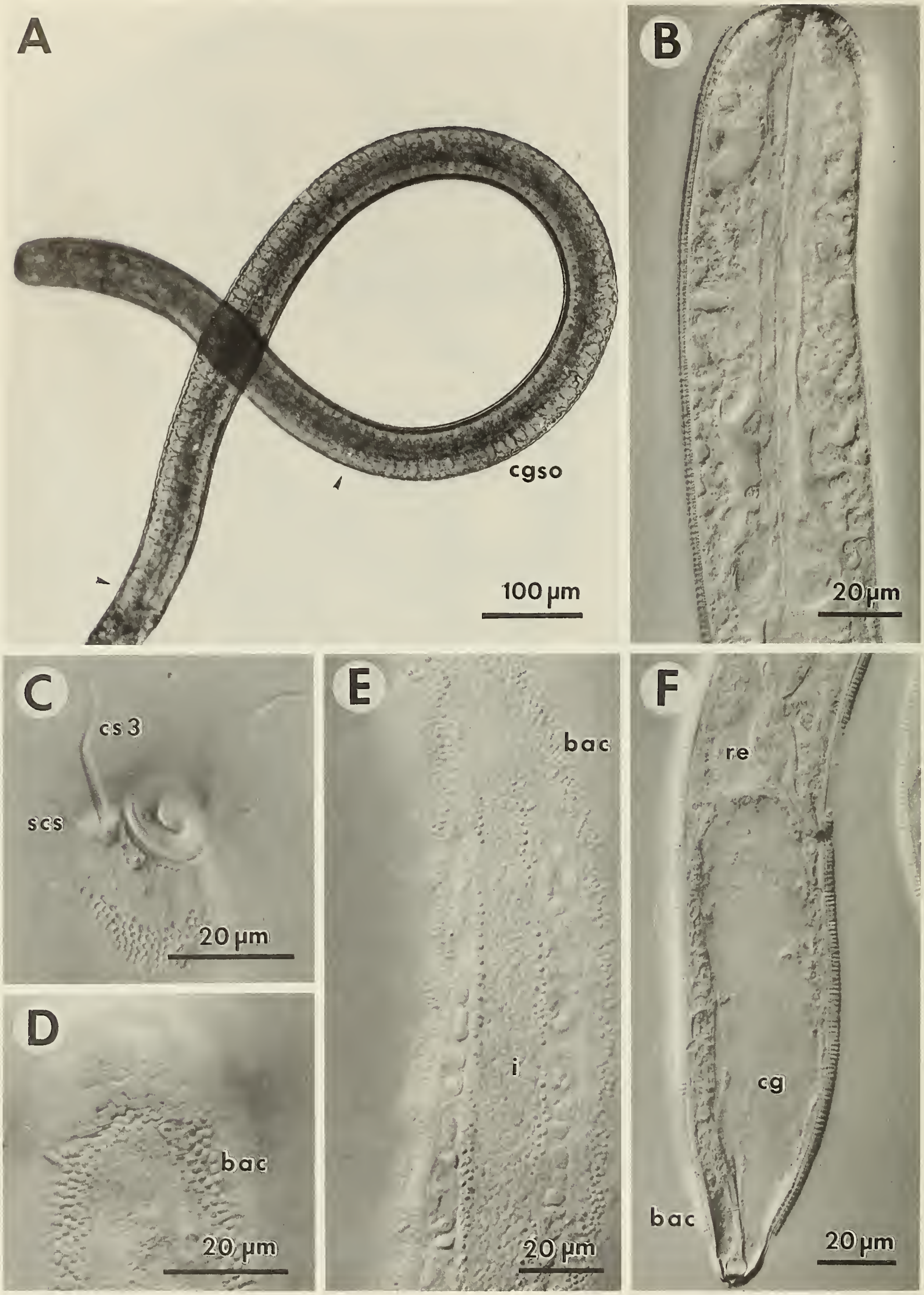


Fig. 11. *Laxus cosmopolitus,* Nomarski interference contrast microphotographs. A. Anterior body region showing concentration of *gso.* B. Anterior end and pharyngeal region. C. Head showing amphid, block layer of cephalic capsule and beginning of bacterial coat. D. Posterior end of cephalic capsule, annulated cuticle and microbial coat. E. Optical section through midgut region showing gut filled with bacteria similar to the ecto-symbiotic bacteria on the cuticle. F. Posterior end of female showing rectum, anus and caudal glands. (For abbrevations see Fig. 1.)

the Maldives (3.98–6.6 mm, $\bar{X} = 4.95 \pm 0.85$ mm, $n = 8$) (Kruskal-Wallis one-way analysis by ranks, $P = 0.005$, pairwise test of significance of differences after Conover 1980). The tail is strongly curved ventrally in males from Rovinj and regularely conical, in the Red Sea specimens it is almost straight, conical with a distinctly set-off cylindrical end part, whereas in the Maldives the tail is almost cylindrical over most of its length and narrows abruptly only near the tip. The two rows of subventral setae on the male tail are slender in the Rovinj specimens, stouter in those from the Red Sea and triangular thorns in males from the Maldives. The spicula in the Maldive males are more distinctly cephalate, less curved and have only a small velum (Fig. 13). Additional specimens provided by G. Boucher (Paris) from New Caledonia resemble the Red Sea animals.

Diagnosis.—Characters of the genus; corpus occupying 50% of the length of the pharynx, being 30–50% wider than the isthmus (34% of pharynx length), bulbus small (16%); subcephalic setae ca. 30% of length of cephalic setae; annulation relatively coarse (1.3 μm); concentration of glandular sense organs ventrally, in males in the postpharyngeal and praecloacal region, in females in the pre- and post-vulvar region; bacterial coat extends into region of cephalic capsule.

Remarks.—*Laxus cosmopolitus* is regularely found in coarse subtidal sand at the type locality and in several locations in the vicinity of Rovinj (Bay of Cisterna, Punta Croce). It is, however, never abundant. Both the Red Sea and the Maldive Island material comes from shallow subtidal coralline sand. The association of the worms with sulfidic sediments and the similarity between the bacteria found in the gut and on the cuticle together with their ultrastructure suggest a similar biology as in *L. oneistus.*

Discussion

The genus *Laxus* was proposed by Cobb in 1894 for two nematodes collected from such different regions of the world as the Gulf of Naples and the Australian coast. Although the description of the type species, *L. contortus,* is on the basis of a female only and is not accompanied by a figure, it is sufficiently precise to warrant the assumption, that it is congeneric with the second species, *L. longus.* In fact, Cobb himself designated the latter as the genotype in Stiles & Hassal (1905) (see also Baylis & Daubney 1926). This allows an identification on the genus level with our species described above. In particular, the genus *Laxus* is recognized by the special structure of the tripartite pharynx with its swollen corpus, which is not as clearly set off as in the genera *Catanema* Cobb, 1920 or *Robbea* Gerlach, 1956; the lack of cervical papillae (which distinguishes it from *Robbea*); and the spicular apparatus with a large cephalate spiculum having a velum in its distal half and a simple, slightly curved gubernaculum with a straight, dorsally directed apophysis (which distinguishes it from *Catanema*). Additional characters are the four long setae of the third circle of cephalic sensillae, which are flanked by shorter setae ("two setae of unequal size placed on each submedian line," Cobb 1894:415) and the presence of additional setae adding up to the eight elongated setae that constitute the first circle of somatic setae; the apparent lack of an excretory system; the shape and position of the amphid; the shape of the tail and the prominent rows of subventral setae pre- and postanally. Although none of the forgoing characters is unique for the genus, the combination is. Cobb's fig. 11/II also indicates the reinforcement of the cephalic cuticle by the block layer.

Laxus septentrionalis, described by Cobb in 1914 from Antarctica, however, does certainly not belong to this genus. Neither does the conical head nor the amphid depicted in the description resemble the foregoing species. The pharynx ("oesophagus" in Cobb's description) is explicitely described as "cylindroid," there is a distinct excretory

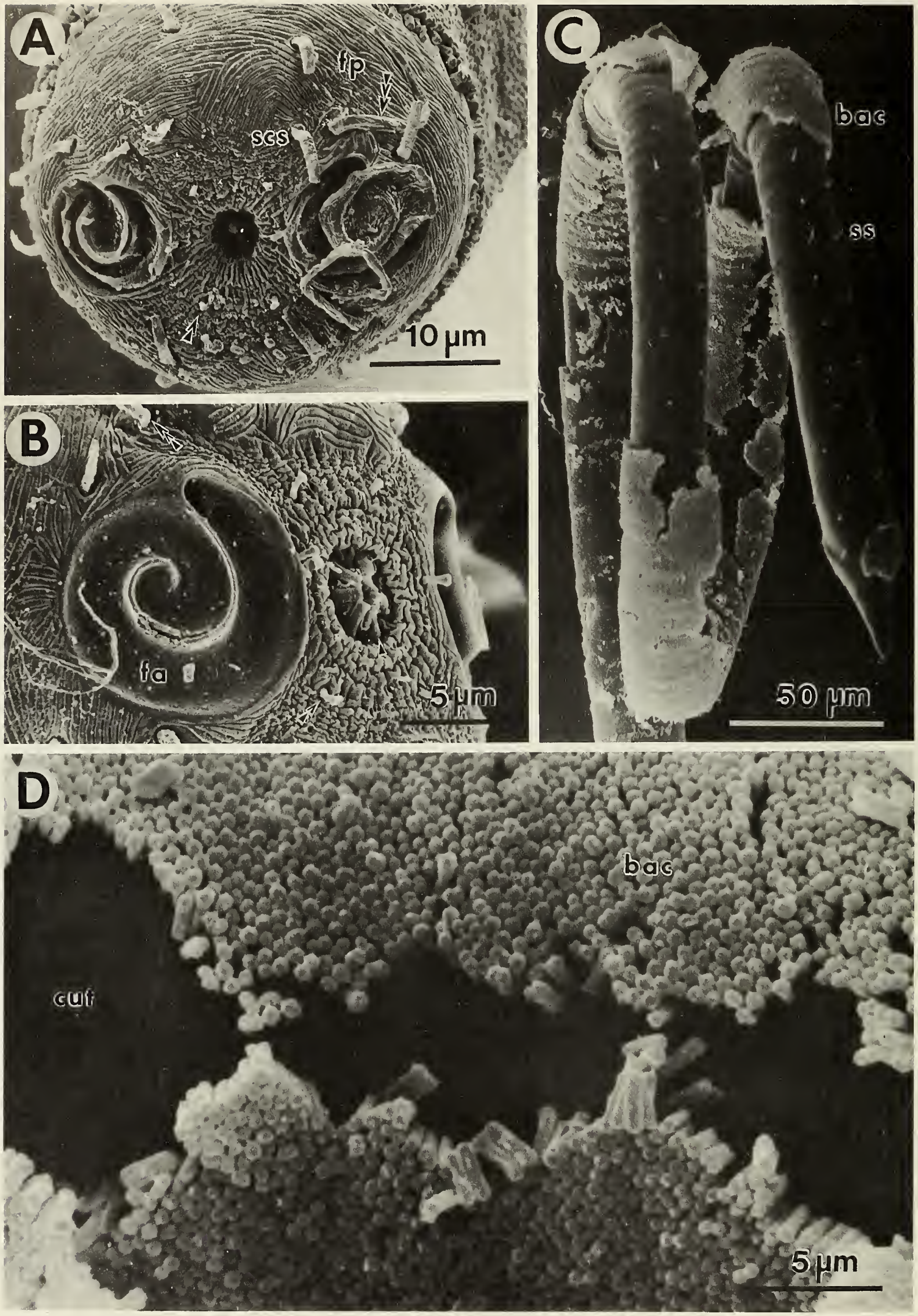


Fig. 12. *Laxus cosmopolitus,* SEM microphotographs. A. En-face view of anterior end showing fingerprint region, amphids, mouth opening surrounded by second circle of six cephalic sensillae (double arrow), third circle of four *cs* (triple arrow) and subcephalic setae. Note that bacterial coat reaches the fingerprint region. B. Close-up of amphid and mouth opening with first (single arrow), second (double arrow) and third circle (triple arrow) of *cs.* C. Posterior end of female showing rows of somatic setae. The disruption of the bacterial coat is an artefact

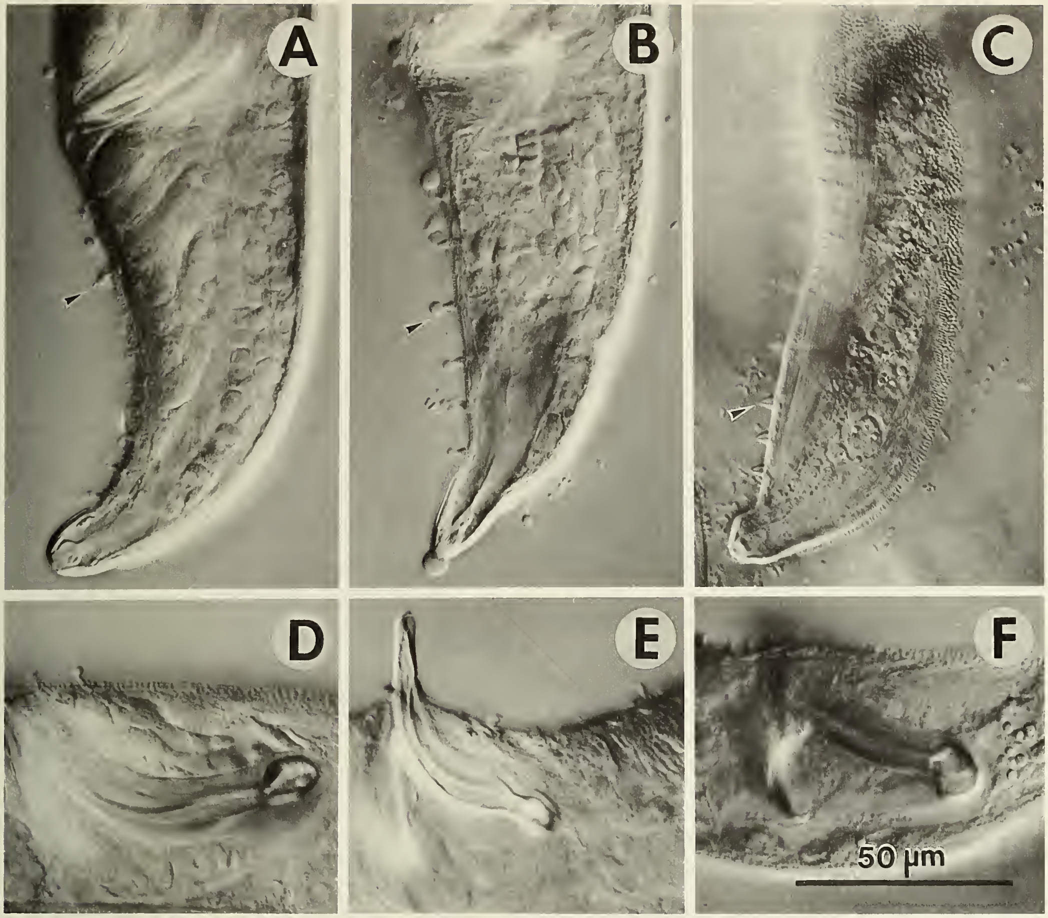


Fig. 13. *Laxus cosmopolitus,* Nomarski interference contrast microphotographs. Variations in the shape of the tail, postanal setae and spicular apparatus between male specimens from the Mediterranean Sea (A, D), the Red Sea (B, E) and the Maldive Islands (C, F). (For abbrevations see Fig. 1.)

system, and the gubernaculum is described to have an apophysis perpendicular to "the part which is applied to the spicula."

In contrast, *Catanema cobbi* Inglis, 1967 certainly has to be transferred to the genus *Laxus* on the basis of the special structure of the pharynx and the distinct block layer reinforcing the head cuticle. Inglis also mentiones that the annulation extends over the region of the block layer. It is very similar to *L. longus* because of the length of the first circle of eight setae and the relative proportions of the three regions of the pharynx, but differs in the number of postcloacal subventral setae (or "tube-like organs"). In the present state of knowledge and in the absence of type specimens it is better to refrain from synonymizing these two species.

The genus *Laxus* may be redefined as follows: Desmodoridae, Stilbonematinae, cu-

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←

of preparation. D. Close-up of bacterial coat in the midbody region showing closely packed rods standing perpendicular to the annulated surface of the cuticle. (For abbrevations see Fig. 1.)

ticle finely annulated, with "fingerprint" pattern on the anterior end. In this region a cephalic capsule is developed by a special "block-layer" inserted between the median and basal zone of the cuticle; pharynx tripartite, with a swollen corpus that is not distinctly set off from the isthmus; spicula curved, cephalate; gubernaculum without apophysis, straight to slightly S-shaped. Symbionts are rod-shaped bacteria arranged in a single layer in which the longitudinal axis of the microorganisms is perpendicular to the cuticle surface.

The following species belong to the genus: *Laxus longus* Cobb, 1894 (type species), *Laxus contortus* Cobb, 1894, *Laxus cobbi* (Inglis, 1967) (syn. *Catanema cobbi* Inglis, 1967), *Laxus oneistus* new species., *Laxus cosmopolitus* new species.

It is peculiar, that neither Cobb nor Inglis—both being keen observers—mention the bacterial ectosymbiosis. Most of the stilbonematids that have been described previously and practically all specimens in our collection (comprising all genera so far described) show the conspicuous and species-specific coat of microorganisms. Also, in Cobb's descriptions of the type species of the genera *Stilbonema, Leptonemella, Catanema* and *Laxonema* (Cobb 1920), no mention is made of the ectosymbionts. Especially in *Stilbonema* the multilayered bacterial coat cannot be overlooked. Since no type material exists, we cannot be sure whether the bacterial ectosymbiosis is absent in these species (which seems improbable), whether the bacteria had been lost during preparation, or whether they were deliberately ignored because the authors believed them to be contaminants.

The small proportion of juveniles in the collection is consistent with other indications of a slow development, low reproduction rate and longevity of adults in *L. oneistus*. Both juveniles and adults could be kept alive for up to three weeks in dishes during which time neither molting or egg-laying was observed.

There is a notable difference between the mean body length of the type specimens and the adults from the quantitative cores, the latter being significantly smaller. This could be an indication of seasonal or year to year variation in size (the type specimens were collected in May 1989, the cores were taken in February 1991). Another explanation could be an unconscious bias when choosing type specimens from qualitative collections where larger "representative" specimens may be preferentially selected. Therefore, size differences between haphazardly selected material and type specimens should not be overrated.

Acknowledgments

We thank Werner Urbancik, Rudolf Novak and Martin Polz for providing several SEM pictures and Hubert Keckeis for help with the biometrical analysis. This study was supported by grants #7814 BIO and #9189 BIO of the FFWF (Austria) and grants from the CCRE project of the National Museum of Natural History, Washington, D.C. The generous help of Klaus Ruetzler and the staff of the Carrie Bow Cay Laboratory is gratefully acknowledged. Collections in the Adriatic were made possible through the help of the Center for Marine Research, Rovinj, Croatia. This is contribution #438 from the Carrie Bow Cay Laboratory (CCRE).

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Neotropical Monogenoidea. 26. *Annulotrematoides amazonicus*, a new genus and species (Dactylogyridae: Ancyrocephalinae), from the gills of *Psectrogaster rutiloides* (Kner) (Teleostei: Characiformes: Curimatidae) from the Brazilian Amazon

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Abstract.—Annulotrematoides, a new genus, is proposed to include species with the following characteristics: presence of a longitudinal ventral groove on the posterior trunk; incomplete tegumental annulations; a vaginal aperture on the left margin of the trunk; overlapping gonads; dorsal and ventral anchor-bar complexes; 14 hooks with ancyrocephaline distribution; ventral bar with anteromedial process; and articulated accessory piece and male copulatory organ. The first two characters are unique to the new genus; *Annulotrematoides* is monotypic. *Annulotrematoides amazonicus,* new species, is described from the gills of *Psectrogaster rutiloides* (Kner) from Furo do Catalão near Manaus, Amazonas, Brazil.

Although phylogenetic analyses are wanting, current evidence suggests that some Monogenoidea from Neotropical fishes have ancient evolutionary links to those of Africa. Gusev (1976a) considered *Jainus* Mizelle, Kritsky & Crane, 1968, from Neotropical Characiformes to be a senior synonym of the Ethiopian *Characidotrema* Paperna & Thurston, 1968, and used this synonymy in part to support a postulated relationship of the two biogeographical faunas. While Kritsky et al. (1987) did not recognize the synonymy, they indicated that the two genera may be sister taxa based on common morphological features of the haptoral armament. Kritsky & Kulo (1992) suggested that a Neotropical-Ethiopian link might also be supported by relationships of species of the Neotropical *Trinigyrus* Hanek, Molnar & Fernando, 1974, the marine *Hamatopeduncularia* Yamaguti, 1953 and *Chauhanellus* Bychowsky & Nagibina, 1969, and the Ethiopian *Schilbetrema* Paperna & Thurston, 1968, all parasites of siluriform fishes. In the present paper a new species of *Annulotrematoides,* new genus, is figured and described from Neotropical Characiformes. This species appears to have an evolutionary relationship with species currently included in *Annulotrema* Paperna & Thurston, 1968, from Ethiopian characiforms.

Materials and Methods

Hosts, *Psectrogaster rutiloides* (Kner), were collected by seine from the Furo do Catalão (Amazon River System) near Manaus, Amazonas, Brazil (5 January 1989). Methods of parasite collection from the hosts' gills, preparation of the helminths for study, measurement, and numbering of hook pairs are those of Kritsky et al. (1986). Terminology is that of Mizelle & Kritsky (1967) and Kritsky & Mizelle (1968). Measurements, in μm, include the average followed by the range and number (n) of structures measured in parentheses. Type specimens are deposited in the helminthological collections of the Instituto Oswaldo Cruz, Rio de Janeiro, Brazil (IOC), the United States National Museum, Beltsville, Maryland (USNPC), the University of Nebraska State Museum, Lincoln, Nebraska (HWML).

Class Monogenoidea Bychowsky, 1937
Order Dactylogyridea Bychowsky, 1937
Dactylogyridae Bychowsky, 1933
Ancyrocephalinae Bychowsky, 1937
Annulotrematoides, new genus

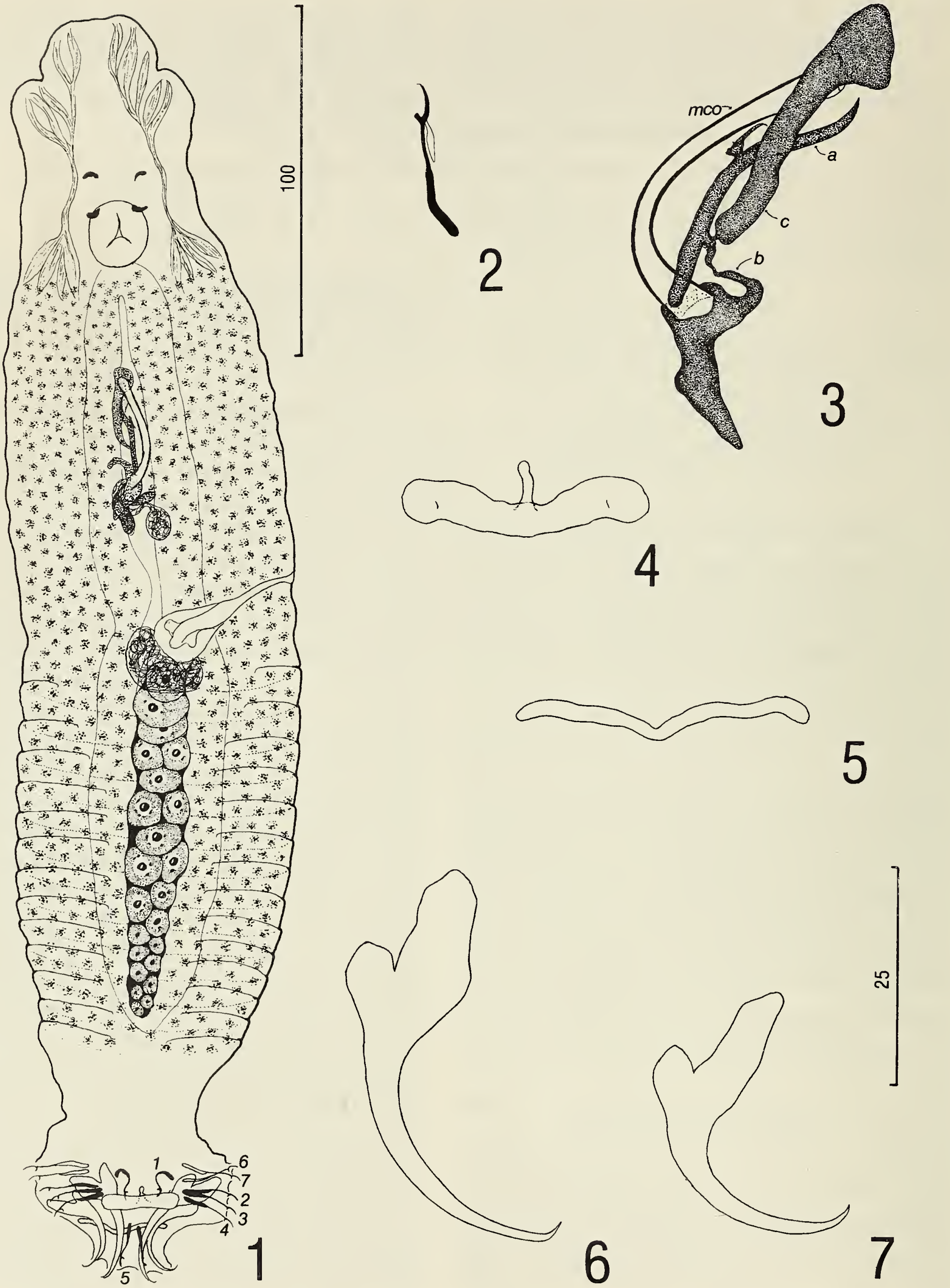
Diagnosis.—Body comprising cephalic region, trunk, peduncle, haptor; longitudinal ventral groove between ends of incomplete tegumental annulations on posterior trunk. Tegument thin. Cephalic lobes, head organs, cephalic glands present. Eyes present. Mouth ventral; pharynx muscular, glandular; esophagus short to nonexistent; intestinal ceca 2, confluent posterior to gonads, lacking diverticula. Genital pore midventral. Gonads intercecal, overlapping; testis dorsal to germarium. Seminal vesicle a dilation of vas deferens; 2 prostatic reservoirs; copulatory complex comprising tubular copulatory organ, accessory piece; accessory piece comprising proximal articulation process, distal rod. Oviduct short; uterus delicate; vaginal aperture on left margin of trunk; seminal receptacle a dilation of vaginal duct. Vitellaria present in trunk, absent in regions of reproductive organs. Haptor armed with ventral, dorsal anchor/bar complexes; 14 hooks with ancyrocephaline distribution (Mizelle 1936, see Mizelle & Price 1963). Anchors simple; ventral bar with anteromedial projection; hooks similar, each with erect thumb, shank comprising 2 subunits. Parasites of gills of Neotropical curimatid fishes.

Type species, host, and locality.—*Annulotrematoides amazonicus,* new species, from gills of *Psectrogaster rutiloides,* Furo do Catalão, Manaus, Amazonas, Brazil.

Etymology.—The generic name reflects similarity of the genus to *Annulotrema.*

Annulotrematoides amazonicus,
new species
Figs. 1–7

Description (based on 46 specimens).—Body 354 (274–438; $n = 32$) long, fusiform; greatest width 86 (73–117; $n = 33$) usually in posterior trunk or near midlength. Tegumental annulations unscaled, each terminating at margin of longitudinal ventral groove. Cephalic margin broad; 2 indistinct terminal, 2 bilateral cephalic lobes. Eyes 4, equidistant; eye granules subspherical to subovate, variable in size; accessory granules absent. Pharynx spherical, 19 (16–22; $n = 33$) in diameter. Peduncle narrow; haptor subhexagonal, 54 (42–64; $n = 32$) long, 71 (62–85; $n = 31$) wide. Ventral anchor 42 (38–45; $n = 10$) long, with broad well-differentiated roots, evenly curved shaft, point; superficial root longer than deep root; point tip recurved; base width 17 (16–19; $n = 10$). Dorsal anchor 27 (21–30; $n = 10$) long, with elongate superficial root, short broad deep root, curved shaft, recurved point; base width 17 (15–18; $n = 10$). Ventral bar 28 (25–30; $n = 27$) long, platelike, with slightly enlarged ends, elongate anteromedial projection; dorsal bar 31 (28–35; $n = 25$) long, slender, with medial bend. Each hook with erect thumb, delicate point; proximal subunit of shank expanded; hook pr. 1—18 (15–21; $n = 4$); pr. 2—20 (17–23; $n = 4$); pr. 3—21 (19–23; $n = 7$); pr. 4—22 (20–25; $n = 5$); pr. 5—16–17 ($n = 2$); pr. 6—24 (23–26; $n = 4$); pr. 7—23 (22–26; $n = 6$) long; filamentous hooklet (FH) loop extending to just short of union of shank subunits. Male copulatory organ 41 (34–49; $n = 10$) long, an arcuate tube with slightly flared termination; base with elongate variable proximal flange. Rod of accessory piece 30 (26–32; $n = 10$) long, acute terminally, with variable



Figs. 1–7. *Annulotrematoides amazonicus,* new species: 1, Composite drawing of whole mount (ventral view; hook pairs numbered respectively); 2, Hook (of pair 3); 3, Copulatory complex (dorsal view); 4, Ventral bar; 5, Dorsal bar; 6, Ventral anchor; 7, Dorsal anchor. Abbreviations: mco, male copulatory organ; a, distal bar of accessory piece; b, proximal articulation process; c, spatulate arm of accessory piece. All figures are drawn to the 25 μm scale except Fig. 1 (100 μm).

flattened projection near midlength; spatulate arm arising from distal end of short articulation process located between base of copulatory organ and rod of accessory piece. Margins of testis undefined; seminal vesicle small; prostatic reservoirs saccate. Germarium elongate, 90 (68–113; $n = 25$) long, 27 (20–35; $n = 23$) wide; ootype not observed; vagina pyriform, with thick proximal wall, opening into large central seminal receptacle.

Specimens studied.—Holotype, IOC 33664; 45 paratypes, USNPC 84822, HWML 38340.

Etymology.—The specific name reflects the Brazilian state from which the species was collected.

Discussion

Gusev's (1976a, 1976b, 1978) thesis that the monogenoidean faunas of the Neotropical and Ethiopian biogeographical regions have ancient evolutionary relationships may be supported by the discovery of *Annulotrematoides amazonicus.* This species possesses characters and host preferences suggesting that it may share a common ancestor with species of the African *Annulotrema.* Both genera are characterized by species with tegumental annulations, and while restricted to their respective biogeographical regions, species of *Annulotrema* and *Annulotrematoides* are exclusively parasites of characiform fishes.

With the exception of Paperna's (1979) drawings, description of the internal anatomy has been lacking in studies dealing with *Annulotrema* (see Guégan et al. 1988, Ergens 1988, Paperna 1973). However, Paperna's (1979) depictions of the internal anatomy are not clear regarding the dorsoventral orientation of the internal organs. Examination of four specimens of two unidentified *Annulotrema* species in the collection of the senior author and collected from the gills of *Alestes* cf. *nurse* (Rüppell) in Togo indicated anatomical features that serve to separate *Annulotrematoides* from *Annulotrema.* Although Paperna (1979; 110) states that the vagina opens on the left in all African *Annulotrema* species, three of the above specimens clearly show the vaginal aperture on the right margin (vagina opens on left margin in *Annulotrematoides amazonicus*). The tegumental annulations in *Annulotrema* are complete ventrally, and the gonads are slightly overlapping (testis dorsoposterior to germarium) while in *Annulotrematoides amazonicus* the testis is dorsal to the germarium.

Within the Neotropics, *Annulotrematoides amazonicus* is probably most closely related to the complex of Ancyrocephalinae reported by Boeger & Kritsky (1988) from the gills of the red-breasted piranha, *Pygocentrus nattereri* (Characiformes). Species in the complex comprise *Amphithecium* Boeger & Kritsky, 1988, *Notothecium* Boeger & Kritsky, 1988, and *Notozothecium* Boeger & Kritsky, 1988, and possess comparable internal anatomy, haptoral organization, and structure of the copulatory complex to those of *A. amazonicus.* In addition, some species in all of these genera have an annulated tegument, which is usually scaled in those from piranha. The copulatory complexes in *Annulotrematoides amazonicus* and the piranha's species include a distal rod in the accessory piece, a possible synapomorphy for the four genera.

Acknowledgment

The authors are grateful to Michel Jégu, Convention ORSTOM/CNPq, Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil, for identifying the hosts.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(3):533–550. 1995.

New records of azooxanthellate stony corals (Cnidaria: Scleractinia and Stylasteridae) from the Neogene of Panama and Costa Rica

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Abstract.—Five new species of azooxanthellate Scleractinia are described from the Panamanian-Costa Rican Neogene: *Septastraea altispina, Antillocyathus gracilis, Paracyathus adetos, Oxysmilia pliocenica,* and *Asterosmilia irregularis.* Three additional species of azooxanthellate stony corals are also reported for the first time in the fossil record: *Gardineria minor, Schizocyathus fissilis,* and *Stylaster roseus.* The records of *S. roseus* are the first fossil occurrence of a stylasterid in the western Atlantic.

The specimens that form the basis for this paper were collected in the first seven years (1986–1992) of the Panama Paleontology Project, a multiphyletic survey of the marine invertebrate Neogene fauna of the Neotropics, especially southern Central America. The purpose of the first phase of the project was to determine the biotic response to the Neogene closure of the Caribbean-eastern Pacific seaway through a detailed analysis of the stratigraphic and geographic distributions of various invertebrate groups. An early review of this project was published (Coates et al. 1992, Collins 1993), which included a general description of the Panama and Costa Rica localities, their lithostratigraphy, and their biostratigraphic correlations. A much more detailed analysis of the stratigraphy of various groups, including Scleractinia, is now in preparation (Collins & Coates in lett) as an edited volume. In that volume I (Cairns 1996) list and document the 18 species of azooxanthellate stony corals that are known to occur in the Panamanian and Costa Rican Neogene, eight of which are discussed herein, i.e., the five new species and the three previously described species that are new to the fossil record.

Species synonymies are considered to be complete or give a reference to a complete synonymy. In the Material Examined sections, each record begins with a PPP locality number, followed by the number of specimens in that lot, followed by its catalog number. The PPP collection sites, with their original "CJ" field numbers, are listed in the Appendix. Absolute ages were derived from biostratigraphic dating using planktic foraminifera, calcareous nannoplankton, and the geological time scale of Berggren, et al (1985).

The following abbreviations are used in the text: GCD, Greater Calicular Diameter; GCD:LCD, Ratio of greater calicular diameter to lesser calicular diameter; H:W, Ratio of height to width of a corallum; PD:GCD, Ratio of pedicel diameter to greater calicular diameter; PPP, Panama Paleontology Project; Sx, Cx, Px, Cycle of septa, costae, or pali (respectively) designated by numerical subscript; USGS, United States Geological Survey; USNM, United States National Museum (part of the National Museum of Natural History, Smithsonian Institution, Washington, D.C.).

Systematic Account

Class Anthozoa
Order Scleractinia
Suborder Faviina
Family Rhizangiidae d'Orbigny, 1849
Septastraea d'Orbigny, 1849

Diagnosis.—Encrusting or ramose colonies having closely spaced cerioid corallites. Intercorallite coenosteum sparse. Corallites with two, rarely three, cycles of septa. Inner edges of septa finely dentate. Pali absent; fossa shallow; columella a solid fusion of inner septal edges. Miocene to Pleistocene: eastern and southern U.S., Central America, Colombia, Europe.

Type species.—Hinde (1888) argued that d'Orbigny's (1849) originally designated type species (and only species listed by him in 1849) of *Septastraea subramosa* could not be considered the type species of the genus because it was not described by d'Orbigny in 1849. Because Milne Edwards & Haime (1849) described four species of *Septastraea* later in the same year, including *S. forbesi*, and because d'Orbigny (1852) later synonymized *S. forbesi* with his *S. subramosa*, Hinde logically reasoned that *S. forbesi* must be the type species, being the only apparent valid species of the pair. However, the ICZN (1985), written long after Hinde's intellectual exercise, clearly states in Article 12b6 that a description of a new genus before 1931 that includes reference to a new species without further description of that species does constitute availability of the species name through indication, i.e., the generic description also serves as the species description. The type species of *Septastraea* must therefore be *S. subramosa* d'Orbigny, 1849 (=*S. forbesi* Milne Edwards & Haime, 1849; =*S. marylandica* (Conrad, 1841)).

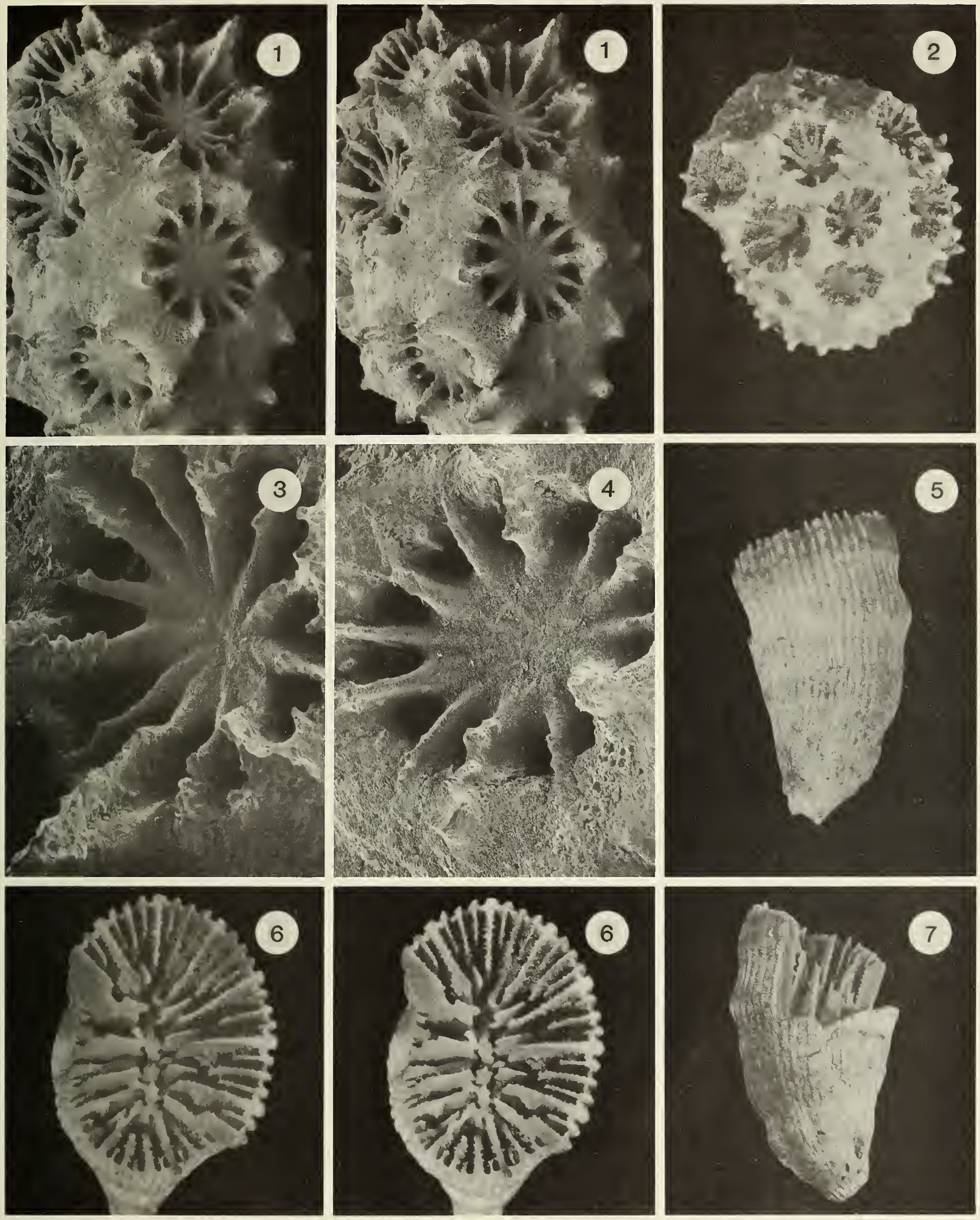
Septastraea altispina, new species
Figs. 1–4

Diagnosis.—Corallum small and cerioid, encrusting gastropod shells. Intercalicular coenosteum well developed. Septa hexamerally arranged in two cycles (12 septa). CS1 highly exsert, each rising to a massive, reddish-brown coensteal spine that is triangular in cross section. Columella massive and flat.

Description.—Corallum cerioid, known only to encrust gastropod shells, the largest colony examined (the holotype) a spherical mass about 11 mm in diameter consisting of approximately 25 corallites. Calices circular to elliptical, larger calices up to 3.3 mm in GCD. Coenosteum well developed: corallites not directly adjacent but separated by 0.50-0.75 mm of coenosteum. In one specimen (USNM 95738), a shallow sulcus surrounds several corallites. Otherwise, coenosteum finely granular (nonspinose) and white, the exsert portions of the 6 CS1 being reddish-brown.

Septa hexamerally arranged in two cycles (12 septa), with no indication of additional S3. S1 highly exsert (up to 1.1 mm), the distal portion of each S1 forming a massive spine that is triangular in basal cross-section (up to 0.3 mm thick), resulting in a crown of 6 CS1 guarding each calice. Inner edges of S1 finely dentate and inclined obliquely toward columella. S2 nonexsert and sometimes rudimentary, their inner edges also finely dentate and oriented obliquely to horizontally, fusing with the columella lower in fossa. Septa relatively thin (0.05–0.11 mm) and well separated from one another by a distance of about four times a septal width (0.3–0.4 mm). Fossa shallow. Columella a solid, massive central structure up to 1.2 mm in diameter, which is flat to slightly concave and granular like the coenosteum.

Discussion.—It may seem inadvisable to describe a new species of *Septastraea* when most, if not all, of the five or six nominal species in this genus have been previously



Figs. 1–7. (1–4, *Septastraea altispina*: 1, 3–4, paratype from PPP326, USNM 95738; 2, holotype, USNM 95735): 1, Stereo view of corallum showing highly exsert costoseptal spines, ×8.1; 2, Holotype, ×4; 3–4, Two corallites illustrating the massive columella, both ×22. (5–7, holotype of *Antillocyathus gracilis*, USNM 95469): 5, 7 Lateral views of holotype, both × 2.6; 6, Stereo view of calice, ×3.8.

synonymized (see Vaughan 1904, Weisbord 1971, Meeder 1987) as the morphologically variable and stratigraphically widespread (New Jersey to Louisiana, ?Colombia; Miocene to Pleistocene) *Septastraea marylandica* (Conrad, 1841). Nonetheless, although both species are similar in habit (encrusting shells), have the same number of septa, and have a massive columella, *S. altispina* differs in having highly exsert, massive, pigmented S1, which are easily seen on all specimens examined and are not present on *S. marylandica.*

Etymology.—The species name *altispina* (from the Latin *altus,* high + *spina,* thorn) refers to the six prominent CS1 that crown each calice.

Material examined.—Holotype: PPP326, 1 colony, USNM 95735.—Paratypes: PPP195, 1 corallite, USNM 95736; PPP196, 1 colony and 2 corallites, USNM 95737; PPP326, 10 colonies, USNM 95738; PPP379, 2 colonies, USNM 95739; PPP422, 2 corallites, USNM 95740.

Type locality.—PPP326: Caribbean Panama, Cayo Agua, north side Pta de Nispero (9°10′4.8″N, 82°02′0.6″W); Cayo Agua Formation, 2.9–3.6 Ma (early Late Pliocene).

Distribution and Age.—Cayo Agua, Isla Popa, and Valiente Peninsula, all Bocas del Toro, Caribbean Panama. Cayo Agua Formation (early Late Pliocene), Shark Hole Point Formation (early Late Pliocene).

Suborder Caryophylliina
Family Caryophylliidae Dana, 1846
Antillocyathus Wells, 1937

Diagnosis.—Corallum solitary and usually highly compressed. Septotheca costate and granular. One crown of pali before S3 or before penultimate septal cycle when hexameral symmetry lost. Columella lamellar or formed of aligned, fused papillae. Dissepiments rare or absent. Miocene to Pliocene: West Indies, Central America.

Type species.—*Placotrochus maoensis* Vaughan *in* Vaughan & Hoffmeister (1925), by original designation.

Antillocyathus gracilis, new species
Figs. 5–7

Diagnosis.—Corallum ceratoid and usually curved about 45° in plane of GCD. GCD:LCD = 1.1–1.3. Small edge crests present on both concave and convex thecal edges near base. Septa hexamerally arranged in four cycles (S1–2>S3>S4). One crown on 12 P3.

Description.—Corallum ceratoid (edge angle 14°–19°), compressed, and usually slightly curved about 45° in plane of GCD. Largest specimen examined (USNM 95539) 13.5 × 10.3 mm in calicular diameter and 27.0 mm in height; holotype slightly smaller and somewhat damaged, but otherwise in excellent preservation, measuring 10.3 × 7.7 mm in calicular diameter and 18.6 mm in height. Calice elliptical, GCD:LCD = 1.12–1.33. Pedicel quite small, only 0.4–0.9 mm in diameter, and invariably detached from substrate. Costae equal, convex, and highly granular. Costae 0.40–0.45 mm wide, separated by shallow intercostal furrows about 0.15 mm wide. Thecal edge crests present on lower 2–3 mm of corallum, best preserved in juvenile coralla before they become broken or worn. Edge crests quite thin, semi-circular in shape, and up to 2.6 mm in height, occurring on both concave and convex thecal edges, but usually more prominent on convex edge. On upper convex thecal edge of many coralla a second, lower crest may be present or the principal costa on that edge may be slightly more produced. Corallum white to reddish-brown.

Septa hexamerally arranged in four cycles (some large coralla have some pairs of S4, up to 60 septa) according to the formula S1–2>S3>S4. S1–2 slightly exsert (about 1 mm) and have straight, vertical inner edges that reach about three-quarters distance to columella. S3 less exsert and about half width of S1–2. Each S3 bordered by a wide (up to 1.6 mm), lamellar palus, the 12 P3 forming a distinct elliptical crown encircling the columella. S4 about half width of an S3. Fossa moderate in depth, containing an elongate,

Table 1.—Diagnostic characters of the four species of *Antillocyathus*.

Character	*A. maoensis*	*A. alatus*	*A. cristatus*	*A. gracilis*
Typical size (GCD)	13–18 mm	9–11 mm	22–26 mm	10–13 mm
Shape; lateral edge angle	Straight, compressed; 45°–80°	Straight, full; parallel in upper corallum	Curved, full; 36°–44°	Curved, compressed; 14°–19° (ceratoid)
GCD:LCD	1.75–2.50	1.3–1.75	1.6–1.7	1.1–1.3
Edge crests	Basally only	Basally only	Basally and convex edge	Basally and convex edge
Septal arrangement	19–24:19–24:38–48:0–8 (78-*80*-104)	14–16:14–16:24–32:0–8 (48-*64*-72)	>S5 (106 septa)	S1–2 > S3 > S4 (*48*-60)
Pali	19–24 secondary pali (P2)	14–16 P2	24 P4	12 P3
Columella	Solid, lamellar	Solid, lamellar	Lamellar to spongy	Fused papillose to sublamellar
Age and Distribution	Late Miocene to early Pliocene of Dominican Republic	Late Miocene to early Pliocene of Dominican Republic	Late Miocene to early Pliocene of Dominican Republic; Pliocene of Panama and Costa Rica	Early to middle Pliocene of Panama

papillose to lamellar columella consisting of three or four fused papillae or a thin, dissected lamella.

Discussion.—*Antillocyathus gracilis* is compared to the three other species in the genus in Table 1. To summarize, it is distinguished by having a curved, slender corallum; a low GCD:LCD; hexamerally arranged septa in four cycles; and 12 P3.

Etymology.—The species name *gracilis* (from the Latin *gracilis,* slender) refers to the slender ceratoid growth form of the species.

Material examined.—Holotype: PPP63, 1 corallum, USNM 95469. Paratypes: PPP56, 15, USNM 95524; PPP57, 3, USNM 95522; PPP63, 18, USNM 95470; PPP196, 27, USNM 95523; PPP345, 17, USNM 95521. Nontypes: PPP55, 2, USNM 95525; PPP193, 27, USNM 95527; PPP194, 2, USNM 95526; PPP197, 8, USNM 95528; PPP198, 25, USNM 95529; PPP208, 1, USNM 95530; PPP294, 7, USNM 95532; PPP295, 2, USNM 95533; PPP298, 1, USNM 95534; PPP306, 1, USNM 95535; PPP307, 8, USNM 95536; PPP308, 2, USNM 95537; PPP311, 3, USNM 95538; PPP335, 1, USNM 95539; PPP346, 6, USNM 95540; PPP348, 1, USNM 95541; PPP350, 3, USNM 95542; PPP355, 3, USNM 95543; PPP357, 1, USNM 95544; PPP423, 1, USNM 95545.

Type locality.—PPP63: Caribbean Panama, Cayo Agua, small island offshore (9°10′44.0″N, 82°03′11.0″W); Cayo Agua Formation, 3.5–3.6 Ma (early Late Pliocene).

Distribution and Age.—Most records from Cayo Agua, Bocas del Toro, Caribbean Panama; also known from Isla Colon and Isla Popa, both also Caribbean Panama. Cayo Agua Formation (early Late Pliocene).

Paracyathus Milne Edwards & Haime, 1848a

Diagnosis.—Corallum solitary; trochoid to turbinate; fixed or free. Base often polycyclic. Paliform lobes usually multilobate, occurring before all but last cycle of septa. Columella papillose, elements often indistinguishable from lower paliform lobes. Eocene to Recent: cosmopolitan.

Type species.—*Paracyathus procumbens* Milne Edwards & Haime, 1848a, by subsequent designation (Milne Edwards & Haime 1850: xv).

Paracyathus adetos, new species
Figs. 8–14

Diagnosis.—Corallum tympanoid, cylindrical, or trochoid, often overgrowing its substrate of attachment to become free. Base polycyclic. Septa hexamerallay arranged in four cycles: $S1>S2>S4\geq S3$. Each S1–3 bears several narrow paliform lobes. Columella papillose or solid.

Description.—Corallum solitary, attached when young but often incorporating the substrate into its base (Fig. 13) and thus becoming free in adult stage. Young coralla cylindrical and squat (tympanoid); older coralla persist as short cylinders if the substrate is too large to overgrow, but become bowl-shaped to trochoid or turbinate if the substrate is overgrown. Largest specimen examined (holotype) 6.7 mm in circular calicular diameter and 3.9 mm in height, the height usually being about half the calicular diameter. Base polycyclic (Figs. 10, 12, 14), larger coralla having up to five concentric thecal rings occurring at the following approximate diameters and septal complements: first ring, 0.5–0.7 mm (6 septa); second, 1.05–1.20 mm (12 septa); third, 1.4–1.9 mm (about 18 septa); fourth, 2.2–3.6 mm (24 septa); and fifth, 2.6–6.7 mm (48 septa). Coralla usually attach to a small bivalve shell or piece of a bivalve shell or to a small gastropod shell, and less frequently to another coral, a brachiopod shell, or a bryozoan colony. Costae highly ridged and dentate, the C1–2 up to 0.4 mm in height, the C3–4 less prominent.

Septa hexamerally arranged in 4 complete cycles above a GCD of about 4.3 mm according to the formula: $S1>S2>S4\geq S3$. S1 highly exsert (up to 0.7 mm) and have straight inner edges that extend about 0.8 distance to columella. Inner edges of each S1 bears one small, blunt paliform lobe adjacent to the columella. S2 less exsert and extend only 0.6 distance to columella, each S2 internally bordered by two or three small, blunt paliform lobes. S3-4 equally exsert, the S3 extending about half the distance to columella, the S4 equal to or slightly wider than the S3. Each S3 internally bordered by three or four tall, blunt paliform lobes; inner edges of S4 finely serrate. Inner edges of each pair of S4 within a half-system fuse to their common S3, each pair of S3 within a system, in turn, fuses to its common S2 through its innermost teeth, directly adjacent to the columella. All septa covered with tall granules. Fossa quite shallow. Columella papillose in small coralla, the papillae fusing in larger coralla to form a massive, slightly concave solid structure.

Discussion.—*Paracyathus adetos* is similar to *P. vaughani* Gane, 1895, a species known from the Late Miocene of the southeastern United States from Virginia to Florida (see Vaughan 1904, Weisbord 1971). Both species have low, tympanoid coralla, polycyclic bases that are often attached to bivalve shells, and similarly shaped paliform lobes. *Paracyathus vaughani,* however, differs in attaining a larger size (e.g., up to 11 mm GCD with 88 septa and eight thecal rings), always remaining attached, having a papillose (never solid) columella, and having a deeper fossa (Figs. 15, 18). *Paracyathus adetos* differs from *P. henekeni* Duncan, 1863 in having a larger corallum and more septa; a lower H:W; and a more solid columella.

Etymology.—The species name *adetos* (from the Greek *adetos,* loose, free, unbound) refers to the tendency of mature coralla of this species to become free attachment by incorporating the substrate into its base.

Material examined.—Holotype: PPP196, 1, USNM 95575. Paratypes: PPP56, 6, USNM 95576; PPP57, 3, USNM 95577; PPP63, 13, USNM 95578; PPP65, 14, USNM 95579; PPP66, 1, USNM 95580;

PPP194, 13, USNM 95581; PPP195, 16, USNM 95582; PPP196, 42, USNM 95583; PPP197, 7, USNM 95584; PPP198, >100, USNM 95585; PPP205, 2, USNM 95586; PPP306, 32, USNM 95588; PPP307, 53, USNM 95589; PPP311, 11, USNM 95590; PPP352, 22, USNM 95591; PPP475, 28, USNM 95587.

Type locality.—PPP196: Caribbean Panama, Cayo Agua, SW Pt. Norte (9°10′42.5″N, 82°03′9.0″W); Cayo Agua Formation, 3.5–3.6 Ma (early Late Pliocene).

Distribution and Age.—All records from Cayo Agua, Bocas del Toro, Caribbean Panama (early Late Pliocene).

Oxysmilia Duchassaing, 1870

Diagnosis (*emended*).—Corallum solitary; ceratoid to trochoid; attached or free. Base composed of concentric, partitioned thecal rings achieved by formation of exothecal dissepiments over ridged costa, or the base may be narrow and unattached. Septotheca costate. Rudimentary paliform lobes occasionally present before S3. Fossa deep. Columella variable, ranging from massive granular papillae to lamellar or aligned fused papillae. Dissepiments absent. Late Pliocene to Recent: Central America, western Atlantic (46–640 m).

Type species.—*Lophosmilia rotundifolia* Milne Edwards & Haime, 1848c, by monotypy.

Oxysmilia pliocenica, new species

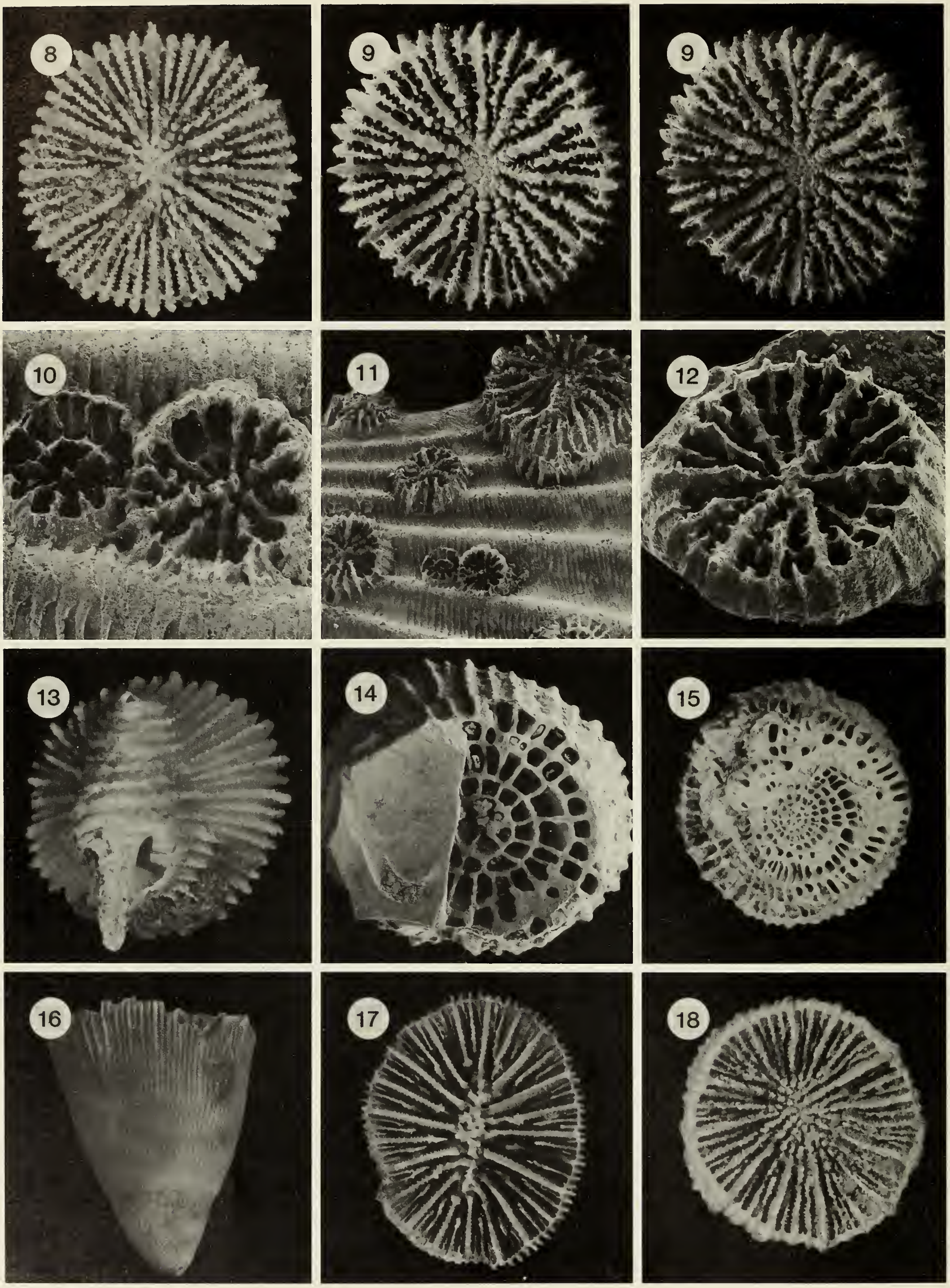
Figs. 16–17

Diagnosis.—Corallum ceratoid and free, with a narrow pedicel. Septa hexamerally arranged in five cycles, the last cycle incomplete: S1–2>S3>S4>S5. Rudimentary paliform lobes (P3) sometimes present. Columella papillose or lamellar.

Description.—Corallum ceratoid and free, the largest specimen examined (holotype) 14.2 × 11.8 mm in calicular diameter and 18.4 mm in height. Pedicel very narrow, only 1.0–1.2 mm in diameter, in most cases partially incorporating a small gastropod shell into its base. Calice elliptical: GCD: LCD = 1.20–1.25. Costae poorly defined on lower third of corallum; broad, slightly convex, and granular on middle third; and ridged and rather thin in upper third adjacent to calice, where intercostal furrows are correspondingly broader. Upper half to third of corallum reddish-brown. Theca quite thin, only about 0.05 mm in thickness.

Septa hexamerally arranged in five cycles, the last cycle incomplete. The holotype has 92 septa and the largest paratype of GCD 13.9 mm has 82 septa, consisting of seven half-systems with both pairs of S5, three with one pair of S5, and two half-systems with no S5. Septal formula: S1–2>S3>S4>S5. Relative exsertness of septal cycles unknown due to poor preservation of calicular edges. S1–2 broad, extending 0.8–0.9 distance to columella, and have straight, vertical, slightly thickened inner edges. S3 about three-quarters width of an S1–2 and have finely sinuous inner edges, some of which extend to the columella low in fossa as irregular trabecular ribbons. S4 half width of S3 and have finely dentate inner edges. S5 rudimentary, about one-third width of an S4. Faces of S1–4 homogeneously covered with low, pointed granules. Fossa moderate in depth. Columella variable in shape: in the holotype and three paratypes it consists of an alignment of slender, fused papillae, but in one paratype (USNM 95594) the columella is a thin, dissected lamella.

Discussion.—*Oxysmilia pliocenica* is quite similar to the only other species in the genus, *O. rotundifolia* (Milne Edwards & Haime, 1848c), a species known only from the Recent western Atlantic from North Carolina to Surinam and the western Gulf of Mexico at 46–640 m (Cairns 1979). Points of similarity include septal number, arrangement, and size; costal shape; and variation in columella shape, the columella of *O. rotundifolia* also ranging from elongate



Figs. 8–18. (8–14, *Paracyathus adetos*: 8, holotype, USNM 95575; 9, paratype, PPP196, USNM 95583; 10–12, paratype, PPP198, USNM 95585; 13, paratype, PPP63, USNM 95578; 14, paratype, PPP475, USNM 95587): 8, Calice of holotype, ×6.4; 9, Stereo view of a paratype, ×7.8; 10–12, Young stages attached to bivale shells (calices of fig. 10 illustrating 2 thecal rings, calices of fig. 12, 3 rings), ×28, ×6.3, ×26, respectively; 13,

papillose to solid lamellar. Also, in both species some specimens bear trabecular processes on the inner edges of their S3 that resemble small paliform lobes. *Oxysmilia pliocenica* differs in having a simple base (not partitioned concentric rings similar to polycyclic development), being smaller in size, and having a reddish-brown corallum.

Lophosmilia Milne Edwards & Haime, 1848b is a closely related genus of three or four species known from the Cretaceous to Eocene of Europe, Texas, and Peru, differing from *Oxysmilia* in having a deep-seated lamellar columella (Wells 1956). But, given the range of columellar variation found in the two known species of *Oxysmilia,* this difference hardly seems significant. In fact, *O. rotundifolia* was originally described in the genus *Lophosmilia.*

Etymology.—Named for the geological epoch in which it occurs.

Material examined.—Holotype: PPP311, USNM 95593. Paratypes: PPP196, 1, USNM 95595; PPP311, 3, USNM 95594.

Type locality.—PPP311: Caribbean Panama, Cayo Agua, S of Pt. de Nispero (9°09′57.4″N, 82°01′48.6″W); Cayo Agua Formation, 2.9–3.6 Ma (early Late Pliocene).

Distribution and age.—Known only from Cayo Agua, Bocas del Toro, Caribbean Panama (early Late Pliocene).

Asterosmilia Duncan, 1867

Diagnosis.—Corallum solitary; ceratoid, trochoid, or flabellate; free or attached. Septotheca costate. Paliform lobes present before penultimate septal cycle. Columella lamellar or fascicular. Vesicular endotheca abundant. Oligocene to Recent: West Indies, Central America.

Type species.—*Trochocyathus abnormalis* Duncan, 1864, by subsequent designation (Vaughan 1919:354).

Asterosmilia irregularis, new species
Figs. 19–20

Asterosmilia abnormalis.—Cairns & Wells, 1987: 37 (in part: USGS 8321).

Diagnosis.—Corallum ceratoid, elongate, and gently curved. Septa arranged in 15–18 sectors, with the following septal complements: 15–18:15–18:30–36:0–10 (up to 76 septa). Paliform lobes present on secondary septa and tertiary septa that are flanked by quaternary septa. Columella lamellar.

Description.—Corallum ceratoid, elongate, and usually gently curved about 90° in basal region. Largest specimen examined (USGS 20468) 19.4 × 16.8 mm in calicular diameter and 72.9 mm in length; holotype 16.3 × 14.6 mm in calicular diameter and 52.1 mm in length. Corallum always free, narrowing to a slender, invariably broken pedicel 1.0–1.5 mm in diameter (PD:GCD = 0.06–0.12), which usually reveals the 6 protosepta. Original object of attachment never seen and apparently not incorporated into base. Calice consistently elliptical: GCD:LCD = 1.15–1.27. Costae slightly convex and equal in width, none more prominent than others. Each costa about 0.5 mm wide near calice and separated by narrow (0.08 mm), shallow intercostal striae. Each costa covered with low, rounded granules about 0.15 mm in diameter, arranged two or three across a costa at any level. Theca not very thick (only about 0.4 mm wide near calice), a deep reddish-brown color.

Septa of adult coralla arranged in 15–18 sectors, each sector flanked by two primary

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Corallum base overgrowing a small gastropod shell, ×5.9; 14, Broken base revealing 5 thecal rings. (15, 18, syntype of *Paracyathus vaughani* from Miocene of Virginia, USNM 68311): 15, 18, Basal view showing thecal rings, and calice, both ×2.8. (16–17, holotype of *Oxysmilia pliocenica,* USNM 95593): 16, 17, Side and calicular views, both ×2.

Table 2.—Diagnostic characters of the three Panamanian Neogene species of *Asterosmilia.*

Character	*A. profunda*	*A. irregularis*	*A. exarata*
Corallum size; shape	GCD max. = 35.7 mm; trochoid to ceratoid, occasionally attached	GCD max. = 19.4 mm; ceratoid, free	GCD max. = 10.4 mm; ceratoid, free
PD:GCD	0.11–0.29	0.06–0.12	0.06–0.11
Costae	C1–2 usually more pronounced than others	All costae equal	C1–2 usually broader than others
Septal arrangement	S1–2 > S3 > S4 > S5 (96–108 septa), S1–2 highly exsert	15–18:15–18:30–36:0–10 (68–76 septa), not exsert	S1–2 > S3 > S4 (48 septa), not very exsert
Paliform lobes	24 P4	16–18 lobes before secondaries and some tertiaries	12 P3
Vesicular dissepiments	Abundant, inclined, 1–5 "rings"	Less common, inclined, 1–2 "rings"	Sparse, horizontal, one ring
Columella	Coarse papillose or crispate	Plate-like (lamellar or labyrinthiform)	Lamellar to crispate

septa and containing a medial secondary septum, two tertiary septa and 0–2 quaternary septa, resulting in a calicular total of 68–76 septa. Septal formula of holotype: 15:15:30:10 (70 septa, 17 well-developed pali and three rudimentary ones); other specimens having: 17:17:34:4 (72 septa, 17 well-developed pali), USNM 95611; 17:17:34:6 (74 septa, 17 well-developed pali and three rudimentary), USNM 95615; and 18:18:36:4 (76 septa, 18 well-developed pali and two rudimentary), USNM 95615. Preservation of most coralla does not allow analysis of septal or palar number. Primary septa only slightly exsert (1.0–1.2 mm), of moderate thickness (about 0.4 mm), and have straight, vertical inner edges that extend about three-quarters distance to columella. Secondary septa less exsert and less thick, and only about half width of a primary. Each secondary septum bordered internally by a broad, lamellar paliform lobe of equal width to the secondary septum. Inner edges of paliform lobes fuse to columella. In sectors lacking quaternaries, tertiary septa are about one-third width of a secondary, but if a pair of S4 flank a tertiary, the tertiary is doubled in width and sometimes bears a broad paliform lobe (P3) of variable size, sometimes as large as a P2 but occasionally rudimentary. S4 rudimentary. Thin vesicular dissepiments occur in upper corallum, inclined and structured as in *A. profunda*, but occurring less abundantly, i.e., only one or two dissepiments present at a level in any interseptal space. Fossa of moderate depth, containing a plate-like columella of variable construction. Often the plate is a single, thin, medial lamella; occasionally it is expressed as several parallel, slightly overlapping plates; and in one case (USNM 95615) the plates were labyrinthiform in arrangement.

Discussion.—*Asterosmilia irregularis* differs from its congeners in having nonhexameral septal symmetry. It is intermediate in size between the two other Neogene species known from Panama and differs from them in other characters as well (Table 2).

Etymology.—The species name *irregularis* (from the Latin *in regularis,* not according to rule) refers to the variable number of septal sectors contained by specimens of this species.

Material examined.—Holotype: PPP1119, USNM 95609. Paratypes: PPP627, 38, USNM 95618; PPP757, 4, USNM 95617; PPP1101, 12, USNM 95610; PPP1102, 2, USNM 95611; PPP1103, 1, USNM 95612;

PPP1104, 1, USNM 95613; PPP1105, 10, USNM 95614; PPP1107, 13, USNM 95615; PPP1118, 1, USNM 95616; USGS 8321, 1, USNM 65323; USGS 20468, 69, USNM 64024; Limon Centro, Costa Rica, 3, USNM 81310; Moin Formation, Costa Rica, 4, USNM 72351.

Type locality.—PPP1119: Lomas del Mar, Limon, Costa Rica, (construction site): 9°59′31.0″N, 83°02′12.2′W; Moin Formation, 1.7–1.9 Ma (Late Pliocene).

Distribution and Age.—All specimens from Lomas del Mar, Limon, Caribbean Costa Rica (Late Pliocene).

Family Flabellidae Bourne, 1905
Gardineria Vaughan, 1907

Diagnosis.—Corallum solitary, ceratoid to turbinate; transverse division lacking. Corallum attached through a pedicel as well as having a massive lateral secondary rootlet. Epitheca transversely wrinkled. Upper, outer septal edges separated from smooth calicular edge by a deep notch. P2 usually present; columella papillose. Late Pliocene (Costa Rica) to Recent (tropical western Atlantic, Hawaiian Islands, Philippines, Antarctica, South Africa).

Type species.—*Gardineria hawaiiensis* Vaughan, 1907, by original designation.

Gardineria minor Wells, 1973
Figs. 21–26

Gardineria minor Wells, 1973: 49–53, figs. 36a–g; Cairns, 1979: 162–163, pl. 31, figs. 7–9 (complete synonymy).

Description.—Corallum small, subcylindrical to ceratoid, and firmly attached to substrate by a small pedicel 0.9–1.3 mm in diameter and a larger, irregularly-shaped lateral rootlet, which issues from the lower side of the theca and appears as a broad thecal adhesion to the substrate. Base polycyclic, usually with only two rings—the protothecal and the outer epithecal—the latter being smooth but circumferentially finely wrinkled. The seven fossil specimens examined range in calicular diameter from 2.6–4.9 mm. Corallum white.

Septa hexamerally arranged in two or three cycles, depending on calicular diameter. Coralla 2.6–3.0 mm in diameter have only 12 septa (Figs. 23, 26), whereas those over 3.3 mm usually have 24 septa arranged: S1>S2>S3 (Figs. 21–22, 24–25). S1 exsert, thick (about 0.25 mm), and have entire inner edges that attain the columella. S2 nonexsert, much thinner than S1, and have sloping, dentate to laciniate inner edges that also merge with the columella. S3 rudimentary, each represented only as a series of spines. Tall, slender P2 sometimes present. Fossa shallow. Columella small and papillose.

Discussion.—The fossil specimens reported herein are indistinguishable from Recent *G. minor* (Figs. 24–25), a species that is common throughout the Caribbean. Large living specimens (e.g., over 5 mm GCD) are known to have a fourth cycle of septa.

Material examined.—PPP466, 1, USNM 95689; PPP710, 6, USNM 95690; type series, USNM; specimens reported by Cairns (1979).

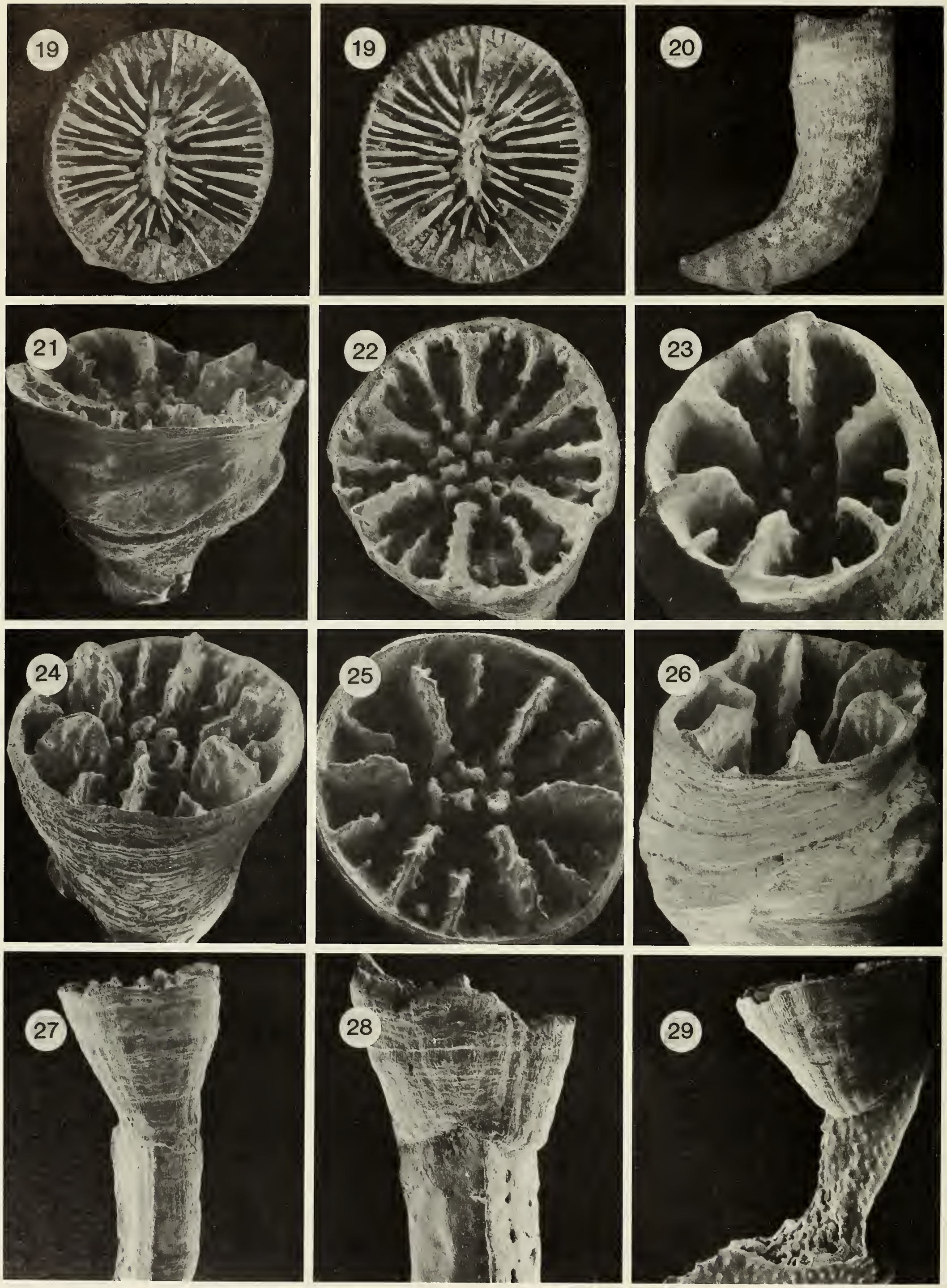
Types.—The holotype and 11 paratypes of *G. minor* are deposited at the USNM (53503-53506) (Cairns 1991).

Type locality.—off Yallahs, Jamaica, 15 m.

Distribution and age.—Santa Rita and Limon, Caribbean Costa Rica; Moin Formation (Late Pliocene). Previously known only from the Recent throughout the Caribbean and Bahamas, including off Panama, at 2–241 m (Cairns 1979).

Family Guyniidae Hickson, 1910
Schizocyathus Pourtalès, 1874

Diagnosis.—Corallum solitary, ceratoid, and invariably attached to a fragment of its parent corallum through longitudinal parricidal budding. Smooth epitheca bears 12



Figs. 19–29. (19–20, holotype of *Asterosmilia irregularis,* USNM 95609): 19–20, Stereo calicular and lateral views of holotype, ×2.5, ×0.9, respectively. (21–26, *Gardineria minor*: 21–23, 26, PPP710, USNM 95690; 24–25, Recent, Jamaica, 31 m, USNM 80892): 21–22, Side and calicular views of a specimen with 3 cycles of septa,

rows of mural pores (spots), a pair of rows flanking each S2. P1 often present; P3 always present, each pair within a system uniting in a V-shaped structure. Columella absent. ?Paleocene, ?Eocene, Late Pliocene to Recent: ?Russia, ? South Australia, Costa Rica, Atlantic (88–1300 m).

Type species.—Schizocyathus fissilis Pourtalès, 1874, by monotypy.

Discussion.—The illustrations of the species described from the Danian of Russia, *S. daschsalachlyensis* Kuzmicheva, 1987, are not typical for the genus. Likewise, the description and figures of *Cyathosmilia velata* Dennant, 1902 (Eocene, South Australia), doubtfully placed in *Schizocyathus* by Vaughan & Wells (1943), are also inconsistent with the type species of the genus. Therefore the early Tertiary records of this genus are strongly doubted.

Schizocyathus fissilis Pourtalès, 1874
Figs. 27–29

Schizocyathus fissilis Pourtalès, 1874: 36–37, pl. 6, figs. 12–13; Cairns, 1979: 166–167, pl. 32, figs. 4–7 (complete synonymy); Zibrowius, 1980: 166, pl. 85, figs. A–O.

Discussion.—The single specimen reported herein measures only 1.9 mm in calicular diameter and 1.5 mm in height, but is attached to a one-sixth sector of its parent corallum, which is 1.6 mm long. Both parent fragment and budded corallum display external mural pores about 0.11 mm in diameter. The septal pattern is obscured by sediment within the calice, but the specimen appears to have three cycles of septa, the S1 being quite exsert.

Even though the Panamanian specimen is small and poorly preserved, there is little doubt it is *S. fissilis.* Asexual fragmentation from a wedge of a parent corallum, usually a longitudinal one-sixth of the corallum, is the most common mode of reproduction in this species (Figs. 27–29). The Panamanian specimen is the first fossil occurrence of this species.

Material examined.—PPP362, 1, USNM 95675; syntype series.

Types.—Forty-one syntypes are deposited at the MCZ (5470 and 2791).

Type locality.—off Barbados, 183 m.

Distribution and age.—Escudo de Veraguas, Bocas del Toro, Caribbean Panama; Escudo de Veraguas Formation, 1.8–1.9 Ma (Late Pliocene). Previously known only from the Recent of Caribbean and Gulf of Mexico, including off Honduras, and northeastern Atlantic, at 88–1300 m (Cairns 1979, Zibrowius 1980).

Class Hydrozoa
Family Stylasteridae Gray, 1847
Stylaster Gray, 1831

Diagnosis.—Gastro- and dactylopores arranged in cyclosystems. Cyclosystems variable in location, ranging from a uniform coverage of all branch surfaces to a strictly sympodial arrangement. Coenosteal texture also variable, but usually linear-imbricate or reticulate-granular. Gastro- and dactylostyles present; gastrostyles usually ridged; ring palisade often present. Ampullae superficial. Oligocene to Recent: cosmopolitan.

Type species.—Madrepora rosea Pallas, 1766, by subsequent designation (Milne Edwards & Haime 1850: xxii).

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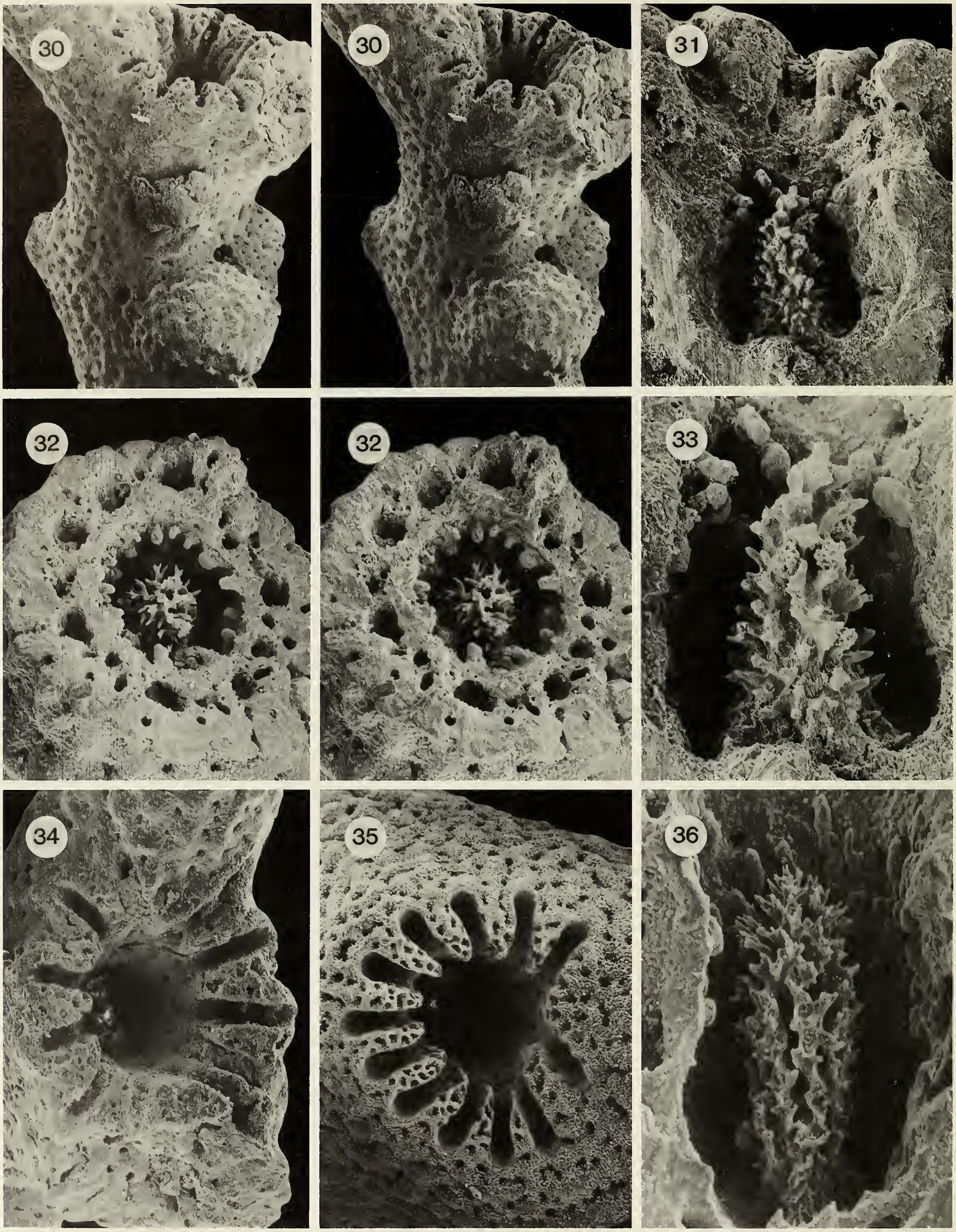
× 13.8, 12.2, respectively; 23, 26, A smaller specimen with only 2 cycles of septa, both × 16.2; 24–25, Oblique calicular and calicular views of a Recent specimen included for comparison to fossil specimens, × 14, × 15, respectively. (27–29, *Schizocyathus fissilis*: 27, Recent, off Barbados, 200 m, USNM 61747; 28, PPP362; 29, Recent, Gulf of Mexico off Florida, 221 m, USNM 61744): 27–28, Small coralla budded asexually from a parent fragment, × 11, × 18, respectively; 29, A three-generation budded corallum, × 10.4.



Figs. 30–36. (*Stylaster roseus*: 30–34, PPP710, USNM 95724; 35–36, Recent, Carrie Bow Cay, Belize, 3 m, USNM 47807): 30, Stereo view of a branch illustrating a cyclosystem and a female ampulla, ×32; 31, 33, Longitudinal fracture through cyclosystems revealing gastrostyles and elements of ring palisade, ×92, ×190, respectively; 32, Stereo view of cross section of a cyclosystem just above gastrostyle tip, illustrating ring palisade and circle of dactylopores, ×80; 34, A cyclosystem, ×50; 35–36, Cyclosystem and gastrostyle of a Recent specimen, ×50, ×155, respectively.

Stylaster roseus (Pallas, 1766)
Figs. 30–36

Madrepora rosea Pallas, 1766: 312-313.
Stylaster roseus.—Cairns, 1986: 61–65, pl. 27, figs. A–H, pl. 28, figs. A–C, pl. 53, fig. D (complete synonymy and distribution map).

Description.—Only relatively small branch fragments are reported herein, the longest (USNM 95724) 9 mm long consisting of nine cyclosystems. Coenosteum composed of slightly convex, worn strips 80–90 μm wide arranged in a reticulate fashion.

Cyclosystems circular to slightly elliptical, 0.8–1.0 mm in greater diameter, and arranged in a strictly sympodial manner. Based on 14 cyclosystems, the range of dactylopores per cyclosystem is 10–13, average = 11.1 ($\sigma = 0.86$), and mode = 11. Gastropores circular (about 0.25 mm in diameter) and contain a well-developed, diffuse ring palisade consisting of robust, cylindrical elements up to 35 μm in height and 14–21 μm in diameter. Gastrostyles lanceolate, highly ridged, and very spinose. Illustrated gastrostyle (Figs. 31, 33) 0.24 mm in height and 0.11 mm in diameter, bearing slender spines up to 35 μm long and only 3–4 μm in basal diameter. Dactylotomes 60–65 μm wide; pseudosepta wedge-shaped and about two times width of a dactylotome. An adcauline diastema three times dactylotome width is often present. Dactylostyles rudimentary, composed of widely-spaced, linearly arranged cylindrical elements up to 25 μm in height and only about 7 μm in diameter.

Female ampullae 0.55–0.65 mm in diameter, sometimes clustered. Lateral efferent pore 0.15–0.18 mm in diameter. Male ampullae not observed.

Discussion.—Direct comparison of the Neogene stylasterids to Recent *S. roseus* shows no significant differences, *S. roseus* being the only shallow-water stylasterid known from the western Atlantic (Cairns 1986). Although the genus *Stylaster* is known from the fossil record, these records are believed to be the first fossil stylasterids of any kind reported from the western Atlantic.

Material examined.—PPP55, 1, USNM 95720; PPP634, 3, USNM 95721; PPP639, 2, USNM 95722; PPP708, 3, USNM 95723; PPP710, 12, USNM 95724; PPP720, 30, USNM 95725; PPP738, 10, USNM 95726.

Types.—Not traced.

Type locality.—off Santo Domingo, depth unknown.

Distribution and age.—Isla Colon, Bocas del Toro, Caribbean Panama; Pueblo Nuevo, Limon, and Santa Rita, Caribbean Costa Rica; Moin Formation (early Late to Late Pliocene). Previously known from Recent throughout Caribbean and Bahamas, including off Caribbean Panama, Costa Rica, Honduras, and Belize, at 0.5–73 m (Cairns 1986).

Acknowledgments

The specimens were collected by the Panama Paleontology Project, and were prepared by Yira Ventocilla (PPP, Smithsonian Tropical Research Institute (STRI), Panama), and Rene Panchaund (Naturhistorisches Museum, Basal, Switzerland). Laurel Bybell and Harry Dowsett (USGS) are acknowledged for their biostratigraphic dating of the PPP samples. The PPP has been funded by the National Science Foundation, STRI, the National Geographic Society, and the Kugler Fund, Basel.

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Zibrowius, H. 1980. Les Scléractiniaires de la Méditerranee et de l'Atlantique nord-oriental.—Mémoires de l'Institut Océanographique 11:283 pp.

Appendix: PPP Collection Sites, Including Original CJ Field Numbers

PPP55 (CJ86-31-1) Isla Colon, Bocas del Toro: 9°25′23.2″N, 82°15′36.8″W; age and formation unknown.

PPP56 (CJ86-32-1) Cayo Agua, Bocas del Toro, SW of Pt. Norte: 9°10′39.1″N, 82°03′8.8″W; Cayo Agua Formation, 3.5–3.6 Ma (early Late Pliocene).

PPP57 (CJ86-33-1) Ibid.: 9°10′48″N, 82°03′6.7″W; Cayo Agua Formation, 3.5–3.6 Ma (early Late Pliocene).

PPP63 (CJ8639-1) Cayo Agua, Bocas del Toro, small island offshore: 9°10′44.0″N, 82°03′11.0″W; Cayo Agua Formation, 3.5–3.6 Ma (early Late Pliocene).

PPP65 (CJ86-40-2) Cayo Agua, Bocas del Toro, S of Pt. de Nispero: 9°09′57.4″N, 82°01′48.6″W; Cayo Agua Formation, 3.4–10.8 Ma (age uncertain).

PPP66 (CJ86-40-3) Ibid.

PPP193 (CJ87-27-1) Cayo Agua, Bocas del Toro, SW of Pt. Norte: 9°10′35.1″N, 82°03′8.7″W; Cayo Agua Formation, 3.5–3.6 Ma (early Late Pliocene).

PPP194 (CJ87-28-1) Ibid.

PPP195 (CJ87-29-1) Ibid.: 9°10′37.0″N, 82°03′9.0″W.

PPP196 (CJ87-29-2) Ibid.: 9°10′42.5″N, 82°03′9.0″W.

PPP197 CJ87-29-3) Ibid.: 9°10′45.8″N, 82°03′8.3″W.

PPP198 (CJ87-29-4) Ibid.: 9°10′48.0″N, 82°03′6.7″W.

PPP205 (CJ87-33-4) Cayo Agua, Bocas del Toro, SW of Pt. Piedra Roja: 9°08′29.3″N, 82°00′43.8″W; age and formation unknown.

PPP208 (CJ87-33-7) Ibid.: 9°08′33.3″N, 82°00′38.4″W; ?Cayo Agua Formation (age uncertain).

PPP294 (CJ88-18-2) Cayo Agua, Bocas del Toro, W side of Pt. de Tiburon: 9°09′18.0″N, 82°01′34.1″W; Cayo Agua Formation, 2.9–3.6 Ma (early Late Pliocene).

PPP295 (CJ88-18-3) Ibid.

PPP298 (CJ88-18-6) Ibid.

PPP306 (CJ88-20-4) Cayo Agua, Bocas del Toro, E side Pt. de Nispero: 9°10′3.1″N, 82°01′48.2″W; Cayo Agua Formation, 2.9–3.6 Ma (early Late Pliocene).

PPP307 (CJ88-20-5) Ibid.

PPP308 (CJ88-20-6) Ibid.

PPP311 (CJ88-21-1) Cayo Agua, Bocas del Toro, S side Pt. de Nispero: 9°09′57.4″N, 82°01′48.6″W; Cayo Agua Formation, 2.9–3.6 Ma (early Late Pliocene).

PPP326 (CJ88-25-12) Cayo Agua, Bocas del Toro, N side Pt. de Nispero: 9°10′4.8″N, 82°02′0.6″W; Cayo Agua Formation, 2.9–3.6 Ma (early Late Pliocene).

PPP335 (CJ88-26-2) Cayo Agua, Bocas del Toro, E tip Pt. de Tiburon: 9°09′11.4″N, 82°01′21.6″W; Cayo Agua Formation, 2.9–3.6 Ma (early Late Pliocene).

PPP345 (CJ88-27-1) Cayo Agua, Bocas del Toro, between Tiburon and Piedra Roja: 9°08′50.2″N, 82°00′54.4″W; ?Cayo Agua Formation (age uncertain).

PPP346 (CJ88-27-2) Ibid.: 9°08′48.5″N, 82°00′56.6″W.

PPP348 (CJ88-27-4) Ibid.: 9°08′45.3″N, 82°01′2.0″W.

PPP350 (CJ88-28-1) Ibid.: 9°08′48.6″N, 82°00′53.1″W.

PPP352 (CJ88-28-3) Ibid.: 9°08′48.4″N, 82°00′50.3″W.

PPP355 (CJ88-28-6) Ibid.: 9°08′47.1″N, 82°00′46.9″W.

PPP357 (CJ88-29-2) Cayo Agua, Bocas del Toro, E end Pt. Piedra Roja: 9°08′35.3″N, 82°00′30.1″W; ?Cayo Agua Formation (age uncertain).

PPP362 (CJ88-30-5) Escudo de Veraguas, Bocas del Toro, NW coast: 9°06′4.5″N, 81°34′18.3″W; Escudo de Veraguas Formation, 1.8–1.9 Ma (Late Pliocene).

PPP379 (CJ88-32-4) Valiente Peninsula, Bocas del Toro, NW side Bruno Bluff: 9°02′32.2″N, 81°44′42.0″W; Shark Hole Point Formation, 3.5–3.6 Ma (early Late Pliocene).

PPP442 (CJ88-59-1) Isla Popa, Bocas del Toro, NE coast: 9°12′57.7″N, 82°06′24.7″W; ?Cayo Agua Formation (age uncertain).

PPP423 (CJ888-59-2) Ibid.

PPP466 (CJ88-00-35) Limon, Costa Rica, near Progressive Baptist Church: 9°59′28.2″N, 83°02′29.9″W; age and formation unknown.

PPP475 (CJ88-00-44) Cayo Agua, Bocas del Toro, SE of Pt. Norte: 9°10′26.3″N, 82°02′26.9″W; Cayo Agua Formation, 4.6–5.0 Ma (Early Pliocene).

PPP627 (CJ89-14-1) Pueblo Nuevo, Limon, Costa Rica (Cerro Mocho subdivison): 9°59′51.0″N, 83°02′36.0″W; Moin Formation, 1.5–3.5 Ma (early Late to Late Pliocene).

PPP634 (CJ89-16-1) Ibid. (cemetery): 9°59′28.2″N, 83°02′29.2″W; Moin Formation, 1.9–2.4 Ma (Late Pliocene).

PPP639 (CJ89-17-2) Lomas del Mar, Limon, Costa Rica (construction site): 9°59′46.3″N, 83°02′26.2″W; Moin Formation, 1.7–1.9 Ma (Late Pliocene).

PPP708 (CJ89-33-1) Santa Rita, Limon, Costa Rica (near stream): 9°58′24.5″N, 83°07′22.4″W; formation unknown, 2.4–3.4 Ma (early Late Pliocene).

PPP710 (CJ89-35-1) Limon, Costa Rica, Santa Eduviges subdivision: 10°00′14.9″N, 83°02′30.9″W; Moin Formation, less than 1.8 Ma (Late Pliocene).

PPP720 (CJ89-39-1) Santa Rita, Limon, Costa Rica (near stream): 9°58′10.3″N, 83°07′48.9″W; formation unknown, 2.2–3.4 Ma (Late Pliocene).

PPP738 (CJ89-47-1) Limon, Costa Rica, Hotel Olas: 10°00′41.1″N, 83°02′49.3″W; formation unknown, 0.01–1.7 Ma (Pleistocene).

PPP757 (CJ89-00-19) Limon, Costa Rica (Lomas del Mar construction site): 9°59′46.3″N, 83°02′26.2″W; Moin Formation, 1.7–1.9 Ma (Late Pliocene).

PPP1101-1119 (CJ92-00-21 to 40) Ibid.: 9°59′31.0″N, 83°02′12.2″W; Moin Formation, 1.7–1.9 Ma (Late Pliocene).

USGS 8321 Costa Rica, north shore of Provision Island, Gatun Formation; Late Miocene.

USGS 20468 Puerto Limon, Costa Rica; ?Late Pliocene.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(3):551. 1995.

BIOLOGICAL SOCIETY OF WASHINGTON

122nd Annual Meeting, 12 May 1995

The meeting was called to order at 12:10 p.m. in the Waldo Schmitt Room, National Museum of Natural History, by President Janet Reid. Janet asked Treasurer, Chad Walter, and Editor, Brian Robbins, for a summary of the year's activities.

Income for the period of 1 January 1994 to 31 December 1994 was $67,877.14, of which $37,190.00 was received for publication charges, $23,107.00 from dues and subscriptions, $4,331.00 from the sale of back issues and bulletins, and $3,249.14 from interest on the Society's accounts. Expenditures were $66,153.57, of which $56,818.22 was associated with publishing the *Proceedings*, the remainder with management costs and bank charges. The net income for the period was $1,723.57, but Chad noted that this figure does not reflect all income and expenditures associated with the publication of issue 107-4. Financial loss per issue of Volume 107 resulting from unpaid page charges ranged from $2,626.76 for 107-3 to $8,003.54 for 107-4. Income from dues, subscriptions, and sales of past volumes of the *Proceedings* and *Bulletin* compensated for these losses, and there was no significant increase or decrease in the net worth of the Society.

Four issues of Volume 107 of the *Proceedings* were published, comprising 78 papers and 779 pages. There were 87 submissions in 1994, the same as in 1993. As of 1 May 1995, there were 36 submissions, up slightly from 34 in 1994. Brian announced that effective 1 October 1995, Dr. Thomas A. Munroe, our Vertebrate Zoology editor will resign. He will be replaced by Dr. Gary R. Graves, Curator of Birds, NMNH.

Dr. David L. Pawson has been named Chairman of the Nominating Committee for the officers and council members for the 1996 election.

The Society notes with sorrow the death on May 3, 1995, of past president John W. Aldrich, who served from 1947–1949. Among his many services to the Society, Dr. Aldrich was the author of "The Biological Society of Washington: a Centennial History 1880–1980," *Bulletin of the Biological Society of Washington,* No. 4:1–40, published 1980.

The meeting was adjourned at 12:25 p.m.

Respectfully submitted,
Carole C. Baldwin, Secretary

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. If subsidized manuscripts result in more than 12 printed pages, the additional pages must be financed by the author(s). Multiple authorship will not alter the 12 page limit (each author will be viewed as having used his/her 12 subsidized pages). 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.

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OF THE
BIOLOGICAL SOCIETY
OF
WASHINGTON

VOLUME 108 NUMBER 4
28 DECEMBER 1995

ISSN 0006-324X

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Known office of publication: National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Printed for the Society by Allen Press, Inc., Lawrence, Kansas 66044

Second class postage paid at Washington, D.C., and additional mailing office.

POSTMASTER: Send address changes to PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON, P.O. Box 1897, Lawrence, Kansas 66044.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):553–559. 1995

Paraturbanella solitaria, a new psammic species (Gastrotricha: Macrodasyida: Turbanellidae), from the coast of California

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Baton Rouge, Louisiana 70803, U.S.A.

Abstract.—A new species of marine gastrotrich is described. Adults of *Paraturbanella solitaria* new species are simultaneous hermaphroditic, ribbon shaped, up to 530 μm long and up to 64 μm wide. The head bears a pair of sensorial piston pits and its anterior-most portion is hexagonally shaped. The adhesive apparatus consists of anterior and posterior adhesive tubules in addition to bilateral "Seitenfüßchen" organs that take origin in the middle of the pharyngeal region. The new species is placed and discussed within the "*teissieri*" species assemblage. This is the first gastrotrich reported from the coast of California.

Marine gastrotrichs in recent years have been the object of an increasing number of taxonomical and biogeographical studies; extensive faunistic surveys have been carried out in northern Europe (Hummon & Warwick 1992, Jouk et al. 1992), the Mediterranean Sea (Hummon et al. 1990, 1992, 1993, 1994; Balsamo et al. 1992; Todaro 1992; Todaro et al. 1992), the Atlantic coast of the United States (Todaro et al. 1991; Evans 1992, 1994), and the northern Gulf of Mexico (Todaro 1994, Todaro et al. 1995). Unlike fauna of these regions, gastrotrichs of the Pacific coast of the United States are poorly known, the only contributions being those of Wieser (1957) and Hummon (1966, 1969, 1972). Accounts of these authors were limited respectively to gastrotrichs from Puget Sound and the San Juan Archipelago, both within the state of Washington. In an attempt to expand the knowledge of the gastrotrich-fauna of the west coast of the United States, I arranged to obtain some sediment from California beaches. This paper deals with the description of a new *Paraturbanella,* the only gastrotrich species found in a sample of marine sand collected near Los Angeles.

Materials and Methods

Sand was collected on 26 November 1994, from Huntington Beach, California (Fig. 1). After digging a 30 cm deep hole at MLLW, 200 cm^3 of sediment was removed from the wall and bottom of the hole, placed in a plastic bag and shipped to the laboratory within 72 h. In the laboratory the sediment was kept in a cold-room at 14°C and processed within 3 days. Specimens were extracted by the narcotization-decantation technique using an isosmotic magnesium chloride solution (Pfannkuche & Thiel 1988). Supernatant was poured in 5-cm plastic dishes and gastrotrichs were located under a M 5 Wild dissecting microscope. Twenty-five sexually mature, living, relaxed individuals were transferred by a glass micropipette to slides and observed using either differential interference contrast optics with a Microphot-FXA Nikon microscope or phase contrast with a Wild M 20 microscope. At that time gastrotrichs were photographed and/or recorded on S-VHS video tape. Measurements of all specimens observed were obtained form the microscope using an ocular micrometer, or

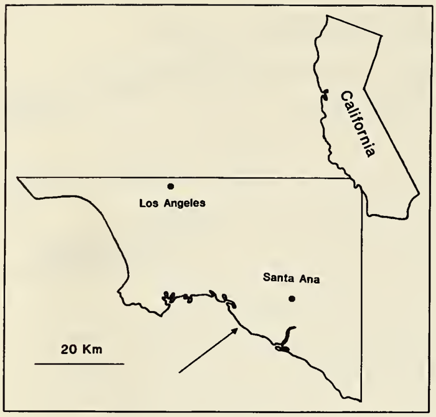

Fig. 1. Location of study site, Huntington Beach (arrow), in southern California.

from photographs or video images. A type specimen has been deposited at the National Museum of Natural History, Washington, D.C., U.S.A. (USNM). Photographs and video images of several individuals are kept in the author's collection (ref. no. PS23-28/94).

Granulometric analysis of the sediment was carried out according to Giere et al. (1988). Mean grain size, sorting coefficient, kurtosis, and skewness were calculated by a computerized program based on the equations of Seward-Thompson & Hail (1973).

Order Macrodasyida Rao & Clausen, 1970
Family Turbanellidae Remane, 1925
Genus *Paraturbanella* Remane, 1927
Paraturbanella solitaria new species
Fig. 2

Holotype.—An adult 460 μm long, formalin-glycerin wholemount (USNM ref. no. 169956).

Type locality.—Huntington Beach, California, U.S.A. (33°41′N; 118°24′W).

Etymology.—The specific name *solitaria* Latin meaning lonely, alludes to the fact that this was the only gastrotrich species found in the sample.

Diagnosis.—*Paraturbanella* with adults up to 531 μm long and 64 μm wide. Head bearing lateral sensorial piston pits and lacking ventral sensorial papillae. Anteriormost portion of the head hexagonally shaped. Eight to ten anterior and ten posterior adhesive tubules; lateral adhesive tubules absent. Caudal cone 7–9 μm long. Caudal lobe 40 μm long. "Seitenfüßchen" organs at the middle of the pharyngeal region, shorter tubules 13–17 μm, longer 25–28 μm. Large, heavily cuticularized buccal cavity; pharynx up to 150 μm long with pharyngeal pores 14–16 μm from the pharyngeal-intestinal junction.

Description.—Mature specimens attain a total body length of 460-531 μm and a width of 47–64 μm (Fig. 2; Table 1). The body is transparent, dorsoventrally flattened and slightly tapering towards the posterior end where it is 23–33 μm wide. The head is 29–30 μm wide and somewhat hexagonal in shape (Fig. 2A). It bears marginal cilia as well as several sensory bristles 10–14 μm long. The posterior margin of the head is demarcated from the rest of the body by a slight constriction, 25–26 μm wide. Located just posterior to the constriction, on each side, is a sensorial piston pit 3.8 μm in diameter (Fig. 2A, C). No other sensorial organ (i.e., ventral sensorial papillae) is present. The adhesive apparatus consists of anterior and posterior adhesive tubules in addition to bilateral "Seitenfüßchen" adhesive organs. Eight to ten anterior tubules (2–5 μm long) are arranged in two ventral symmetrical, hand-shaped, groups (Fig. 2C). Ten posterior tubules (6–21 μm long) are part of the 39–41 μm long caudal lobes. A caudal cone, 7–9 μm long, occurs between the symmetrical caudal lobes (Fig. 2A, B). The two "Seitenfüßchen" adhesive organs, literally "lateral foot," referred also as "dorni" tube groups by Evans & Hummon (1991), consist each of two tubules of unequal length originating ventrolaterally, about in the middle of the pharyngeal region, and directed backwards; the longer tube is 25–28 μm in length while the shorter one is 13–17 μm (Fig. 2C).

The body, dorsally and laterally, bears 18–20 pairs of sensory bristles (9–12 μm long); ventrally it bears the locomotory cil-

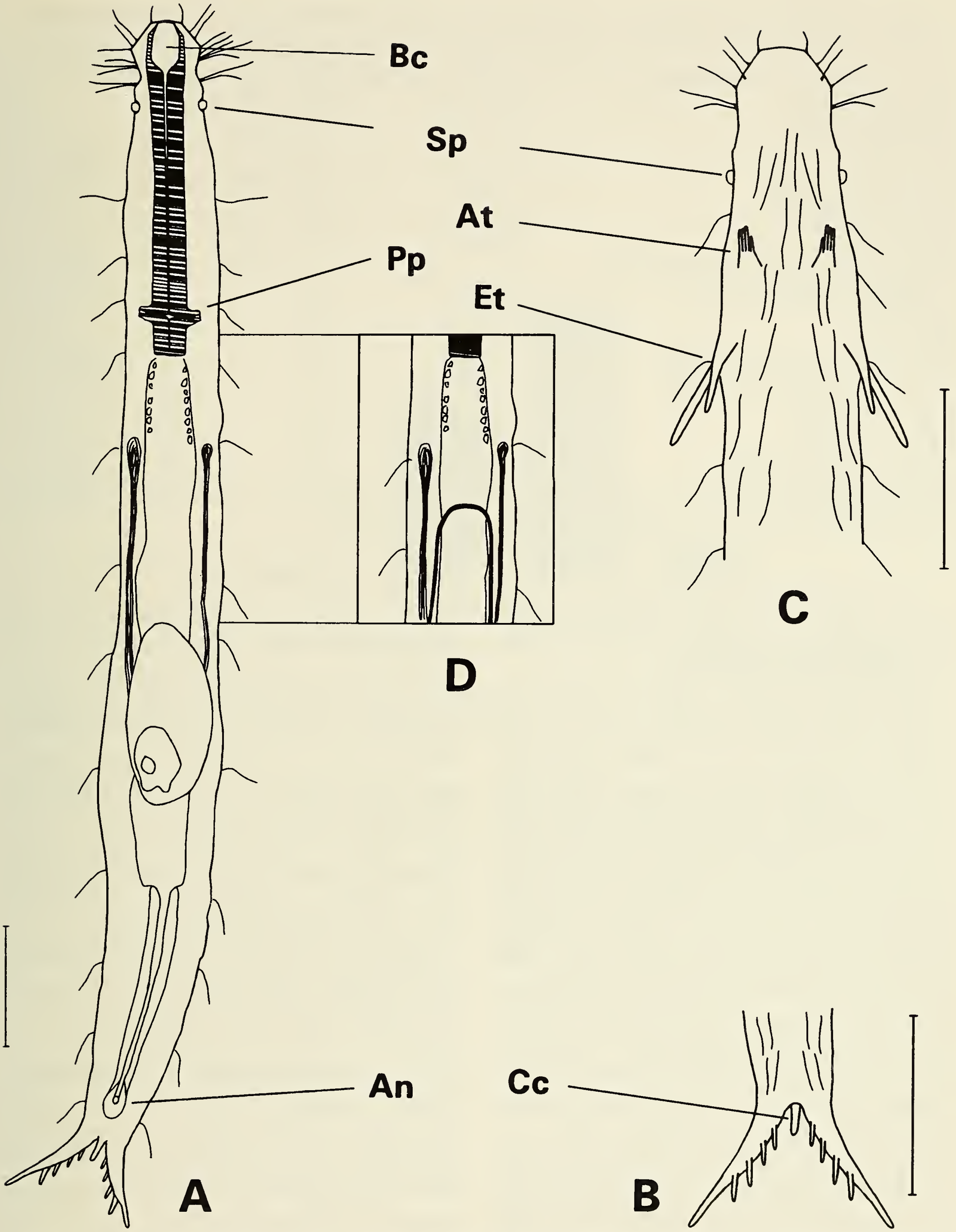

Fig. 2. *Paraturbanella solitaria* new species. A. Habitus; B. Caudal lobes, ventral; C. Anterior end, ventral. D. Mid intestine, ventral. An, anus; At, anterior adhesive tubules; Bc, buccal cavity; Cc, caudal cone; Et, Seitenfüßchen organs; Pp, pharyngeal pores; Sp, Sensorial piston pits. Scale bars represent 50 μm.

Table 1.—Morphometrical parameters of *Paraturbanella solitaria* new species (measurements are in μm).

	Range	$\bar{X}$	*SD*	*n*
Total body length	477.0–531.0	505.9	21.6	25
Caudal lobe length	35.2–41.1	37.5	2.4	24
Head width	29.4–30.4	29.8	0.5	23
Head constriction width	25.0–27.0	25.9	0.8	23
Maximum trunk width	47–64	53.9	6.6	19
Posterior trunk width	23.5–33.4	28.8	3.9	23
Pharynx length	125.0–144.0	132.0	5.2	20
Distance of the pharyngeal pores from the pharyngo-intestinal junction	14.6–17.6	15.6	1.1	21
Mouth length	19.4–21.6	19.6	1.3	20
Mouth width	10.5–11.7	10.9	0.4	19
Seitenfüßchen longer tubule length	25–28.4	27.2	1.3	17
Seitenfüßchen shorter tubule length	11.7–17.6	15.6	2.2	17
Piston pits diameter	3.0–3.9	3.6	0.3	20
Caudal cone length	7.0–9.8	8.9	1.1	19
Number of anterior tubules	8–10	9.6	0.8	25
Number of posterior tubules	10.0	10.0	0.0	25

$\bar{X}$, mean value. *SD,* standard deviation. *n,* number of specimens studied.

ia. The latter are arranged in two bands that run parallel to each other from the head to the base of the caudal lobes.

The buccal cavity is spacious with a thick cuticular wall and measures 19–21 μm in length by 10.7–12 μm in width. The pharynx is 125–150 μm long and 15–16 μm wide; the pharyngeal pores open about 14–16 μm from the pharyngeal-intestinal junction (Fig. 2A). The intestine is straight and morphologically recognizable in two parts. The anterior part is wider and has a thinner wall compared to the posterior part. The anus opens ventrally at 24–30 μm from indentation between the caudal lobes. The reproductive system is made up of paired bilateral testes and probably bilateral ovaries. Testes originate 32–38 μm posterior to the pharyngeal-intestinal junction, thence tapering in sperm ducts (vasa deferentia) that run backward laterally to the intestine until the mid-trunk, where apparently they turn anteriorly to join at the midline, ventrally to the intestine, 65–70 μm posterior to the pharyngeal-intestinal junction (Fig. 2D). A single mature ovocyte, 55–70 μm in length, was visible dorsal to the mid-intestine in most of the specimens studied. Neither additional accessory reproductive organs or genital orifices have been observed.

Habitat.—A large population of individuals representative of all age classes inhabits the fine, silicious, clean sand of the intertidal zone of Huntington Beach shore. There, sand granules are of low sphericity, sub-angular and moderately well sorted (Fig. 3). At the time of the collection, water temperature and salinity were 19°C and 35 ppt respectively. Major associated taxa were nematodes and turbellarians.

Remarks.—In these specimens the head lacks laterally projecting tentacles, the buccal capsule does not extend beyond the mouth, the anterior tubules are borne on fleshy projections (hands), and the "Seitenfüßchen" organs are located in the mid-pharyngeal region. These characteristics, according to Evans & Hummon (1991), affiliate them with the genus *Paraturbanella.* Among the thirteen species so far ascribed to this genus, because of the morphology of the cephalic region, the absence of lateral adhesive tubes and the morphology of the intestine, the present specimens resemble more closely to species that fall within the "*teissieri*" group, namely: *P. mesoptera*

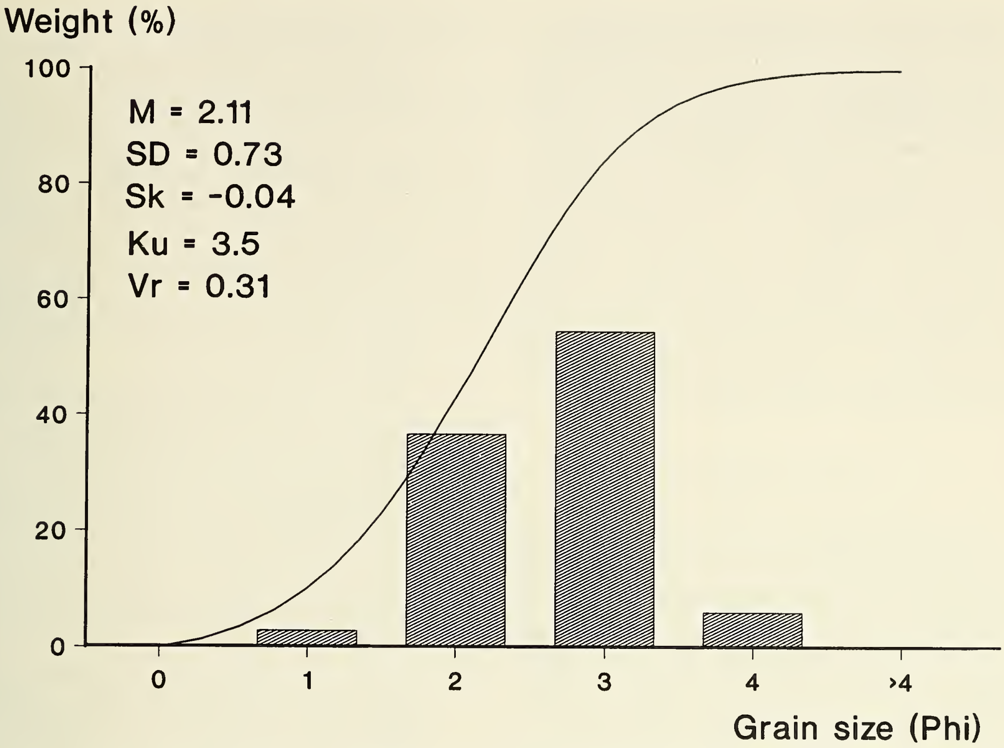

Fig. 3. Granulometric analysis: Histogram by weight and cumulative curve. M, mean grain size; SD, sorting coefficient; Sk, skewness; Ku, kurtosis; Vr, roundness value.

Rao, 1970, *P. microptera* Wilke, 1954, and *P. teissieri* Swedmark, 1954. The specimens from California differ from the ones described from India as *P. mesoptera,* in that they are of a larger size, 460–531 μm vs. 360–380 μm, and in that they bear fewer adhesive tubules in both the anterior groups, 4–5 vs. 9, and in the caudal lobes, 5 vs. 9. The present specimens differ from those affiliated with the European *P. teissieri* in that they lack the ventral sensorial papillae and also because they bear a smaller number of anterior as well as posterior adhesive tubules, 8–10 vs. 12 and 10 vs. 12–20 respectively. Recently Kisielewski (1987), discussed synonymizing *P. microptera* (originally found near Naples, Italy) with *P. teissieri* noticing that the two taxa were described almost simultaneously and that both species were considered by their authors as the second within the genus, and consequently only differences from *P. dorni* Remane, 1927, were included in their discussions. This clearly indicates that Swedmark and Wilke were unaware of each other's findings. The possible synonymy of *P. teissieri* and *P. microptera* was mentioned previously by Schmidt & Teuchert (1969), and an oversight of piston pits (one of the possible differences between the two species) by Wilke was suggested by these authors. On this subject Kisielewski (1987), pointed out that the piston pits were not mentioned either in the original description of *P. teissieri,* and thus, their later findings could not be used as an argument for separating both forms. Kisielewski's conclusions were agreed with by Todaro et al. (1993) on the basis of an extensive faunistic survey around the Italian peninsula that yielded only specimens whose morphological characteristics were in full accordance with the description of the north European *P. teissieri* (M. Balsamo, W. Evans, W. D.

Hummon, M. A. Todaro & P. Tongiorgi, unpubl. data). Among the morphological traits shared between the Italian and the north European specimens, were also sensorial piston pits and sensorial papillae. Since neither one of these organs were reported in the original description of *P. microptera* it was assumed by Todaro et al. (1993), that they were both overlooked by Wilke. On this ground, therefore, I think it is appropriate to affiliate the Californian specimens with a new taxon, proposing the name *Paraturbanella solitaria* new species for it.

Acknowledgments

I am indebted to Neil Scott, surfer and friend, for providing me with the sand from Huntington Beach. I am grateful to Dr. John W. Fleeger for his encouragement and support. The paper benefitted from the comments of Maria Balsamo, Wayne Evans, William Hummon and Paolo Tongiorgi.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):560–567. 1995

Rissoella ornata, a new species of Rissoellidae (Mollusca: Gastropoda: Rissoelloidea) from the southeastern coast of Brazil

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Abstract.—*Rissoella ornata*, a new species, is described from the northern coast of São Paulo State, Brazil. Characters of the shell and anatomy are described, demonstrating, among several interesting anatomical characters, that this species has eyes on small stalks with tentacles far removed from them, a special chamber in the right side of the mantle cavity delimited by the thickness of the mantle and head skin, simultaneous hermaphrodite gonad, the gonoducts free in the haemocoel of the body and two genital pores (a small penis and a female pore) behind the head. The analysis of these characters suggests a relationship of the Rissoellidae with the Euthyneura-Pulmonata.

Only one species of the genus *Rissoella* J. E. Gray, 1847 (type species *R. glaber* J. E. Gray, 1847), Rissoelloidea, Rissoellidae, which comprises very small animals, is known from Brazil. This is *Rissoella caribaea* Rehder, 1943 (Rios 1985:40, 1994: 181).

In studies on associated fauna of the coral *Mussismilia hispida* (Verrill), carried on by João Miguel M. Nogueira (doctoral thesis) on the São Paulo coast in the years 1993–1994, several specimens belonging to the genus *Rissoella* were found. Analysis of the shell characters suggested these specimens are a new species.

Probably due to miniaturization (Fretter 1948), and consequent simplification of structures, the systematic placement of the Rissoellidae has been problematic. They were, for example, included in the Mesogastropoda (Rios 1985), Heterogastropoda (Ponder & Yoo 1977), Neogastropoda (Vaught 1989) and Opisthobranchia (Fretter & Graham 1954) (for a discussion on this subject see Ponder & Yoo 1977). Haszprunar (1985:29) considered that the Rissoellidae appears to represent an intermediate level of organization between the Prosobranchia and the Heterobranchia. Haszprunar (1988) re-analyzed the position of the Rissoellidae, considering the group as part of a superfamily within Allogastropoda (Heterobranchia). This systematic problem has been aggravated by scanty knowledge of the anatomy of the Rissoellidae, for only two species have been described anatomically (Fretter 1948).

The family Rissoellidae includes only one genus, *Rissoella*, which was subdivided in four subgenera (Ponder & Yoo 1977), mainly characterized by the radula.

Materials and Methods

The specimens were collected by scuba diving, fixed in 4% formalin, preserved in 70% ethanol, and deposited in "Museu de Zoologia da Universidade de São Paulo" (MZUSP) collection.

Twenty specimens for anatomical studies were decalcified in Railliet-Henry fluid. Some of them were dehydrated in ethanol series, stained in carmine, cleared and fixed in creosote. Serial sections of three specimens were stained in haematoxylin and eosin. Shells, radulae, jaws and opercula were examined under SEM, in the "Laboratório de Microscopia Eletrônica do Instituto de Biociências da Universidade de São Paulo", using the technique described by Solem (1970, 1972). All drawings were made with the aid of a camera lucida. Systematic and shell terminologies were based on Ponder & Yoo (1977), and the anatomical terminology on Fretter (1948).

In the figures the following abbreviations are used:

ag:	albumen gland
an:	anus
cg:	capsule gland
da:	anterior lobe of the digestive gland
dc:	duct to capsule gland
dd:	duct of posterior lobe of the digestive gland
dg:	posterior lobe of the digestive gland
ec:	egg covering
ey:	eye
fa:	fold parallel to mantle border
fc:	phaecal chamber
fh:	flap of the head adjacent to the phaecal chamber
fm:	fold perpendicular to the mantle border
fp:	female genital opening
ft:	foot
gi:	gill vestiges
hd:	hermaphrodite duct
hg:	hypobranchial gland vestiges
hs:	head-foot skin
in:	intestine
ja:	jaw
ki:	kidney
ll:	left lobe of the columellar muscle
ls:	longitudinal posterior slit of the foot
mb:	mantle border
od:	odontophore
oe:	oesophagus
og:	opercular peg
op:	operculum
ow:	outer wall of egg capsule
pc:	posterior lobe of the capsule gland
pe:	penis
pt:	prostate
ra:	radula
rl:	right lobe of the columellar muscle
rt:	rectum
sn:	snout
ss:	style sac
st:	stomach
te:	tentacle
vd:	vas deferens
vm:	visceral mass
yg:	yolk granules of the egg

Systematics

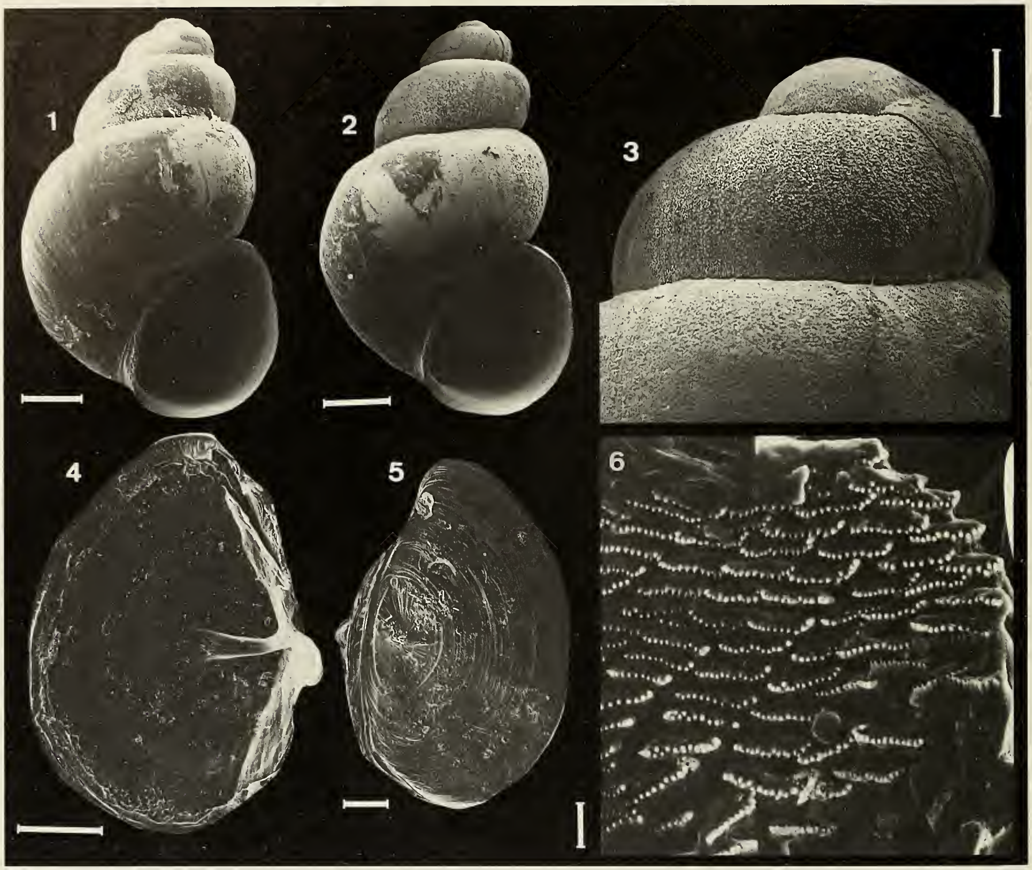
Rissoella (*Rissoella*) *ornata*, new species
Figs. 1–18

Types.—Holotype MZUSP 28004 (length 1.00 mm by 0.60 mm). Paratypes: MZUSP 28005, 1 specimen (1.10 mm by 0.65 mm); MZUSP 28006, 1 specimen (1.10 mm by 0.68 mm); MZUSP 28007, 5 shells (1.40 by 0.71 mm; 1.00 by 0.62 mm; 0.90 by 0.55 mm; 0.83 by 0.53 mm); MZUSP 28008, 1 shell (1.20 by 0.61 mm); MZUSP 28009, 13 specimens and anatomical slides; MZUSP 28010, 24 specimens; 28012, 7 specimens; 28013, 25 specimens; 28015, 24 specimens; all these from type locality. MZUSP 28014, 3 specimens, São Paulo, São Sebastião, Búzios Island. MZUSP 28011, 1 specimen, São Paulo, Ubatuba, Palmas Island. Museu Oceanográfico da Fundação Universidade de Rio Grande: MORG 32289 (2 specimens from type locality). Museu Nacional da Universidade Federal do Rio de Janeiro, MNRJ 6934 (2 specimens from type locality).

Type locality.—Brazil, São Paulo State, São Sebastião Municipality, Vitória Island, 23°45′S 45°01′W.

Diagnosis.—South Atlantic species with tall spire, smooth surface of the shell, deep suture, umbilicus deep and bordered by thin walls.

Description.—Shell: minute (to 1.5 mm), thin, tall, smooth and shiny (Figs. 1, 2, 14), transparent, colorless. Protoconch with one smooth whorl, relatively large (Fig. 3). Spire length slightly longer than the length

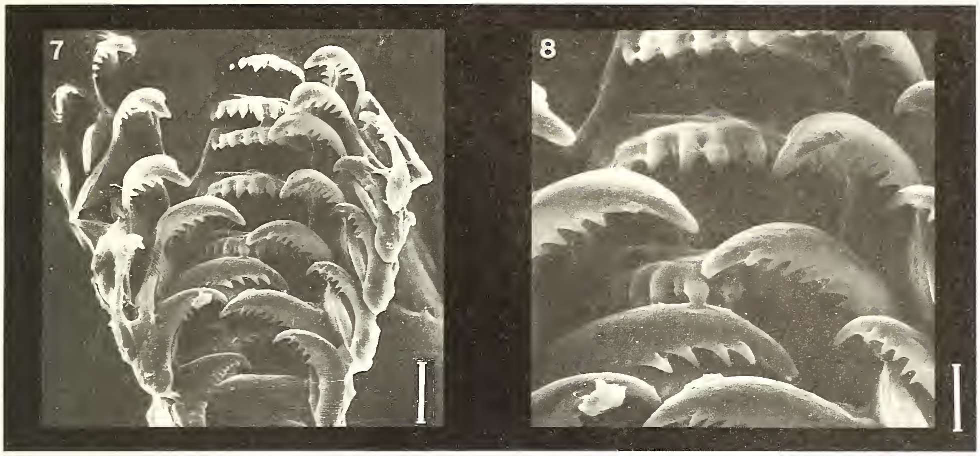


Figs. 1–6. *Rissoella ornata.* 1, frontal view of a paratype shell, scale = 200 μm; 2, the same for other specimen, scale = 200 μm; 3, detail of the specimen of Fig. 2, showing a profile of the protoconch and first teleoconch whorl, scale = 50 μm; 4, inner view of the operculum, scale = 100 μm; 5, outer view of the operculum, scale = 50 μm; 6, detail of a jaw plate, scale 5 μm.

of the aperture. Teleoconch to three convex whorls. Suture deep. Surface with distinct growth lines, slightly undulated axially. Periostracum thin, velvet-like (Fig. 3). Aperture oval, of moderate size (discretely smaller than a half of total shell length). Inner lip slightly thickened. Umbilicus conspicuous, externally bordered by a sharp edge (Figs. 1, 2, 14). Outer lip rounded and simple.

Operculum: somewhat rounded, occupies entire aperture, pale-yellow, transparent. Externally with concentric growth lines, nucleus near mid region of the inner edge (Fig. 5). Internally (Fig. 4), the slightly convex columellar edge is bordered on its inner side by a sharp ridge from which arises a short, blunt peg; a short, rounded ridge arises from the base of the peg and passes across less than half of the inner surface of the operculum at right angles to the columellar edge. Outer edge simple, convex.

Head-foot: yellowish-white with brown pigment on lateral region of the foot and around eyes (Fig. 15). Snout bifid (Figs. 11, 13), with two rounded lobes and two tentacles, which arise one at the base of each lobe; tentacles cylindrical, tapering slightly towards a blunt tip (Figs. 11, 13). Eyes well-developed, dark, on short stalks far back on the neck; lens massive and very-large. Foot slightly lanceolate, its opercular



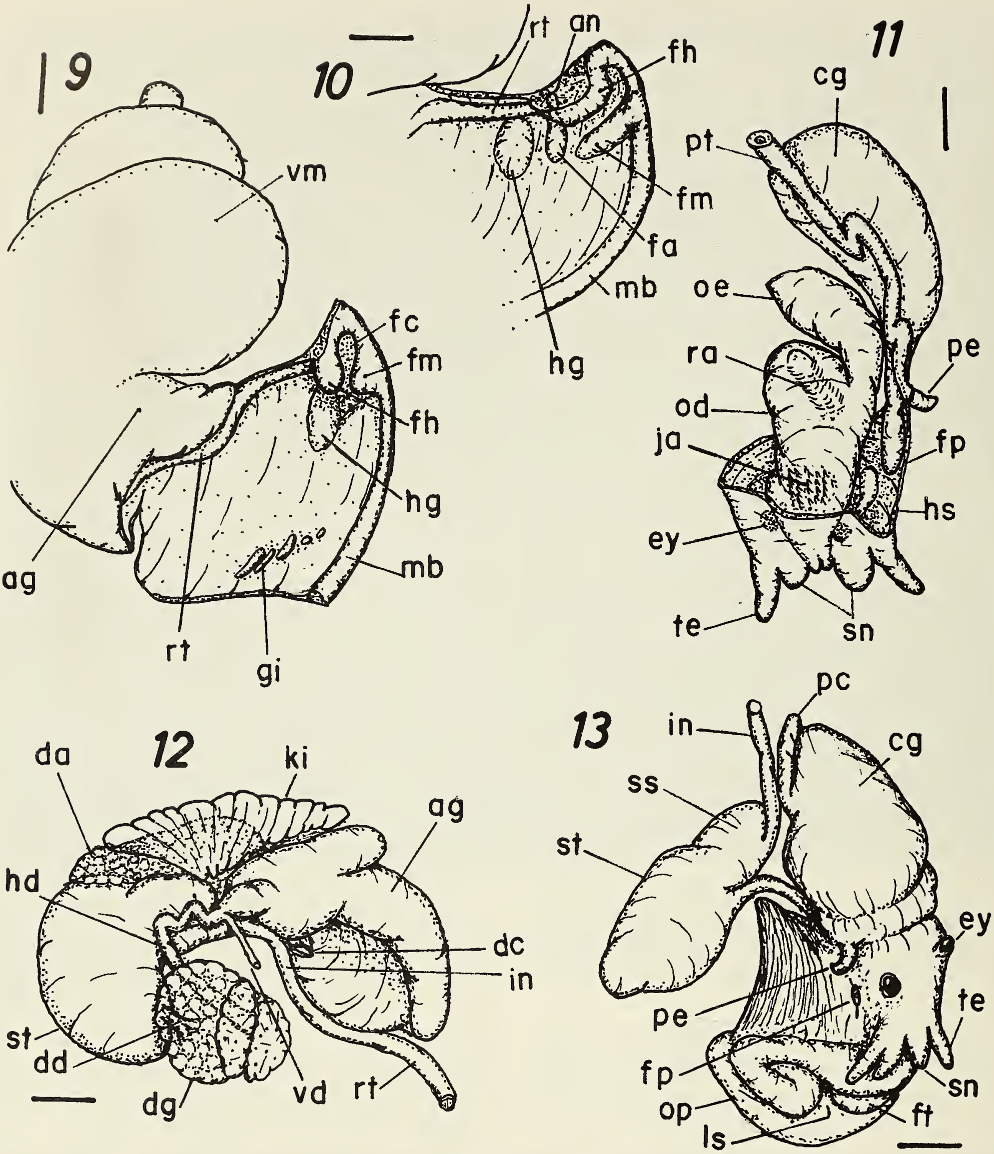
Figs. 7–8. *Rissoella ornata.* Details of the radular teeth, 7, scale = 10 μm; 8, scale = 5 μm.

lobe on each side projects beyond the lateral margins of the sole. Posterior pedal mucous gland opening in a median longitudinal slit sited in posterior half of the pedal sole (Figs. 13, 16). Head-foot greatly compressed posteriorly by the developed capsule gland (Fig. 13); upon dissection, a large concavity appears separating the head-foot from visceral mass, which are united only by oesophagus. Columellar muscle distally bilobed (Fig. 16), oesophagus and the female duct running between both lobes; right lobe thick, left lobe thin (Fig. 16).

Visceral mass: visible through the transparent colorless shell (Fig. 15); in the posterior half of each whorl a yellowish-white digestive gland is present, in the anterior half of each whorl a beige gonad, in the form of several arcs (with convexity posterior) (Fig. 15). Some specimens (MZUSP 28015) have a dark pigment in the mantle. In these specimens, the above cited structures are difficult to see.

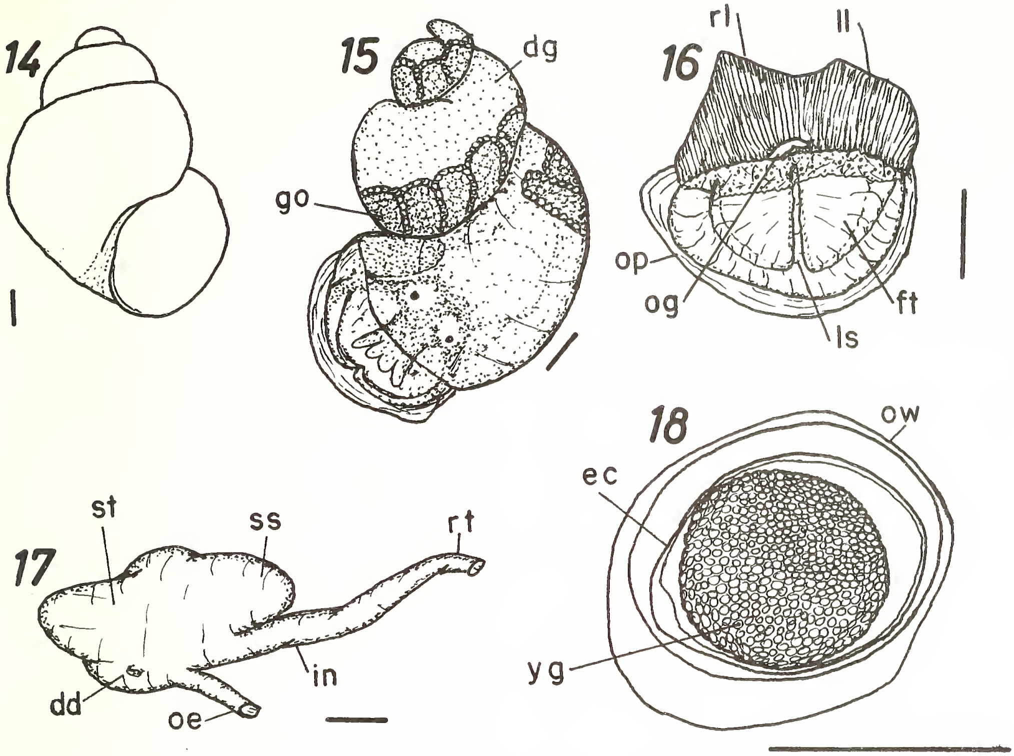
Pallial cavity: shallow (about a half of whorl) (Figs. 9, 10), mostly occupied by the female glands (albumen and capsule glands). No special structures found, except the faecal chamber (described bellow) on right side, and gill vestiges on left extremity (Fig. 9). These gill vestiges, which have functional cilia, present great variation in number and form of the leaflets. Mantle border rather thickened, without tentacles or siphon (Fig. 10).

Digestive system: jaw in two lateral plates (Fig. 11), which have several scales turned backward, each scale has an aligned series of minute cusps on its cutting edge (Fig. 6). Odontophore very long, cylindrical (Fig. 11). Radula short—about 10–12 rows; rachidian tooth large, wide, with convex cutting edge bearing about 10 similar-sized cusps (Figs. 7, 8); lateral teeth large, convex, triangular, with 4-6 pairs of small sharp cusps and one large terminal cusp (Fig. 8); inner marginal teeth similar to (but smaller than) the lateral teeth (Fig. 7); outer marginal teeth missing. Oesophagus originates in ventral-right region of the odontophore, flattened and wide (Fig. 11), skirts the columellar muscle, inserting in mid-ventral region of the stomach (Figs. 12, 13, 17). Stomach (Figs. 12, 13, 17) large, rather flattened, with style sac differentiated. Digestive gland with two lobes (Fig. 12), one small and anterior, bound posteriorly by the stomach, ventrally by the style sac, dorsally by the kidney and anteriorly by the albumen gland. The large and posterior lobe of the digestive gland, which opens ventrally in stomach (Fig. 12), spreads through the



Figs. 9–13. *Rissoella ornata.* 9, inner view of the pallial cavity, mantle border in frontal view; 10, mantle border in inner view, showing the faecal chamber; 11, ventral view of the head, foot removed, showing the anterior region of the digestive and genital systems; 12, ventral view of the posterior half of the first whorl and the second whorl; 13, dorsal-right view of the head-foot and stomach. Scales = 100 μm (see Materials and Methods for abbreviations).

posterior half of the coils of the visceral mass (Fig. 15). Intestine a wide tube, originates near the insertion of the oesophagus in stomach (Figs. 13, 17) and lies ventrally to the style sac and the albumen gland in the right margin of the pallial cavity (Fig. 12), running in this cavity for a short distance and opening into a special faecal chamber (Figs. 9, 10), which is located in the right angle of the mantle edge. This chamber is delimited (Fig. 10) posteriorly by a mantle fold from anus until a short



Figs. 14–18. *Rissoella ornata.* 14, shell of a young specimen in frontal view; 15, outer view of a specimen extracted from the shell; 16, ventral view of the posterior half of the foot and the columellar muscle, anterior half of the foot extracted; 17, ventral-right view of the stomach; 18, mature egg capsule. Scales = 100 μm (see Materials and Methods for abbreviations).

distance to the left (fa); right and dorsally by the mantle wall; on the left by a mantle fold rather perpendicular to the mantle border (fm); and ventrally by a flap of the head skin (fh).

Reproductive system: gonad (Fig. 15) on the columellar side of the visceral mass (described above), hermaphrodite, with sperm and ova developed in the same tubules. Gonadial duct single (Fig. 12) and coiled with thick walls, running along the columella until the posterior end of the body whorl, where it divides into two divergent branches. One of these branches leads to the pallial vas deferens (vd) and the other to the albumen gland (ag).

Vas deferens, initially narrow and thin-walled (Fig. 12), anteriorly passes forward on the right side of the head. Posterior to the odontophore it becomes larger, with thick walls and rather coiled (prostate) (Fig. 11), turns at an opened angle along the dorsal surface of the body whorl to the right side, where it ends in a relatively short tubular penis, which has a rather pointed tip (Figs. 11, 13).

Albumen gland amorphous (Fig. 12), of considerable size, flattened between the kidney and the capsule gland. Capsule gland (Figs. 11, 13) well-developed, attached to the head-foot complex and not to the mantle. Between the albumen and capsule glands a flattened posterior lobe of the capsule gland is generally present (Fig. 13: pc). Anteriorly the capsule gland leads forward above the oesophagus and to the right side of the head, projecting from the dorsal wall as an opaque white mass (Fig. 11). The capsule gland opens into the right side of the head by way of a small pore, which is anterior-ventral to the root of the penis, behind the tentacles (Figs. 11, 13: fp).

Development: the proportionally large egg capsules are manufactured apparently one at a time in the pallial oviduct, when developed, occupies most of the space within the capsule gland. The egg capsules (Fig. 18) are similar to that described by Fretter (1948) for *Rissoella diaphana* (Alder) and *R. opalina* (Jeffreys). The capsule contains only one egg. Outer wall thick and transparent, between this and the thin transparent membrane, which covers the egg, a transparent fluid (Fig. 18). About half of examined specimens have a developed capsule within the capsule gland. Even small specimens have developed gonad and egg capsules. Animals of several sizes are found together, which probably indicate that *R. ornata* is not annual like its European relatives (Fretter 1948).

Habitat.—*R. ornata* was found moving on coral *Mussismilia hispida,* about 5 m depth. According to the literature, other species of *Rissoella* live on and feed upon intertidal algae.

Range.—Brazil, sub tidal level, northern coast of São Paulo State.

Etymology.—The contrast between the dark gonad and the clear digestive gland, visible through the shell, gives the effect of each whorl is ornamented (lt. *ornata*) by several arches (Fig. 15).

Discussion

Rissoella (*R.*) *ornata* differs from *R.* (*Jeffreysilla*) *caribaea* in having a longer spire, deeper suture, smaller body whorl and the umbilicus bordered by thin walls.

Using the diagnosis of the *Rissoella* subgenera by Ponder & Yoo (1977) the subgeneric allocation of *R. ornata* is doubtful as this species has radular similarity to both *Rissoella* s.s. and *Jeffreysiella* Thiele, 1912. The shape of the lateral and inner marginal teeth, and the similarity between both, resemble *Jeffreysiella*; but the absence of the outer marginal teeth and the shell shape resemble *Rissoella* s.s.

Based on the anatomical knowledge of three species: *Rissoella diaphana, R. opalina* (apud Fretter 1948) and *R. ornata* described herein, some interesting comments on the relationship of the Rissoellidae may be done. On the one hand, the Rissoellidae have small size, palcispiral operculum, snout, small gill (although vestigial), ripidoglossate-like radula, large stomach with style sac, oesophagus insertions near intestine origin, among other characters, which reveal some similarity with the Rissoidea (= Hydrobioidea, "basal" Cenogastropoda). On the other hand, the Rissoellidae have eyes on small stalks with tentacles far removed from them, a special chamber in the right side of the mantle cavity delimited by the thickness of the mantle and head skin, jaws, a peculiar arrangement of the digestive glands, simultaneous hermaphrodite gonad, the gonoducts free in the haemocoel of the body and two genital pores (a male and a female) behind the head, which show similarity with the Pulmonata. The gonoducts free in the haemocoel of the body has been considered as a character of the "higher" Heterobranchia (Haszprunar 1985) and synapomorphy of the Euthyneura (Haszprunar 1988). Based on this fact, the Rissoelloidea may be considered as Euthyneura.

Acknowledgments

Special thanks to João Miguel M. Nogueira for collecting material.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):568–576. 1995

Description of a new viviparous species of *Dentatisyllis* (Polychaeta: Syllidae) from Belize with an assessment of growth and variation, and emendation of the genus

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Abstract.—*Dentatisyllis mangalis,* a new viviparous species of syllid polychaete, is described from mangrove and adjacent shallow-water habitats of Twin Cays, Belize. The new species is distinguished by a combination of short dorsal cirri with only a few articles and compound falcigers with long tapering blades bearing bifid tips. Analysis of meristic and linear characters used in classical syllid taxonomy revealed that the mean number of articles per dorsal cirrus per individual increases only slightly with increasing body length (growth); proventricle length increases linearly with body length; and the ratio of proventricle length to width is relatively independent of body length. Furthermore, overall growth is accomplished more by the addition of segments than the elongation of existing ones. The genus diagnosis is emended to include the presence of nuchal organs.

An investigation of the diversity and distribution of syllid polychaetes inhabiting shallow-water habitats at Twin Cays, Belize, has recorded a number of known and previously unknown species of the subfamilies Exogoninae and Eusyllinae (Russell 1989a, 1989b, 1991). Species of the subfamily Syllinae collected from these habitats include the new viviparous species of *Dentatisyllis* Perkins, 1981, described herein. The new species is illustrated and the variability of selected linear and meristic characters is evaluated.

The viviparous mode of reproduction, exhibited by the new species and documented herein, is particularly noteworthy. Brooding, however, is quite common in syllids, and internal brooding with direct development (viviparity) has been reported (including the present paper) for seven species (San Martín 1984, Wilson 1991).

Materials and Methods

Specimens were obtained from core samples collected along a 40-m transect spanning a continually submerged mangrove forest, a shallow unshaded algal flat, and a turtlegrass (*Thalassia testudinum*) meadow. Depth along the transect at time of sampling ranged from 9 to 130 cm. Further description of the habitats sampled and explanation of the core sample labels (used below under "Type material") are provided by Russell (1989a).

Material was fixed in a seawater solution of approximately five percent formaldehyde and one percent methanol, stained with Rose Bengal, and preserved in 70% ethanol. Specimens were examined by mounting them temporarily on slides in a medium of glycerin and 70% ethanol (1:1).

Linear measurements were made using an ocular micrometer. Body length was measured from the posterior margin of the tentacular segment to the posterior tip of the pygidium; body width across the proventricle without the parapodia. The mean number of articles per dorsal cirrus was determined for each type specimen by counting the articles in one dorsal cirrus on each setiger, provided a dorsal cirrus was present and could be seen in its entirety. Occasionally both dorsal cirri of one setiger were counted and the number of articles comprising each cirrus differed. In such instances the larger number was used in the calculation of the mean to ensure that the data was not biased toward the conclusion that the species is characterized by short (few articles) dorsal cirri, a possibility that was of particular interest. The dorsal cirri on setiger 1, which appeared to always be longer than other dorsal cirri, and the dorsal cirri on the last three setigers, which typically were shorter than others, were not included in the mean. It was assumed that the number of articles comprising these cirri was strongly determined by their position on the body, and that, in individuals with only a few dorsal cirri (e.g., small individuals or individuals that have lost dorsal cirri), including these cirri in the mean would result in a value that was not representative. Consequently, they were omitted from counts on all individuals.

Summary statistics and the product-moment correlation coefficient (r) were calculated using Microsoft Excel (version 4.0). Prior to the calculation of r for the relationship between body length and the ratio of proventricle length to width, the latter was transformed using a $\log_{10}$ transformation due to the tendency of ratios not to be normally distributed (Sokal & Rohlf 1981).

Type material has been deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C., U.S.A. Comparative material was borrowed from the Museo Nacional de Ciencias Naturales de Madrid (MNCNM), Madrid, Spain.

Systematics

Family Syllidae Grube, 1850
Subfamily Syllinae Rioja, 1925
Genus *Dentatisyllis* Perkins, 1981, emended

Diagnosis.—Holotype of the type species, *Dentatisyllis carolinae* (Day, 1973) with two ciliated slits along the posterior margin of the prostomium, one on either side of the dorsal midline, each indicating the presence of a nuchal organ.

Remarks.—Nuchal organs were reported absent in the original generic diagnosis (Perkins 1981), which is otherwise complete and accurate.

Dentatisyllis mangalis, new species
Figs. 1–3; Tables 1, 2

Dentatisyllis brevicirra—Wilson, 1991:506 *nomen nudum.*

Type material.—Holotype: T-4LB (USNM 102495). Paratypes: M-3, 1 (USNM 102496); C-3, 2 (USNM 102499); C-5, 1 (USNM 102500); C-8, 1 (USNM 102502); T-2LF, 3 (USNM 102510); T-2LB, 2 (USNM 102511); T-4UB, 1 (USNM 102512); T-4LB, 4 (USNM 102513); T-5UB, 1 (USNM 102514); T-5LF, 1, (USNM 102515); T-7F, 3 (USNM 102516); T-7B, 3 (USNM 102517); T-9F, 2 (USNM 102518); T-9B, 2 (USNM 102519); T-11F, 3 (USNM 102520); T-11B, 4 (USNM 102521). All types from West Bay, Twin Cays, Belize (16°50′N, 88°05′W); 9–130 cm depth; collected Nov 1983.

Additional material examined.—*Dentatisyllis carolinae* (Day, 1973), holotype (USNM 43146); 4 paratypes (USNM 43147) off Beaufort, North Carolina, North Atlantic: 20 m, May 1965. *Dentatisyllis* sp. A of Uebelacker, 1984, 1 specimen (USNM 65669), id. by Barry Vittor and Associates, off Crystal River, Florida, Gulf of Mexico: 38 m, Nov 1977. *Dentatisyllis junoyi* López & San Martín, 1992, holotype (MNCNM, 16.01/802), off Curral Velho, Boavista Island, Cape Verde Islands, North Atlantic, 15 m, Aug 1985; paratype (MNCNM, 16.01/803), off Salamanza, Sao Vicente Island, Cape Verde Islands, North Atlantic.

Description.—All type specimens complete. Body slender and approximately oval in cross-section; pale yellow without markings; length without palps, prostomium, and tentacular segment, 0.8–3.9 mm; width

Table 1.—Summary statistics for selected features of *Dentatisyllis mangalis.*

Feature	Range	$\bar{X}$	*SD*	*n*
Body				
length (mm)	0.8–3.9	2.1	0.7	35
width (mm)	0.1–0.2	0.17	0.32	18
number of setigers	19–47	33	7.4	35
Proventricle				
length (μm)	200–430	308.6	61.1	35
width (μm)	70–150	103.6	17.7	33
length/width	2.1–3.9	3.0	0.4	33
Number of articles				
median antennae	7–13	10.6	1.7	28
lateral antennae	4–8	6.1	1.2	37[a]
dorsal tentacular cirri	4–10	7.3	1.8	24[a]
ventral tentacular cirri	2–5	3.0	1.2	5[a]
dorasl cirri of setiger #1[b]	4–10	7.9	1.6	28
anal cirri	4–10	6.4	1.3	33

[a] Some on same individual.

[b] Summary statistics for other dorsal cirri are presented in Table 2.

across proventricle without parapodia 130–230 μm; number of setigers 19–47. (Table 1 provides descriptive statistics for these and other quantitative features.)

Prostomium oval, 1.5–3 times wider than long, with two pairs of lensed eyes on posterior half of prostomium in a flattened trapezoidal arrangement (Fig. 1A). A third pair of smaller eyes (eyespots) present on anterior portion of prostomium, one at the base of each lateral antenna. Median antenna with 7–13 articles, arising between posterior pair of eyes; lateral antennae with 4–8 articles, originating on anterior portion of prostomium. Palps triangular, free for most of length; appear strongly contracted in most specimens. A pair of nuchal organs, each in a narrow ciliated groove on either side of the dorsal midline along posterior margin of prostomium (Fig. 1A).

Dorsal tentacular cirri with 4–10 articles; ventral tentacular cirri with 2–5 articles. Dorsal cirri on setiger 1 longest with 4–10 articles, all other dorsal cirri with 3–8 articles, fewer in posteriormost 3–4 setigers. Mean number of articles per dorsal cirrus increases with body length (Fig. 3A). (Table 2 provides descriptive statistics on the number of articles in dorsal cirri by individual.) First article of tentacular and dorsal cirri typically slender and cylindrical (Fig. 1B), arising from a short broader cirrophore; other articles of these cirri larger, rounded or bulbous. Ventral cirri short, not extending beyond parapodia, larger and bulbous in anterior setigers (Fig. 1C), becoming digitiform and tapering slightly in middle and posterior setigers (Fig. 1B). Pygidium short, semicircular, with terminal anus (Fig. 1D) and two anal cirri each with 4–10 articles usually larger than articles of dorsal cirri; with or without a third short smooth anal cirrus arising midventrally between articulated anal cirri.

Aciculae slightly enlarged distally, tips protruding from parapodia through cuticle; 2 slender aciculae per parapodium in anterior setigers, tip of one less oblique than the other (Fig. 1E); aciculae solitary and heavier in middle and posterior setigers (Fig. 1F). Simple setae present only in posterior setigers: superior simple setae (Fig. 2A) solitary, about as long as shafts of compound falcigers, blunt bilobed to bifid tips, fine distal serrations typically along superior surface, approaching plumose condition; inferior

Table 2.—Summary statistics by specimen of *Dentatisyllis mangalis* for number of articles in dorsal cirri.

Holotype (H) or Paratype (P)	Range	$\bar{X}$	*SD*	n^a	n as Percentage of Total Number of Setigers
H	4–8	6.0	0.7	31	94
P	4–7	5.9	0.8	30	70
P	5–6	5.1	0.4	15	58
P	4–6	4.9	0.9	21	76
P	6–8	6.6	0.7	8	23
P	3–7	5.2	0.9	17	74
P	4–7	5.4	0.9	21	55
P	4–7	5.2	0.9	15	50
P	6–7	6.3	0.5	15	35
P	3–5	4.1	0.5	13	72
P	4–6	5.2	0.5	18	62
P	5–7	5.5	0.6	19	54
P	4–5	4.4	0.5	20	91
P	4–5	4.6	0.5	21	84
P	4–5	4.7	0.4	21	100
P	5–8	6.4	0.7	37	88
P	4–6	5.2	0.6	24	77
P	4–6	5.5	0.6	24	89
P	4–6	5.1	0.6	21	78
P	4–7	5.9	0.7	23	82
P	3–4	3.8	0.4	13	81
P	4–6	5.3	0.6	21	75
P	4–6	5.1	0.7	17	57
P	3–6	5.4	0.8	28	76
P	3–4	3.9	0.3	16	94
P	3–5	4.2	0.6	19	86
P	4–6	4.9	0.5	27	96
P	5–7	6.1	0.5	35	92
P	5–7	5.6	0.6	33	94
P	3–6	5.1	0.6	25	89
P	4–6	5.0	0.5	18	64
P	4–7	5.8	0.7	30	94
P	4–5	4.2	0.4	13	62
P	5–7	5.7	0.5	34	100
P	4–5	4.1	0.3	15	100

[a] Number of dorsal cirri examined. Only one cirrus (when present and visible) from each setiger was included in count.

simple setae shorter, solitary, slightly curved (Fig. 2B), with bifid tips and fine distal serrations along inferior surface. About 9 compound setae per anterior fascicle, number gradually decreasing posteriorly to 3 or fewer per fascicle in last few posterior setigers. Compound falcigers with bifid serrated blades (Fig. 2C–E). Blades of superiormost falcigers long, narrow, tapering to minutely bifid tips with knob-like terminal tooth; longest in middle and posterior setigers. Commonly 2 of these long-bladed falcigers per fascicle in anterior setigers, usually 1–2 per fascicle in other setigers, occasionally absent from a fascicle.

In mature specimens, pharynx usually extending to setiger 7 when inverted, to setiger 5 when everted, about equal in length to proventricle, with an anterior mid-dorsal tooth; anterior end surrounded by 10 large papillae or lobes, tips ciliated; anterior margin of pharynx denticulate (Fig. 2F), with 10 distinct teeth arranged in opposition to pharyngeal lobes, tooth shape sometimes rough and irregular. Proventricle length 200–430 μm, width 70–150 μm, length to width ratio 2.1–3.9, with about 32 muscle rows. Proventricle length exhibiting a more or less linear relationship with increasing body length (Fig. 3B). Proventricle length to width ratio remaining relatively constant or increasing slightly with increasing body length (Fig. 3C).

Reproduction through viviparity; holotype and numerous paratypes with from 1 to 4 young present in coelom (Fig. 2G). Young not enclosed within a membrane; with up to 13 setigers bearing setae similar to those of adult.

Etymology.—The species name refers to the mangrove community or mangal (*sensu* MacNae 1968; Tomlinson 1986) that is a conspicuous feature of the type locality.

Discussion

Synonymy.—Dentatisyllis brevicirra, as used by Wilson (1991:506, table 2), is a *nomen nudum* according to the International Code of Zoological Nomenclature (Third Edition 1985). That name had been, prior to Wilson's paper, only informally proposed by me in a conference poster for the concept herein established as *D. mangalis.*

Comparison to congeners.—Dentatisyllis mangalis agrees with the generic diagnosis (as emended above) and resembles *Dentatisyllis carolinae* (Day, 1973), Perkins

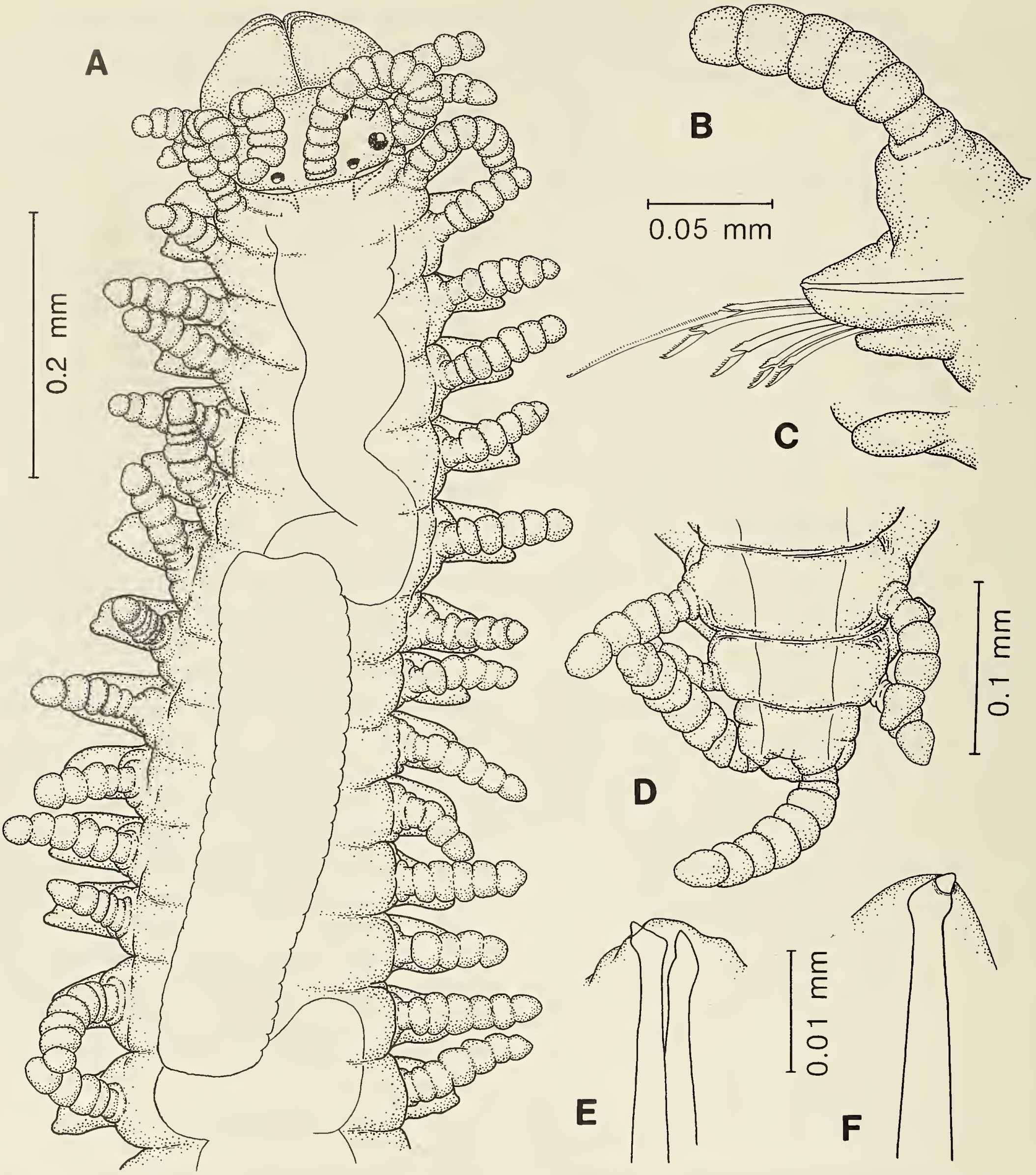

Fig. 1. *Dentatisyllis mangalis,* new species. A. Anterior end, contracted (setae not drawn). B. Parapodium from middle setiger, posterior view. C. Ventral cirrus on anterior setiger, posterior view. Scale same for B and C. D. posterior end, dorsal view (setae not drawn). E. Aciculae and tip of parapodium from anterior setiger. F. Acicula and tip of parapodium from middle setiger. Scale same for E and F. A from paratype USNM 102515; B, C, E, F from paratype USNM 102516; D from paratype USNM 102511.

(1981:1166, fig. 38a–h) with respect to the bifid simple setae and superior compound falcigers, but differs by having antennae, tentacular cirri, and especially dorsal cirri comprised of relatively few articles, with the first article of dorsal cirri consistently more slender and cylindrical than others; only two aciculae per anterior parapodium; superiormost compound falcigers with long narrow blades; blades of other compound

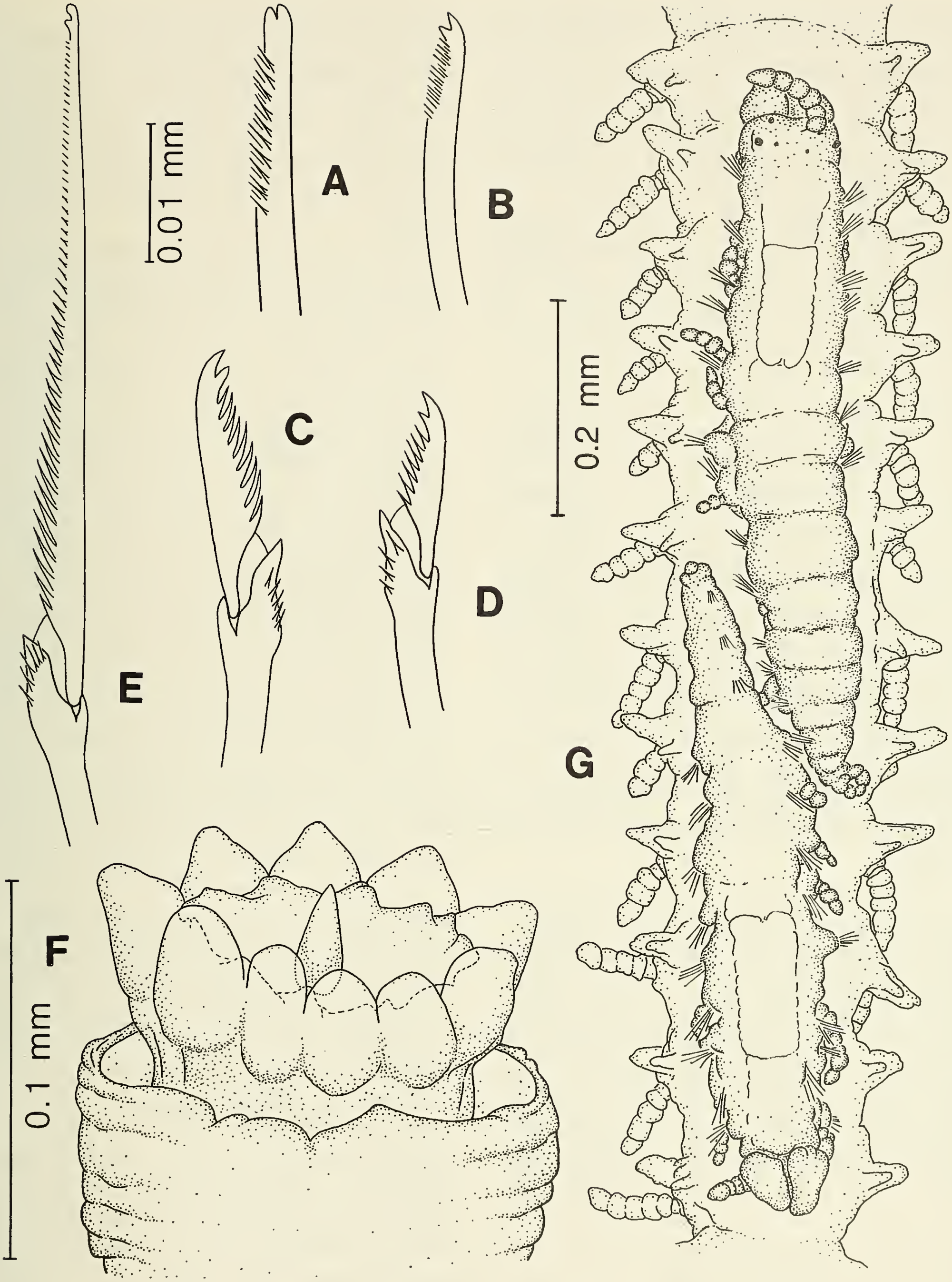

Fig. 2. *Dentatisyllis mangalis,* new species. A. Superior simple seta from posterior setiger. B. Inferior simple seta from posterior setiger. C. Superior compound falciger from middle setiger. D. Inferior compound falciger from anterior setiger. E. Compound spiniger-like seta from anterior setiger. Scale same for A–E. F. Anterior end of everted pharynx, ventral view. G. Two offspring prior to release, dorsal view of one, ventral view of other, inside setigers 21–32 of adult in ventral view, setiger 21 at top of figure (some external structures of offspring obscured by adult's internal structures, especially musculature associated with aciculae in each parapodium; setae of offspring included where visible; setae of adult not drawn). A, B from paratype USNM 102510; C–E from paratype USNM 102516; F from paratype USNM 102511; G from holotype USNM 102495.

falcigers with sharply pointed terminal and subterminal teeth; blades of inferior compound falcigers without enlarged subterminal tooth; and a typically smaller body size. *Dentatisyllis mangalis* differs in the same ways from *Dentatisyllis* sp. A of Uebelacker (1984:30.115, fig. 30.110 a–d).

The new species also resembles *Dentatisyllis junoyi* López & San Martín, (1992: 219, fig. 1a–l) particularly with regard to the superiormost compound falcigers with long narrow blades bearing bifid tips (called "spiniger-like setae" by López and San Martín, 1992), but differs by having antennae, tentacular cirri, and, most notably, dorsal cirri comprised of relatively few articles, with the first article distinctly cylindrical. *Dentatisyllis mangalis* differs further by having ventral cirri clearly shorter than parapodial lobes, compound falcigers without an enlarged subterminal tooth or long slender serrations (or spines) arising from the distal margin of the blade, superiormost compound falcigers with long narrow blades along the entire body (sometimes two per fasicle in anterior setigers), and blades of these falcigers without long slender serrations arising from the distal blade margin.

Viviparity, growth, and morphological variation.—One of the most interesting aspects of the new species is its viviparous reproduction. Setigerous young are present in the coelom of a number of type specimens (Fig. 2G), including a paratype with as few as 30 setigers and a length of 1.6 mm. The brooded young were originally overlooked in some adult specimens. Their presence can be obscured by the alimentary tract, acicular and parapodial muscles, and other organs of the adult. The brooded young are most easily recognized by their proventricle, palps, and dark eyes. The apparent lack of a membrane enclosing each offspring, including those removed from brooding adults for closer study, suggests that ovoviviparity is unlikely.

The means by which offspring leave the adult is not known; however, once released, individuals appear to grow more by the addition of setigers than by the elongation of existing setigers, as indicated by a fairly linear relationship between body length and the number of setigers (Fig. 3D). This close relationship indicates that setigers grow to full size fairly rapidly, soon after they are formed.

Perhaps the most distinguishing and conspicuous feature of *Dentatisyllis mangalis* is the dorsal cirri, each consisting of relatively few articles (from three to eight), except for those on setiger 1 which are typically longer. In contrast, *D. carolinae* has 27 articles per dorsal cirrus on some anterior setigers (excluding setiger 1), thereafter about 30 on "short" dorsal cirri and about 55 on "long" dorsal cirri (Perkins 1981). Similarly, *D. junoyi,* has 7 to 9 articles on "short" dorsal cirri and 14 to 21 articles on "long" dorsal cirri (López & San Martín 1992). (Except on a few anterior setigers, "short" and "long" dorsal cirri in the latter two species, as in many Syllinae, alternate throughout the body. Such alternation was observed on only a few specimens of *D. mangalis*; the difference between "short" and "long" cirri was only one or two articles.) Observations I have made of numerous specimens from Belize belonging to other genera of the subfamily Syllinae, as well as the observations of others (e.g., Perkins, 1981:1169), have suggested that within a species the length of dorsal cirri and the number of articles comprising them probably increases with body size; small individuals have fewer articles per dorsal cirrus, larger individuals more. Although, such size-related variation does exist in *D. mangalis* and the relationship appears quite linear, the mean number of articles per dorsal cirrus per individual does not change considerably with body length, even when the latter increases nearly five-fold (Fig. 3A). Furthermore, not only is the number of articles comprising a dorsal cirrus on *D. mangalis* small compared to *D. carolinae* and *D. junoyi,* but it also varies little along any one individual (Table 2).

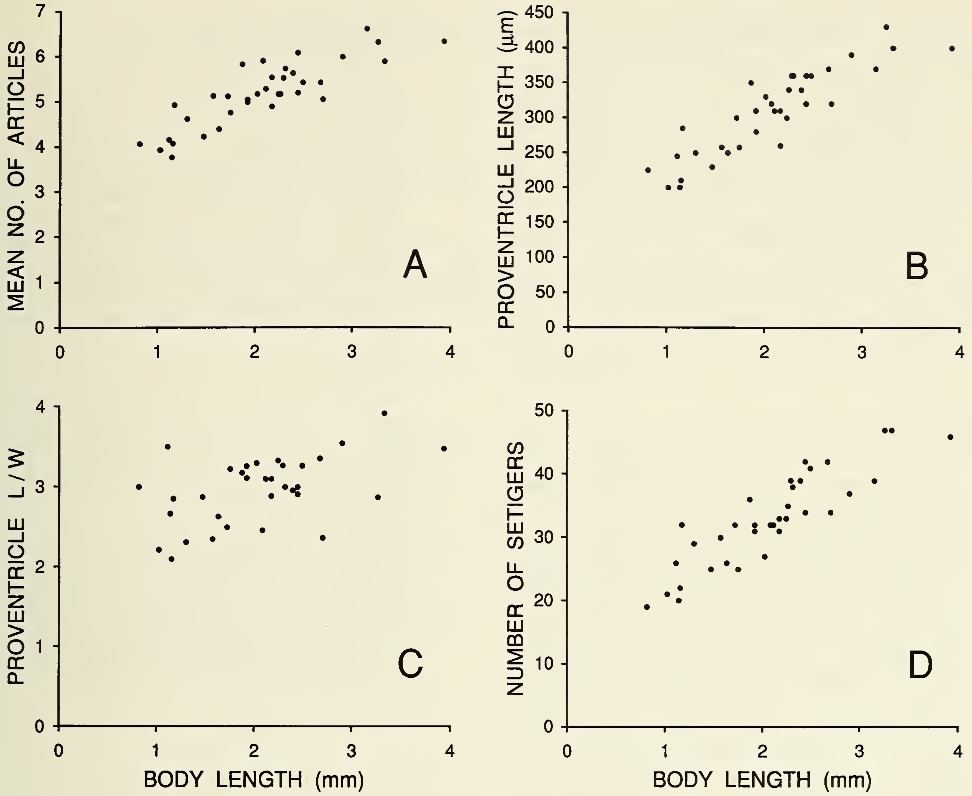

Fig. 3. *Dentatisyllis mangalis* type material. Relationship between body length and (A) mean number of articles in dorsal cirri for each individual ($r = 0.858$, $n = 35$, see Table 2 for variation associated with each mean), (B) proventricle length ($r = 0.892$, $n = 35$), (C) proventricle length to width ratio ($r = 0.503$, $n = 33$), and (D) total number of setigers ($r = 0.886$, $n = 35$).

Other observations on the relationship between morphological variation (such as that in proventricle length or the proventricle length to width ratio) and growth have been noted in the species description.

Acknowledgments

I thank Dr. Kristian Fauchald, National Museum of Natural History (NMNH), Smithsonian Institution for use of a microscope equipped with a drawing tube, and for critically reading the manuscript; and, Dr. Jerry Kudenov, University of Alaska, Anchorage, Mr. Thomas Perkins, Florida Department of Natural Resources, and Dr. Guillermo San Martín, Universidad Autonoma de Madrid, for critically reviewing the manuscript. Thanks are also due Mr. Oscar Soriano, Museo Nacional de Ciencias Naturales de Madrid, for the loan of specimens; and Ms. Linda Ward, NMNH, for sharing office space and equipment and for cataloguing specimens. Financial support from the Caribbean Coral Reef Ecosystems (CCRE) Program, NMNH (Dr. Klaus Rützler, Program Director), is gratefully acknowledged. This paper is CCRE Contribution No. 454.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):577–582. 1995

New genera for two polychaetes of Lepidonotinae

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Abstract.—Among the Lepidonotinae, two species of *Lepidonotus* are referred to new genera: *L. dictyolepis* Haswell, from Australia, to *Augenerilepidonotus,* and *L. kumari* Rullier, from Malaya, to *Olgalepidonotus.*

As part of an on-going study on the polynoid polychaetes, two species that were described under *Lepidonotus* Leach, 1816, *L. dictyolepis* Haswell, 1883, from Australia, and *L. kumari* Rullier, 1970, from Malaya, show differences from *Lepidonotus* and are referred to two new genera: *Augenerilepidonotus,* for the first species, and *Olgalepidonotus,* for the second species.

The specimens examined in this report were received on loan from the Australian Museum, Sydney (AMS), through Elizabeth Pope, Pat Hutchings, and Neville Coleman; from the Western Australian Museum, Perth, through R. W. George; and from Professor Francois Rullier, Laboratoire de Zoologie, Angers, France (LZA).

Family Polynoidae Kinberg, 1856
Subfamily Lepidonotinae Willey, 1902
Augenerilepidonotus, new genus

Type species.—*Lepidonotus dictyolepis* Haswell, 1883. Gender: masculine.

Diagnosis.—Body short, flattened, subrectangular, with 26 segments (first achaetous). Elytra and prominent elytrophores 12 pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, and 23. Elytra large, oval, overlapping, with surfaces mostly covered with chitinous irregular polygonal areas enclosing small secondary areolae, with some spinous microtubercles and lateral fringes of short, wide papillae. Dorsal cirri on nonelytrigerous segments, with bulbous cirrophores and short styles; dorsal tubercles indistinct. Prostomium bilobed, lepidonotoid, with 3 antennae, 2 palps, and 2 pairs of eyes; median antenna with bulbous ceratophore in anterior notch of prostomium; lateral antennae inserted terminally on anterior extensions of prostomium. First or tentacular segment not visible dorsally; tentaculophores lateral to prostomium, achaetous, with 2 pairs of dorsal and ventral tentacular cirri, with bulbous upper lip and small indistinct facial tubercle. Second segment with first pair of elytrophores, biramous parapodia, and long ventral buccal cirri. Biramous parapodia with small, conical notopodia on anterodorsal faces of larger neuropodia; neuropodia with subconical presetal lobe and shorter, rounded postsetal lobe, deeply cut dorsally and ventrally. Notosetae numerous, slender, densely serrated, short, extending only slightly beyond tips of neuropodia, much more slender than neurosetae; few short, tapering to blunt tips and numerous, long, tapering to capillary tips. Neurosetae stout, relatively few (8–12), with few spinous rows (4–5), and curved unidentate tips. Ventral cirri short, subulate. Pygidium with anal ridge and pair of anal cirri. Nephridial papillae small, bulbous, beginning on segment 8. Pharynx (?) not extended.

Etymology.—The genus is named for Herman Augener (1927), whose description and figures of a specimen of *Lepidonotus dictyolepis,* from near the type locality, supplemented Haswell's original description.

Remarks.—*Augenerilepidonotus dictyolepis* differs from other species of *Lepidonotus* by the presence of chitinous polygonal areas on the elytra. Among the Polynoidae, similar types of elytra with chitinous polygonal areas are found in the Iphioninae Baird, including *Iphione* Kinberg, *Iphionides* Hartmann-Schroder, and *Iphionella* McIntosh (See Pettibone 1986, Hanley & Burke 1991), and in Harmothoinae, including *Gaudichaudius* Pettibone, 1986.

Augenerilepidonotus dictyolepis
(Haswell, 1883), new combination
Fig. 1

Lepidonotus dictyolepis Haswell, 1883, 287, pl. 9: figs. 7,8.—Augener, 1927:94, fig. 3a–c.—Not Fauvel, 1932:14 (Gulf of Manaar).—Rullier, 1972:29.—Day, 1975: 178, fig. 1m–q.—Averincev, 1978:69.—Hanley & Burke, 1990:218, fig. 7A–J.—Hanley, 1993:314.

?*Lepidonotus aeololepis* Haswell, 1883: 286, pl. 9: figs. 3–5.

Material examined.—Australia, New South Wales: Watson's Bay, Fort Jackson, Sydney, dredged in shallow water, early June, 2 syntypes of *L. dictyolepis* (AMS G11274).

Western Australia: Cockburn Sound, Harding Rock, east side of Garden Island, burrowed 5–7 inches into old coralline limestone, and Parmelia Bay, 1.6 km west of Woodman Point, washings from *Pinna* shells with *Caulerpa,* 2–3 m, 6/13 Feb 1972, B. R. Wilson, coll., 3 specimens (WAM 43-72; ident. Day, 1975). Hall's Bank, Fremantle, rubble, 8 m, 13 Apr 1972, N. Coleman, coll., 1 specimen (AMS W-5491).

Description.—Body with 26 segments, 7–12 mm long, 3–4.5 mm wide with setae. Elytra with most of surface covered with irregular polygonal areas, enclosing secondary areolae, larger centrally, smaller peripherally, with some smaller areolae, microtubercles, and short, stout papillae near external borders (Fig. 1G, H; Augener 1927: fig. 3a, b; Day 1975: fig. 1n, o; Hanley & Burke 1990: fig. 7A–D). Elytrophores large, bulbous (Fig. 1A, C). Dorsal cirri with cylindrical cirrophores bulbous basally, with short subulate styles, shorter than neurosetae; dorsal tubercles indistinct (Fig. 1A, D; Day 1975: fig. 1m).

Bilobed prostomium with bulbous ceratophore of median antenna in anterior notch, style cylindrical, with tapered tip; slightly shorter lateral antennae inserted on anterior extensions of prostomium; 2 pairs of large eyes; tentaculophores lateral to stout palps and prostomium, with 2 pairs of dorsal and ventral tentacular cirri, similar to median antenna (Fig. 1A; Hanley & Burke 1990: fig. 7E). Segment II without nuchal fold, with first pair of large elytrophores, biramous parapodia and long ventral buccal cirri; neurosetae differing from following neurosetae, more slender, with more numerous rows of spines, tapering to sharp tips (Fig. 1A, B; Hanley & Burke 1990: fig. 7E, G, J).

Biramous parapodia with small, conical notopodium on anterodorsal side of large neuropodium, with subconical presetal lobe and shorter rounded postsetal lobe, deeply cut dorsally and ventrally (Fig. 1C, D). Notosetae numerous, short, extending only slightly beyond neuropodium, slender, densely serrated, few short, tapering to blunt tips and numerous long ones tapering to capillary tips (Fig. 1C, E). Neurosetae relatively few (8–12), all similar, stout, with few spinous rows (4–5) and slightly curved unidentate tips (Fig. 1F; Haswell 1883: pl. 9: fig. 7; Augener 1927: fig. 3c, d; Day 1975: fig. 1q; Hanley & Burke 1990: fig. 7,1).

Distribution.—Western Australia: Rottnest Island, under limestone rubble, 6–7 m (Hanley 1993); South-West Australia: off Albany, low water under rocks (Hanley & Burke 1990; Eastern Australia: Port Jackson, New South Wales, shallow water and

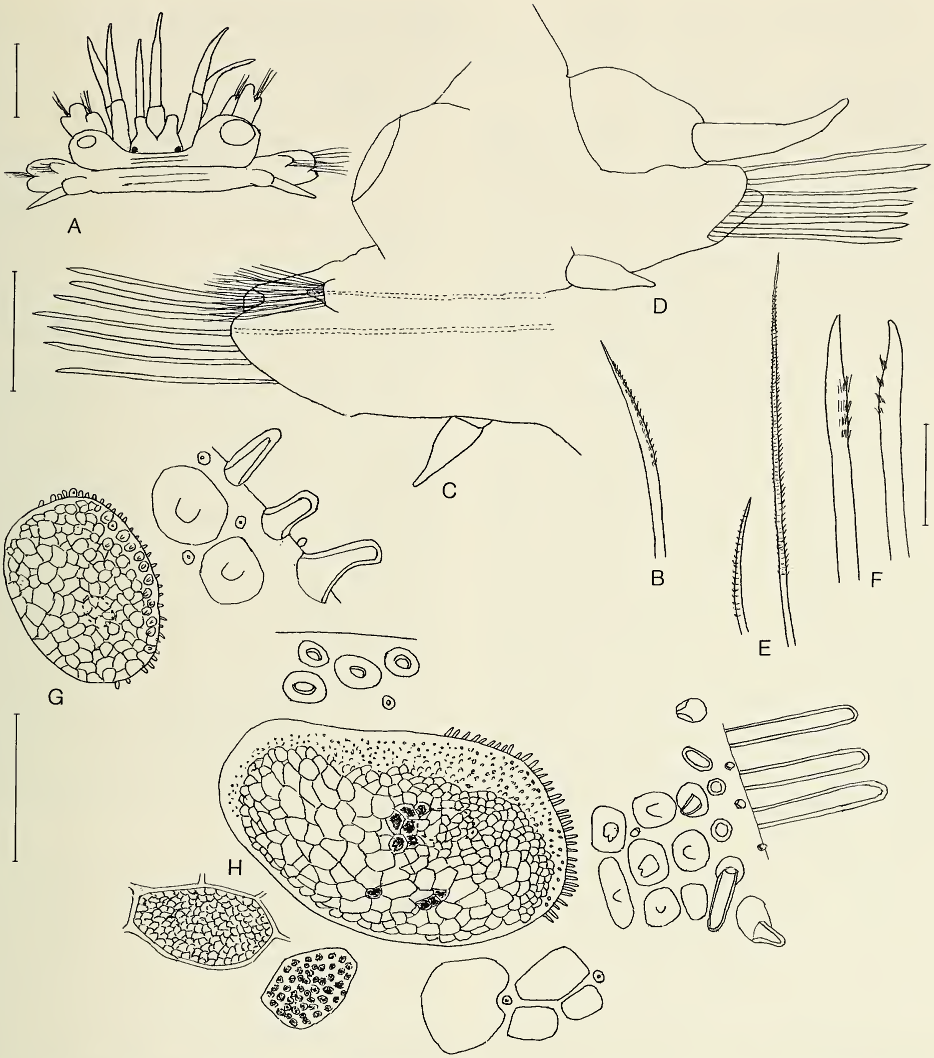

Fig. 1. *Augenerilepidonotus dictyolopis,* paratype of *Lepidonotus dictyolepis* (AMS 11274): A, Dorsal view of anterior end, prostomium partially withdrawn in segment II, with posterior eyes hidden from view; B, Neuroseta from segment II; C, Right middle elytrigerous parapodium, anterior view, acicula dotted; D, Right middle cirrigerous parapodium, posterior view; E, Short and long notosetae from same; F, Two neurosetae from same; G. Right first elytron, with detail of lateral border; H, Right middle elytron, with detail of different areas. Scales = 0.5 mm for A; 0.1 mm for B, E, F; 0.3 mm for C, D; 1.0 mm for G, H.

under stones and algae (Haswell 1883, Augener 1927); Tasman Sea: Norfolk Island, 50 m, coralline sand (Averincev 1978, Vinogradova et al. 1978); and Coral Sea: New Caledonia (Rullier 1972).

Remarks.—Lepidonotus aeololepis Haswell, 1883, from Thursday Island, Australia, from under rocks at low tide, is questionably referred to *A. dictyolepis.* The type specimen in the Queensland Museum is lost (Day & Hutchings 1979:89) and not available for study. The description and figures are deficient but the elytra, showing polygonal areas, and the stout neurosetae with few spinous rows and entire tips, agree with *A. dictyolepis.*

Olgalepidonotus, new genus

Type species.—Lepidonotus kumari Rullier, 1970. Gender: masculine.

Diagnosis.—Body short, flattened, subrectangular, with 26 segments (first achaetous). Elytra and prominent elytrophores 12 pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, and 23. Elytra large, overlapping, covering dorsum, without long fringe of papillae, densely covered with rounded microtubercles and micropapillae. Dorsal cirri on non-elytrigerous segments, with long cylindrical cirrophores and tapered styles extending to tip of neurosetae. Prostomium bilobed, with 3 antennae, 2 palps, and 2 pairs of eyes; median antenna with oval ceratophore in anterior notch of prostomium; lateral antennae inserted subterminally on anterior continuations of prostomium, on same level as median antennae but with line of separation from prostomium. First or tentacular segment not visible dorsally; tentaculophores lateral to prostomium, achaetous, with 2 pairs of dorsal and ventral tentacular cirri, without distinct facial tubercle. Second segment with first pair of elytrophores, biramous parapodia, and long ventral buccal cirri. Biramous parapodia with small conical notopodia on anterodorsal faces of larger neuropodia; neuropodia with subconical presetal acicular lobe and shorter rounded postsetal lobe. Notosetae all one type, much more slender than neurosetae, delicate, finely spinous, tapering to capillary tips. Neurosetae not usual *Lepidonotus* type, rather slender, wider basally, tapering to sharp tips, mostly bare, upper ones with few spines (4–5), Ventral cirri short, subulate. Pygidium with anal ridge and pair of long anal cirri. Nephridial papillae rather long, cylindrical, beginning on segment 8. Pharynx (?) not extended.

Etymology.—The genus is named for Olga Hartman, who contributed so much to the study of the Polychaeta.

Remarks.—Olgalepidonotus kumari differs from the usual *Lepidonotus* types of setae, having all long capillary notosetae and stouter neurosetae mostly bare, with subterminal enlargements, tapering to sharp tips.

Olgalepidonotus kumari (Rullier, 1970), new combination
Fig. 2

Lepidonotus kumari Rullier, 1970:221, Figs. A–I.

Material examined.—Malaya, Port Swettenham, in mangrove, 30 Nov 1968, A. S. Kumar, collector, holotype (LZA).

Description.—Body with 26 segments, 9 mm long, 4.5 mm wide with setae. Elytra large, overlapping, covering dorsum, last twelfth pair extra wide, covering posterior five segments (Rullier 1970: fig. A). Elytra oval to subreniform, densely covered with rounded, colored microtubercles and short micropapillae on surface and posterior and lateral borders (Fig. 2H; Rullier 1970: figs. H, I). Elytrophores large, bulbous (Fig. 2A, D). Dorsal cirri with long cylindrical cirrophores on dorsoposterior faces of parapodia, with styles extending about to tips of neurosetae; dorsal tubercles slightly inflated (Fig. 2E).

Bilobed prostomium with deep red pigmentation on lateral margins and bases of antennae; median antennae with rounded ceratophore in anterior notch of prostomium, with style about as long as stout tapered palps; lateral antennae inserted subterminally on anterior extensions of prostomium, on same level as median antenna but with line of separation, appearing as distinct ceratophores, with styles shorter than median antenna; eyes rather large, anterolateral pair and slightly smaller posterolateral pair; tentaculophores lateral to palps and prostomium, with dorsal tentacular cirri similar to median antenna and slightly shorter ventral tentacular cirri (Fig. 2A; Rullier 1970: fig. B). Segment II without nuchal fold, with first pair of large elytrophores, biramous parapodia, and long ventral buccal cirri, similar to tentacular cirri; notosetae similar to following; neurosetae differing from following, more slender, with spinous rows,

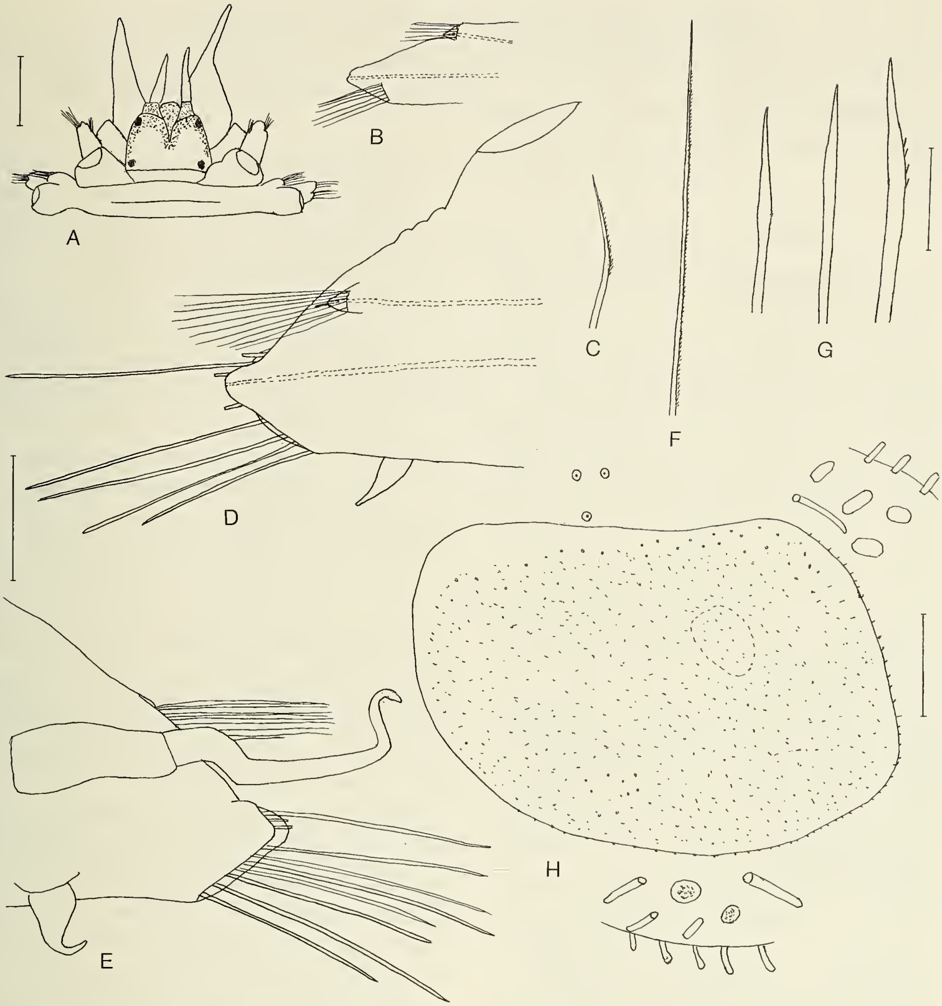

Fig. 2. *Olgalepidonotus kumari,* holotype of *Lepidonotus kumari* (LZA): A, Dorsal view of anterior end, missing: styles of median antenna, right and left dorsal and ventral tentacular cirri, elytra of segment II and styles of dorsal cirri of segment III; B, Right parapodium of segment II, elytrophore and ventral buccal cirrus not shown, acicula dotted; C, Neuroseta from same; D, Right middle elytrigerous parapodium, anterior view, acicula dotted, some neurosetae broken or missing; E, Right middle cirrigerous parapodium, posterior view, some neurosetae broken or missing: F, Notoseta from same; G, Lower, middle and upper neurosetae from same; H, Right middle elytron, with detail of microtubercles and micropapillae. Scales = 0.5 mm for A; 0.3 mm for B, D, E; 0.1 mm for C, F, G; 0.5 for H.

and tapering to delicate tips (Fig. 2A–C; Rullier 1970: fig. B).

Biramous parapodia with short, conical notopodia on anterodorsal sides of large neuropodia, with subconical presetal acicular lobe and slightly shorter, rounded postsetal lobe, notched dorsally (Fig. 2D, E). Notosetae much more slender than neurosetae, single type, delicate, finely spinous, tapering to long capillary tips (Fig. 2D, F; Rullier 1970: fig. D). Neurosetae rather slender, wider subdistally, tapering to sharp tips, few (4–5) supraacicular ones, with few (4–5) spinous rows, and more numerous (15–20) subacicular neurosetae, smooth, without spines, lower ones with slightly curved tips (Fig. 2G; Rullier 1970: figs. E–G). Ventral cirri short, subulate (Fig. 2D, E).

Distribution.—Indian Ocean, Port Swettenhan, west coast of Malaya, in mangrove swamp.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):583–595. 1995

Two new species of *Opisthotrochopodus* (Polychaeta: Polynoidae: Branchinotogluminae) from the Lau and the North Fiji Bac-arc Basins, southwestern Pacific Ocean

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Abstract.—*Opisthotrochopodus segonzaci,* a new species of branchiate polynoid polychaete from the Lau and the North-Fiji Bac-arc Basins, southwestern Pacific Ocean, differs from the other species of the genus in having short dorsal cirri with rounded tips on the anterior segments and achaetous modified parapodia on segment 21. *Opisthotrochopodus trifurcus,* a new species from the North-Fiji Basin, is unique in the genus in having trifurcate neurosetae on the posterior modified segment.

Polynoid polychaetes of the subfamily Branchinotogluminae Pettibone, 1985 include three genera (*Branchinotogluma* Pettibone, 1985; *Opisthotrochopodus* Pettibone, 1985; and *Peinaleopolynoe* Desbruyères & Laubier, 1988) and ten species to date. Most of them are known from deep-sea chemosynthetic communities. The subfamily was established by Pettibone (1985) when *B. hessleri, B. sandersi, B. grasslei,* and *O. alvinus* were described from the Galápagos Spreading Center, and the East Pacific Rise at 21°N. Some of these species were later reported from the Explorer and the Juan de Fuca Ridges, Northeastern Pacific, as well as *O. tunnicliffeae* (Pettibone 1988). From the hydrothermal rift-area of the Mariana Bac-arc Basin in the western central Pacific, two additional polynoids, *B. burkensis* and *O. marianus,* were described (Pettibone 1989). About some hundreds kilometers North of this basin, *O. japonicus* was found associated with the hydrothermal vents of Kaikata seamount by Miura & Hashimoto (1991). A branchiate polynoid species, *Peinaleopolynoe sillardi,* was also described from a non-hydrothermal environment but attracted to enriched sediments in experimental trays disposed on the deep-sea floor in the North Atlantic Ocean to study the influence of organic matter on colonization processes (Desbruyères & Laubier 1988). The genus was newly included in the subfamily by Pettibone (1993), along with the description of the second species, *P. santacatalina,* associated with a whale skeleton in the bathyal Santa Catalina Basin.

Polynoid polychaetes collected by the French submersible *Nautile* from the hydrothermal community of the central part of the North-Fiji and the Lau Basins were studied and *Branchipolynoe pettiboneae* Miura & Hashimoto, 1991 in Branchipolynoinae was reported associated with mytilid mollusks by Desbruyères et al. (1994). Two other polynoids, *Thermopolynoe branchiata* in Lepidonotopodinae and *Thermiphione fijiensis* in Iphioninae, have been described previously (Miura 1994). In this study, two new species of the genus *Opisthotrochopodus* are described. The types are deposited in the Museum National d'Histoire Naturelle de Paris (MNHN), and the National Museum of Natural History, Smithsonian Institution (USNM).

Some additional specimens were used for SEM or histological observation at Kagoshima University (KU).

Subfamily Branchinotogluminae
Pettibone, 1985
Opisthotrochopodus Pettibone, 1985
Opisthotrochopodus segonzaci, new species
(Figs. 1–4)

Material examined.—Vailili, Lau Basin, *Nautile* Dive 10, 22 May 1989, BIOLAU Station 2, 23°13′S 176°38′W, 1750 m, Holotype (MNHN UD 852), 3 paratypes (including 1 modified, MNHN UD 853). White Lady, North Fiji Basin, Dive 20, 15 Jul 1989, STARMER II Station 4, 16°59.50′S, 173°55.47′E, 2000 m, 9 paratypes (4 modified, MNHN UD 854, USNM 171052), 4 specimens (2 modified, KU).

Description.—Holotype 29 mm long, 14 mm wide including parapodia, with 21 segments, including first achaetous tentacular segment. Largest paratype 49 mm long, 19 mm wide, with 21 segments. Body short, spindle-shaped, slightly tapered anteriorly and posteriorly, flattened ventrally, arched dorsally (Figs. 1a, 2a–d). Integument smooth. Preserved specimens pale.

Elytra 10 pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, and 19, large, imbricated, oval, smooth, white or colorless (Fig. 2a); last pair on segment 19 much smaller on holotype and on specimens with modified posterior segments than on others. Dorsal cirri on non-elytrigerous segments with short cylindrical cirrophores, and short styles with rounded tips, extending to tips of neurosetae (Figs. 1e, g, 2c, 3d, e, h, i). Branchiae arborescent, separated into two groups: upper groups on lateral bases of elytrophores or dorsal tubercles; lower groups on bases of notopodia (Fig. 3d–i); present on segments 3–19 on holotype and on specimens with modified posterior segments (Fig. 1c, e, f), or on segments 3–21 on specimens with non-modified segments (Figs. 2c, 3a, d–i).

Prostomium bilobed. Anterior lobes prominent, cylindrical, extending anteriorly, with frontal filaments; median antenna inserted in anterior notch, with short cylindrical ceratophore and subulate style extending to about tip of palp; palps thick, smooth, extending beyond prostomium, with rounded tips (Fig. 2c, d). Tentacular segment fused to prostomium, indistinct; tentaculophores lateral to prostomium, annulated, achaetous, with two pairs of tentacular cirri, stout, short, as long as tentaculophores, with rounded or convex distal tips (Fig. 2c, d).

Segment 2 with first pair of elytrophores, biramous parapodia, and ventral or buccal cirri attached basally on prominent cirrophores lateral to mouth, with styles similar to tentacular cirri, longer than following ventral cirri (Figs. 2c, d, 3c). Mouth opening situated between segments 1 and 2 (Figs. 1a, 2b, d). Muscular pharynx encircled distally by four pairs of small papillae, subequal in size; bearing lateral lamellar expansions with four distal papillae, and numerous small papillae forming proximal band; two pairs of jaws without denticulations on inner border (Fig. 2e).

Segment 3 with first pair of arborescent branchiae, dorsal cirri, short ventral cirri and biramous parapodia similar to segment 2; dorsal cirri short, with rounded tips (Figs. 2c, d, 3d). Following biramous parapodia, with short notopodia on anterodorsal sides of large neuropodia (Fig. 3d–i). Notopodia subconical, with projecting acicular lobes hidden by numerous notosetae, and enclosed antero-dorsally by flaring bracts (Fig. 3d–i). Neuropodia subconical, deeply notched on upper part (Fig. 3d–i).

Ventral segmental papillae long, attached to bases of neuropodia on segment 12, and extending to bases of ventral cirri; 5 pairs of flat semioval ventral lamellae on segments 13–17 on holotype and on half of specimens (Fig. 1a, b), or lacking both papillae and lamellae on other specimens (Fig.

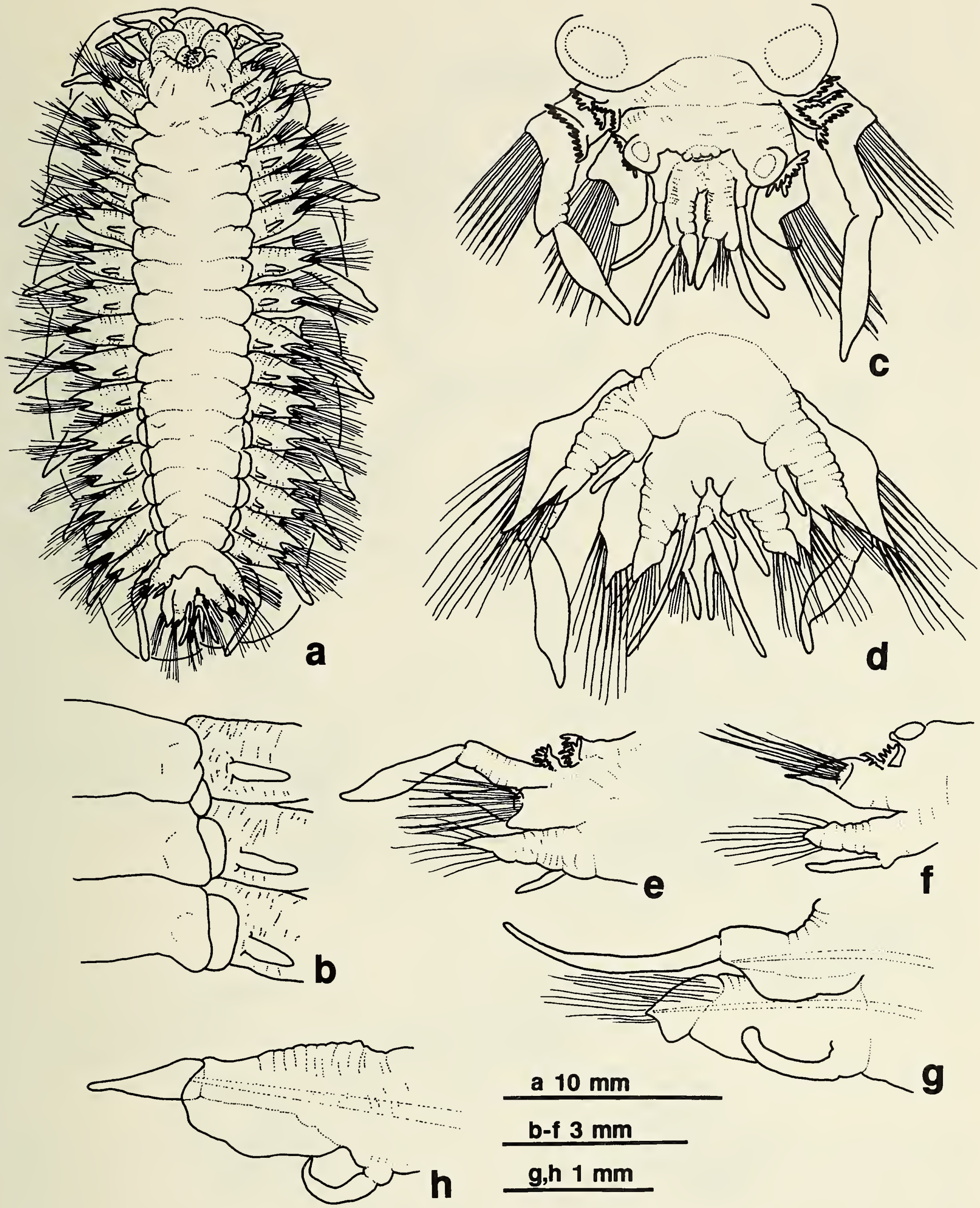

Fig. 1. *Opisthotrochopodus segonzaci,* new species. Holotype (MNHN UD 852): a, Ventral view; b, Left halves of segments 12–14, ventral view; c, Posterior end, dorsal view; d, Same, ventral view; e, Right cirrigerous parapodium from segment 18, anterior view; f, Right elytrigerous parapodium from segment 19, elytron removed, anterior view; g, Right cirrigerous parapodium from segment 20, anterior view; h, Right cirrigerous parapodium from segment 21, anterior view.

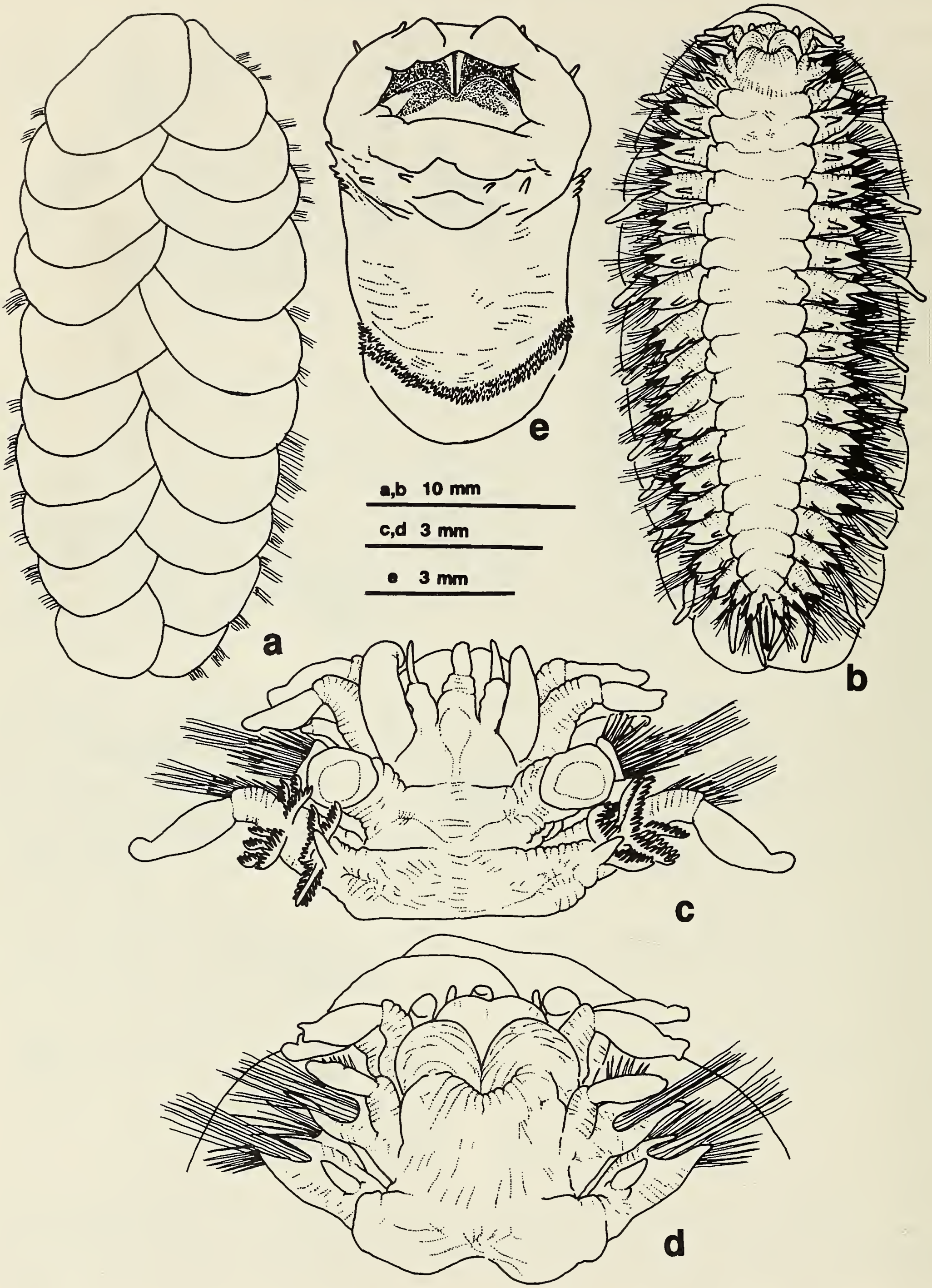

Fig. 2. *Opisthotrochopodus segonzaci,* new species. Paratype (MNHN UD 853): a, Dorsal view; b, Ventral view; c, Anterior end, dorsal view; d, Same, ventral view; e, Pharynx of another paratype (MNHN UD 854), ventral view.

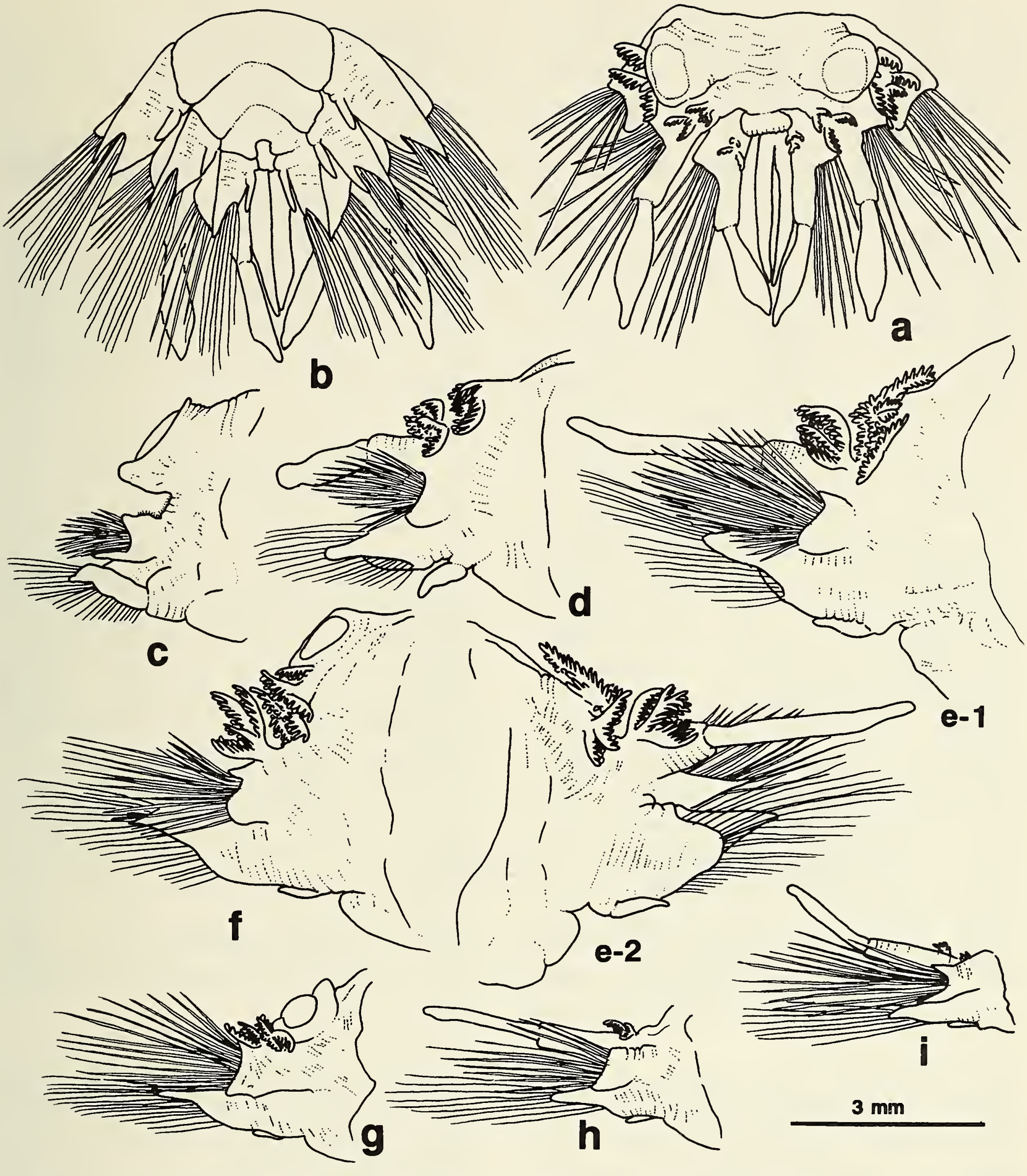

Fig. 3. *Opisthotrochopodus segonzaci,* new species. Paratype (MNHN UD 853): a, Posterior end, dorsal view; b, Same, ventral view; c, Right elytrigerous parapodium from segment 2, elytron removed, anterior view; d, Right cirrigerous parapodium from segment 3, anterior view; e-1, Right elytrigerous parapodium from segment 10, elytron removed, anterior view; e-2, Same, posterior view; f, Right elytrigerous parapodium from segment 11, elytron removed, anterior view; g, Right elytrigerous parapodium from segment 19, elytron removed, anterior view; h, Right cirrigerous parapodium from segment 20, anterior view; i, Right cirrigerous parapodium from segment 21, anterior view.

2b). Segments 18–21 modified, with reduced parapodia on holotype and on specimens with ventral segmental papillae (Fig. 1c–h), or not modified on other specimens (Figs. 2b, 3g–i). Parapodia of segments 18 and 19 biramous, with small notopodia and slender neuropodia; ventral cirri slightly elongated on holotype and on modified specimens (Fig. 1c–f); notopodia developed with numerous notosetae on other specimens (Fig. 3g). Parapodium of segment 20 modified with reduced notopodium and elongated neuropodium, lacking notosetae; notopodial acicular lobe fused to cirrophore of long dorsal cirrus; cirrophore with ventral lamellar expansion and embedded notoacicula; neuropodium with lamellar expansion folding small bundle of neurosetae on holotype and on specimens with ventral segmental papillae (Fig. 1g); notopodia with numerous notosetae on other specimens (Fig. 3h). Parapodium of segment 21 strongly modified, lacking noto- and neurosetae; notopodial acicular lobe fused to cirrophore of short conical dorsal cirrus, ventral lamellar expansion enlarged; ventral cirrus as long as dorsal cirrus on holotype and on specimens with ventral segmental papillae (Fig. 1h); parapodia with noto- and neurosetal bundles on other specimens (Fig. 3i). Pygidium visible dorsally as bulbous lobe, wedged between parapodia of posterior segments, with pair of long ventral anal cirri (Figs. 1c, 3a)

Notosetae numerous, forming radiating bundles, much stouter than neurosetae, serrated on distal margins; tips bare, tapered (Fig. 4a-1, -2). Neurosetae numerous, forming fan-shaped bundles. Supraacicular neurosetae with numerous prominent spines in two rows; tips bare, tapered (Fig. 4b-1, -2). Subacicular neurosetae serrated on distal margins; tips bare, tapered, hooked (Fig. 4c-1, -2).

Variation in paratypes.—Half of the 16 complete specimens have modified parapodia on segments 18–21, with long ventral papillae on segment 12, and flat semi-oval ventral lamellae on segments 13–17 (Fig. 1a), while remaining specimens have no modified segments, papillae, or ventral lamellae (Fig. 2b). This dimorphism is independent of the specimen size.

Etymology.—The species is named for Michel Segonzac, who helped to prepare the materials examined in this study.

Remarks.—*Opisthotrochopodus segonzaci* differs from the other congeneric species in having short dorsal cirri with rounded tips, and achaetous parapodia on segment 21 on specimens with modified posterior segments.

Opisthotrochopodus trifurcus,
new species
(Figs. 5–8)

Material examined.—White Lady, North Fiji Basin, *Nautile* Dive 12, 7 Jul 1989, STARMER II Station 4, 16°59.50′S, 173°55.47′E, 2000 m, Holotype (MNHN UD 855), 7 paratypes (including 3 modified, MNHM UD 856); Dive 10, 5 Jul 1989, 2 paratypes (MNHM UD 857); Dive 11, 6 Jul 1989, 26 paratypes (15 modified, USNM 171053); Dive 13, 8 Jul 1989, 36 specimens (21 modified, KU); Dive 14, 9 Jul 1989, 14 paratypes (7 modified, MNHM UD 858); Dive 16, 11 Jul 1989, 50 paratypes (23 modified, MNHM UD 859); Dive 20, 15 Jul 1989, 23 paratypes (12 modified, USNM 171054).

Description.—Holotype 15 mm long, 7 mm wide including parapodia, with 21 segments, including first achaetous tentacular segment. Body short, spindle-shaped, slightly tapered anteriorly and posteriorly, flattened ventrally, slightly arched dorsally (Figs. 5a, b, 6a, b). Preserved specimens pale.

Elytra 10 pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, and 19; large, imbricated, oval, smooth, white or colorless; first pair subreniform (Figs. 5a, 6a). Dorsal cirri on non-elytrigerous segments with short cylindrical cirrophores, and very long cirriform styles with tapered tips (Fig. 7b, c, e). Branchiae arborescent, separated into two

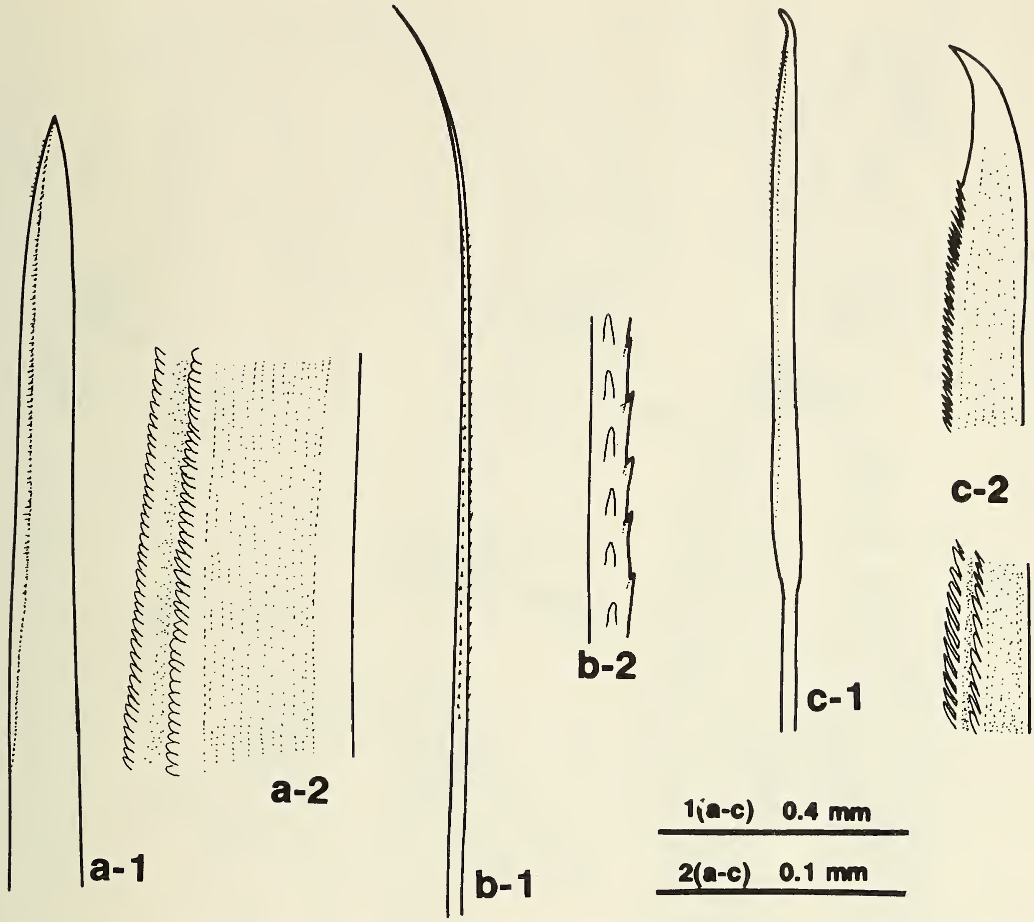

Fig. 4. *Opisthotrochopodus segonzaci,* new species. Paratype (MNHN UD 853): a-1, Notoseta from segment 11; a-2, Same, enlarged; b-1, Supraacicular neuroseta; b-2, Same, enlarged; c-1, Subacicular hooked neuroseta; c-2, Same, enlarged.

groups: upper groups on lateral bases of elytrophores and dorsal tubercles; lower groups on bases of notopodia; present on segments 3–18 on specimens with modified posterior segments (Figs. 5b, 7b–d), or on segments 3–21 on specimens with non-modified parapodia (Fig. 6a–d); dorsal tubercles nodular, projecting (Fig. 7b, c).

Prostomium bilobed. Anterior lobes prominent, cylindrical, extending anteriorly, without frontal filaments; median antenna inserted in widely incised anterior notch, with very short ceratophore and subulate style, half as long as palp; palps thick, smooth, twice as long as prostomium, with slender tips (Figs. 5c, 6c). Tentacular segment fused to prostomium, not distinct dorsally; tentaculophores lateral to prostomium, smooth, achaetous, with two pairs of tentacular cirri, slender, longer than tentaculophores (Figs. 5a–c, 6a–c).

Segment 2 with first pair of elytrophores, biramous parapodia, and ventral or buccal cirri with short cirrophores and styles similar to tentacular cirri, longer than following ventral cirri; notopodium long, conical, with projecting acicular lobe and several notosetae; neuropodium long, conical, with numerous neurosetae (Fig. 7a). Muscular pharynx encircled distally by four pairs of

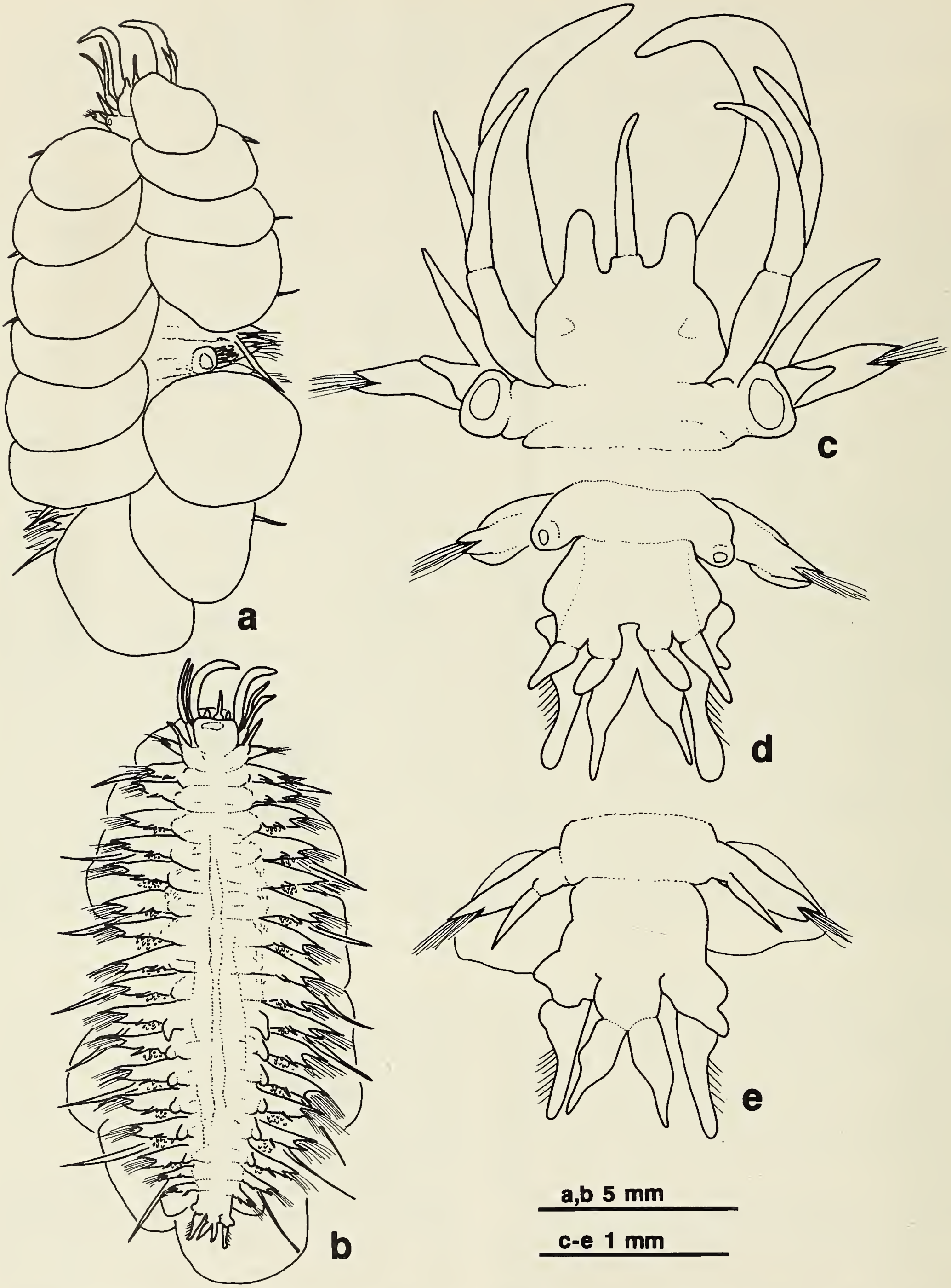

Fig. 5. *Opisthotrochopodus trifurcus,* new species. Holotype (MNHN UD 855): a, Dorsal view; b, Ventral view; c, Anterior end, dorsal view; d, Posterior end, dorsal view; e, Same, ventral view.

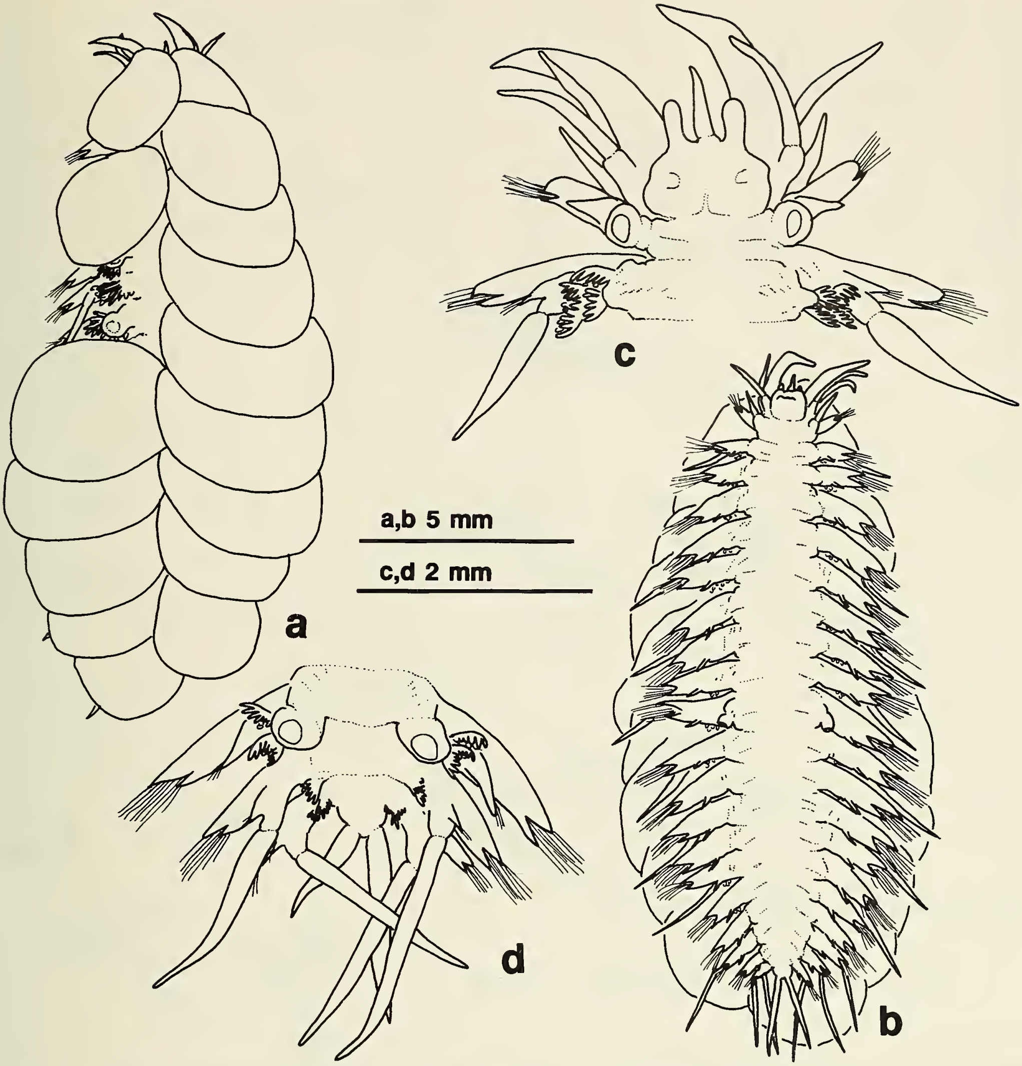

Fig. 6. *Opisthotrochopodus trifurcus,* new species. Paratype (KU): a, Dorsal view; b, Ventral view; c, Anterior end, dorsal view; d, Posterior end, dorsal view.

large papillae, subequal in size; two pairs of jaws with denticulations on inner borders (observation on dissected paratypes).

Segment 3 with first pair of arborescent branchiae, dorsal cirri, ventral cirri, biramous parapodia similar to segment 2, and triangular dorsal tubercles; dorsal cirri long, with tapered tips (Fig. 7b). Following biramous parapodia, with short notopodia on anterodorsal sides of large neuropodia on segments 4–17 (Fig. 7c–d). Notopodia long, conical, with several notosetae; neuropodia long, conical, deeply notched on upper part (Fig. 7c–d).

Ventral segmental papillae on segment 12, as long as segment; 5 pairs of flat semi-oval ventral segmental lamellae present on segments 13–17 on holotype and on half of specimens (Fig. 5b), or lacking semi-oval segmental lamellae and bearing short ventral segmental papillae on segment 11 on other specimens (Fig. 6b). Segments 18–21

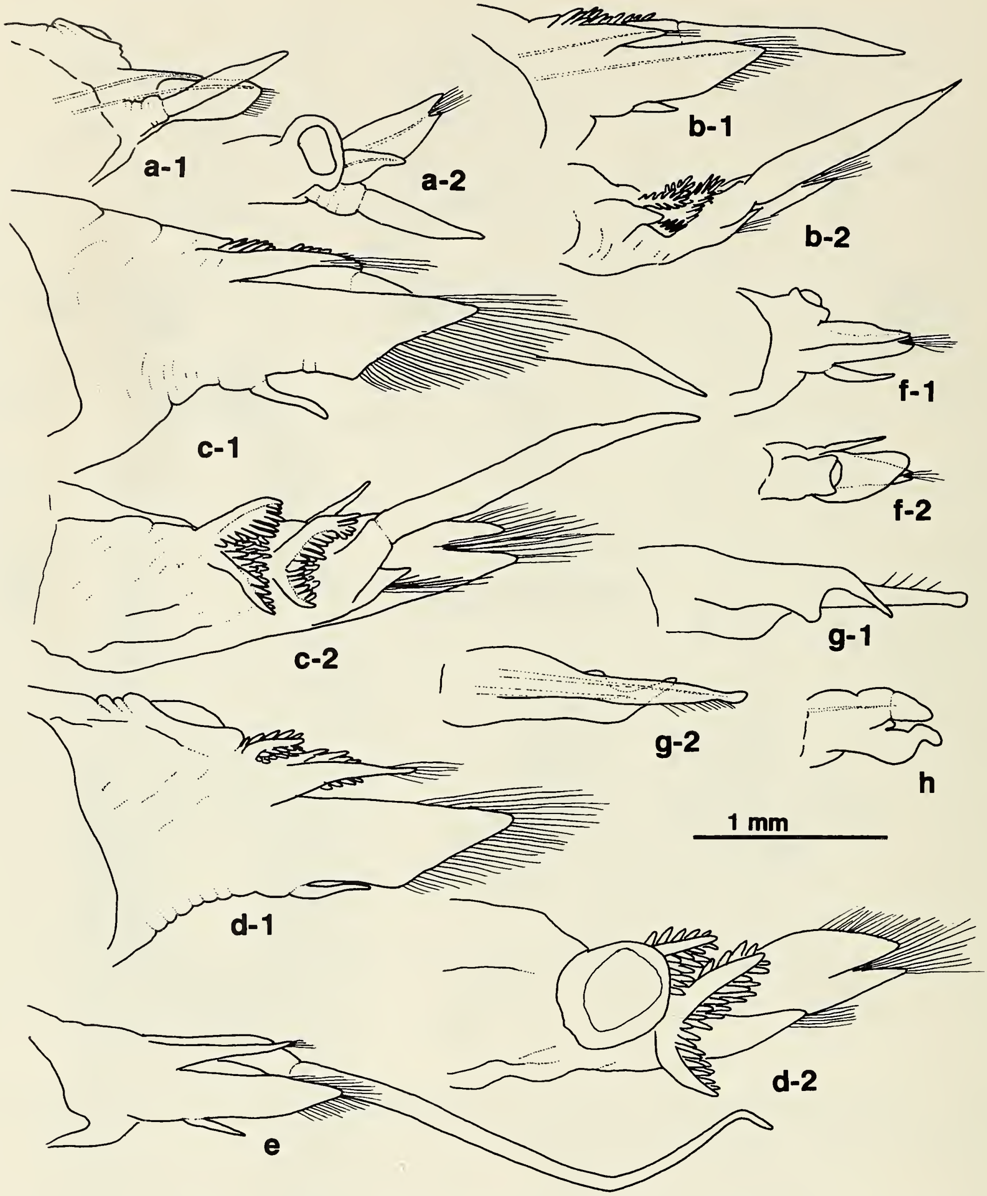

Fig. 7. *Opisthotrochopodus trifurcus,* new species. Holotype (MNHN UD 855): a-1, Left elytrigerous parapodium from segment 2, elytron removed, anterior view; a-2; Same, dorsal view; b-1, Left cirrigerous parapodium from segment 3, anterior view; b-2, Same, dorsal view; c-1, Left elytrigerous parapodium from segment 10, elytron removed, anterior view; c-2, Same, dorsal view; d-1, Left elytrigerous parapodium from segment 11, elytron removed, anterior view; d-2, Same, dorsal view; e, Left cirrigerous parapodium from segment 18, anterior view; f-1, Left elytrigerous parapodium from segment 19, elytron removed, anterior view; f-2, Same, dorsal view; g-1, Left cirrigerous parapodium from segment 20, anterior view; g-2, Same, dorsal view; h, Left cirrigerous parapodium from segment 21, anterior view.

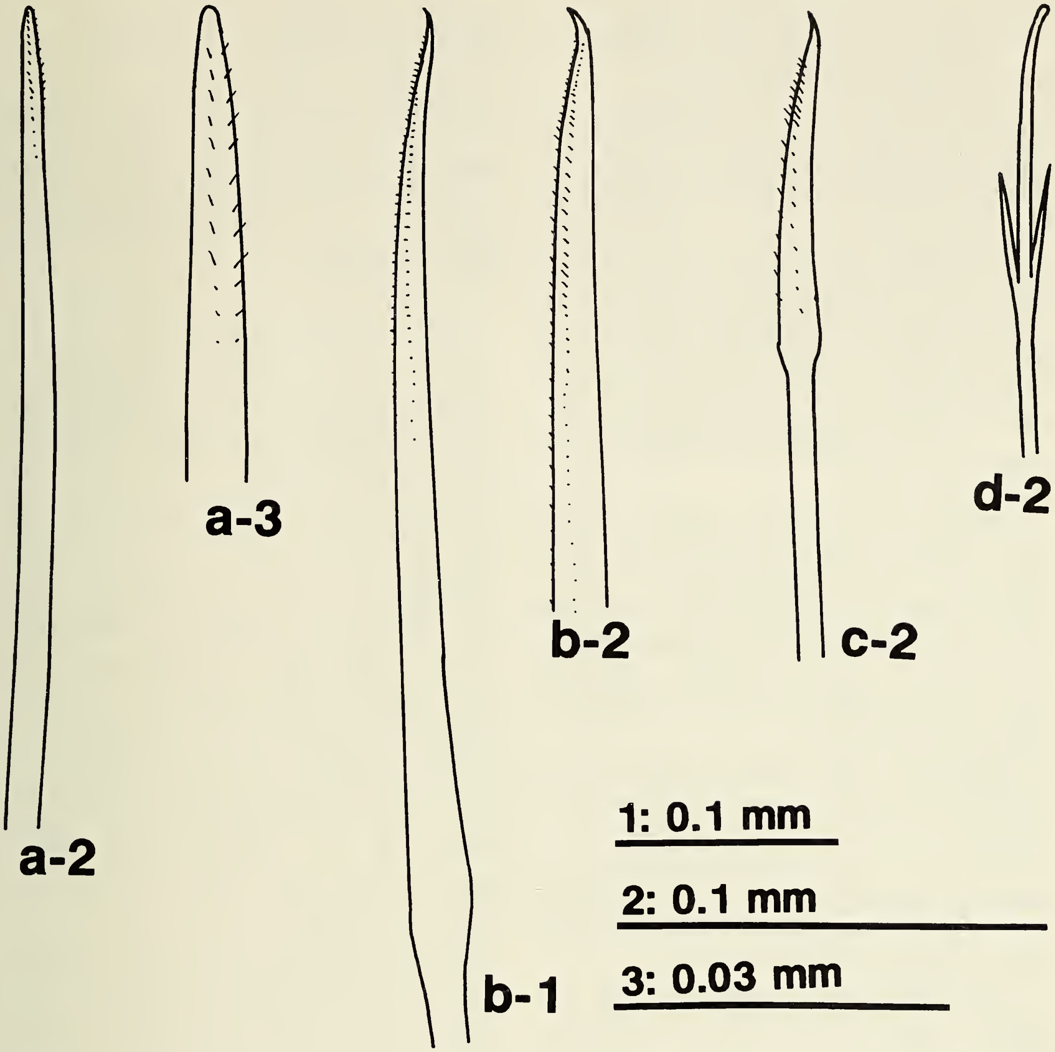

Fig. 8. *Opisthotrochopodus trifurcus,* new species. Holotype (MNHN UD 855): a-2, Notoseta from segment 10; a-3, Same, enlarged; b-1, Supraacicular neuroseta; b-2, Same, enlarged; c-2, Subacicular hooked neuroseta; d-2, Trifurcate neuroseta from segment 20.

modified, with reduced parapodia (Figs. 5b, d, e, 7c–h) on holotype and on specimens with semi-oval segmental lamellae, or not modified on specimens without segmental lamellae (Fig. 6b, d). Segment 18 modified slightly, with parapodia bearing very long dorsal cirri (Fig. 7e). Segment 19 with achaetous notopodia bearing broad dorsal lamellar expansion (Fig. 7f). Segment 20 modified strongly, with long achaetous notopodia bearing bifurcate distal end; dorsal digitiform expansion and ventral fringed lamella; club-shaped neuropodia fringed by trifurcate neurosetae found only on segment 20 (Fig. 7g). Segment 21 reduced in size, achaetous, with uniramous parapodia; notopodia digitiform, with embedded acicula and very short cirri; ventral cirri, with basal lamellar expansion and digitiform short cirriform distal end (Fig. 7h). Pygidium with pair of anal cirri; anal cirri short on specimens with modified posterior segments and semi-oval segmental lamellae (Figs. 5b, d, e), or long on others with non-modified posterior segments (Fig. 6b, d).

Notosetae as stout as neurosetae, with short spines on distal margins; tips bare, blunt (Fig. 8a-2, -3). Neurosetae numerous, forming fan-shaped bundles. Supraacicular neurosetae with numerous short spines on distal margins; tips bare, tapered, hooked (Fig. 8b-2). Subacicular neurosetae with short spines on distal margins; tips bare, tapered, hooked (Fig. 8c-2). Trifurcate neuroseta on segment 20 with long blunt central rod-like projection and paired fine lateral extensions half as long as central projection (Fig. 8d-2).

Variation in paratypes.—Half of specimens (83/165) have modified parapodia on segments 18–21, ventral papillae on segment 12, and flat semi-oval ventral lamellae on segments 13–17, while remaining specimens lack posetrior modified parapodia and ventral lamellae, but bear ventral papillae on segment 11.

Etymology.—The species name is derived from the characteristic trifurcate neurosetae.

Remarks.—Opisthotrochopodus trifurcus differs from other species in having trifurcate neurosetae on segment 20 in specimens with modified posterior segments.

Opisthotrochopodus segonzaci and *O. trifurcus* show characteristic dimorphism. One type has modified posterior segments. In this type, ventral segmental papillae and lamellae are fully developed. The other type has no modified posterior segments nor ventral segmental lamellae. The dimorphism is independent of the size of specimen in these species. As none of specimens had matured gametes, it is not clear if this is sexual dimorphism. The dimorphism was reported also in *Themopolynoe branchiata* by Miura (1994).

A couple of species, *Opisthotrochopodus alvinus* and *Branchinotogluma hessleri,* which were recorded from the Galápagos Spreading Center and the East Pacific Rise at 21° (Pettibone 1985, 1988) show almost the same dimorphic state as mentioned above in each species from southwestern Pacific areas. In these species, the former has strongly modified posterior segments and long ventral papillae, and the latter lacks posterior modified segments and long papillae. We think these species have the possibility to be synonymized, but further study is necessary.

Acknowledgments

We thank the captain and the crews of the French research vessel *Le Nadir* and of the submersible *Nautile.* The STARMER project (North Fiji Basin study) was funded by the Science and Technology Agency of Japan and by the Institut Français de Recherche pour l'exploitation de la Mer (IFREMER), France; the BIOLAU (Lau Basin study) was funded by IFREMER, France. Anne-Marie Alayse-Danet was chief scientist of the BIOLAU cruise and Suguru Ohta (with the second author) was co-chief scientist of the STARMER II cruise. The first author thanks Michel Segonzac and Patrick Briand of the Centre National de Tri d'Océanographie Biologique for their kind communication of the materials examined in this study. The manuscript was improved by the careful review and corrections by Marian H. Pettibone and Jon L. Norenburg of Smithsonian Institution. This work was supported in part by grants-in-aid for the first author from the Ministry of Education, Culture and Science, Japan (No. 03640630) and Kato Foundation for the Promotion of the Bioscience Researches.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):596–612. 1995

Two species of *Oxyurostylis* (Crustacea: Cumacea: Diastylidae), *O. smithi* Calman, 1912 and *O. lecroyae,* a new species from the Gulf of Mexico

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Abstract.—A form of *O. smithi* Calman, 1912 and *Oxyurostylis lecroyae,* new species, are described from the northeastern Gulf of Mexico. The specimens of *O. smithi* described herein and those collected near the type locality, Woods Hole, Massachusetts, differ in the development and arrangement of the carapace carinae, and in the shape and relative length of the female fifth thoracic segment. *Oxyurostylis lecroyae* is distinguished from all the other described species of the genus by the presence of a horizontal carina on the carapace of the adult female.

Calman (1912) created the genus *Oxyurostylis* to receive *O. smithi,* a species he described based on a few specimens from the Woods Hole, Massachusetts, area, but in the material examined two specimens from the Gulf of Mexico were also included. Subsequently, numerous authors reported the occurrence of *O. smithi* from the Bay of Fundy to Louisiana (e.g., Bousfield & Leim 1960, Bowen et al. 1979, Farrel 1979, Zimmer 1980, Corey 1984, Modlin & Dardeau 1987, Cahoon & Tronzo 1990, Băcescu 1992).

In addition to *O. smithi,* five other species of the genus *Oxyurostylis* have been described: *O. pacifica* Zimmer, 1936 and *O. tertia* Zimmer, 1943 from California and Baja California; *O. atlantica* Radhadevi & Kurian, 1981 from Florida and Yucatán; *O. antipai* Petrescu et al., 1993 from Jamaica; and *O. salinoi* Brum, 1966 from Brazil.

In the present paper two species of *Oxyurostylis* from the northeastern Gulf of Mexico are described, one designated as *O. lecroyae,* new species, and the other provisionally considered as a form of *O. smithi* Calman, 1912. Although these descriptions clarify some taxonomic aspects of the *Oxyurostylis* from the Gulf of Mexico, comparisons among the species of this uniform and problematic genus still remain incomplete.

Material and Methods

Total body length was measured from the tip of the pseudorostrum to the tip of the telson. Cephalothoracic and thoracic lengths include the distal process of the fifth thoracic segment.

Small juveniles of *O. smithi* could not be identified with certainty; therefore, these specimens were omitted from the list of material examined. Since this limitation also applies to most of the immature instars of *O. lecroyae,* new species, only preparatory female and adults from both sexes are included in the material examined for this species.

Specimens examined under scanning electron microscope (SEM) were dehydrated, critical-point dried, mounted on stubs and coated with 15nm of gold-palladium.

The materials used in this study were

borrowed from museums, donated by colleagues, and collected by the authors. The following museums loaned material to the authors: Museu Nacional do Rio de Janeiro (MNRJ); National Museum of Natural History, Smithsonian Institution (USNM); and Gray Museum, Marine Biological Laboratory, Woods Hole.

In addition to the specimens from the Gulf of Mexico described herein, the following material from the North American Atlantic coast and Southern Brazil was examined for comparative purposes:

Oxyurostylis smithi Calman, 1912.—Woods Hole, Massachusetts, surface: 16 Sep 1882, 1 preparatory ♀, 1 adult ♂, 1 preparatory ♂ (USNM 44145). Date unknown, 1 adult ♂ (USNM 44160). 6 May 1906, 3 adult ♂♂, 1 juvenile (USNM 44163). Date unknown, 1 preparatory ♀, 1 preparatory ♂, 2 juveniles (USNM 44164). Date unknown, 1 preparatory ♀, 2 juveniles (USNM 44165). 2 May 1888, 11 adult ♂♂, 1 juvenile (USNM 63646). Vineyard Sound, Massachusetts: depth unknown, 3 Sep -?, 1 juvenile (USNM 34897). Surface, 29 Jul 1881, 1 adult ♂, 1 juvenile (USNM 44152). Surface, 22 Aug 1881, 1 preparatory ♀, 1 adult ♂, 1 preparatory ♂, 2 juveniles (USNM 44154). Barnstable Harbor, Massachusetts: depth unknown, 7 May 1968, 1 marsupial ♀ (Gray Museum 1125). Off Falmouth Harbor, Massachusetts: 41°31.5′N, 70°36.5′W, depth unknown, 30 Mar 1965, 5 preparatory ♀♀, 1 preparatory ♂, 1 juvenile (Gray Museum 2337). Off New Jersey: 39°21′00″N, 74°05′18″W, 26 m, 7 Nov 1976, 10 marsupial ♀♀, 5 preparatory ♀♀, 2 adult ♂♂, 5 juveniles (USNM 179608). 39°15′18″N, 74°08′00″W, 36 m, 14 Feb 1977, 6 preparatory ♀♀, 1 adult ♂, 1 preparatory ♂, 11 juveniles (USNM 179612). West end of Skull Creek, South Carolina: depth unknown, date unknown, 3 marsupial ♀♀, 9 preparatory ♀♀, 2 preparatory ♂♂, 5 juveniles (USNM 92000). One mile inside May River, South Carolina: depth unknown, 17 Jan 1891, 2 preparatory ♀♀, 1 adult ♂, 2 preparatory ♂♂, 7 juveniles (USNM 92021).

Oxyurostylis salinoi Brum, 1966.—Ubatuba, Praia do Flamengo, São Paulo: 12 m, 18 Oct 1961, Sta. 3(6)II, 5 marsupial ♀♀, 2 preparatory ♀♀, 2 adult ♂♂, 1 preparatory ♂ (Paratypes, MNRJ 4213). Ubatuba, Lagosteiro, São Paulo 6 m, 19 Jan 1962, Sta. 4(6)III: 4 marsupial ♀♀, 2 preparatory ♀♀, 2 preparatory ♂♂ (Paratypes, MNRJ 4215).

Oxyurostylis smithi Calman, 1912
(Figs. 1–22, 35, 36)

Material examined.—Galveston Island, West Bay, Texas, 0.5-1.5m: Feb 1971, 1 marsupial ♀, 5 preparatory ♀♀, 3 adult ♂♂, 2 preparatory ♂♂. Mar 1971, 4 marsupial ♀♀, 1 adult ♂, 2 preparatory ♂♂. Apr 1971, 7 marsupial ♀♀, 1 preparatory ♀, 1 adult ♂, 3 preparatory ♂♂. Jan 1972, 2 marsupial ♀♀, 1 preparatory ♀, 2 adult ♂♂, 5 preparatory ♂♂. Feb 1973, 3 preparatory ♀♀, 3 adult ♂♂, 3 preparatory ♂♂. Feb 1974, 5 marsupial ♀♀, 9 preparatory ♀♀, 2 preparatory ♂♂, 3 juveniles. 2 Apr 1987, 2 marsupial ♀♀. 31 Mar 1988; 1 marsupial ♀, 3 preparatory ♀♀. Biloxi, Mississippi, approx. 1 m depth: 22 Feb 1992, 2 marsupial ♀♀, 1 adult ♂, 1 juvenile. 2 May 1992, 3 marsupial ♀♀, 3 preparatory ♀♀, 2 adult ♂♂, 6 preparatory ♂♂, 2 juveniles. 29 May 1992, 7 marsupial ♀♀, 8 preparatory ♀♀, 8 adult ♂♂, 1 preparatory ♂ (selected reference material: 6 marsupial ♀♀, 6 adult ♂♂, USNM 274182). 9 Jul 1992, 2 marsupial ♀♀, 1 preparatory ♀, 4 adult ♂♂, 3 preparatory ♂♂, 2 juveniles. 7 Nov 1992, 1 marsupial ♀, 18 preparatory ♀♀, 7 adult ♂♂, 3 preparatory ♂♂, 13 juveniles. Horn Island, Mississippi: depth unknown, 11 Jul 1973, 2 marsupial ♀♀, 1 preparatory ♀, 2 adult ♂♂ (USNM 150190). Ship Island, Mississippi: 4 ft; 2 Jul 1959; 10 marsupial ♀♀, 4 preparatory ♀♀, 1 adult ♂ (USNM Acc. #239395). Perdido Key, Florida: lagoon, 0.1–1 m, 1–5 Dec 1991, 46 marsupial ♀♀, 55 preparatory ♀♀, 19 adult ♀♀, 33 preparatory ♂♂, 55 juveniles. 8–9 Mar 1992, 53 marsupial ♀♀, 49 preparatory ♀♀, 36 adult ♂♂, 54 preparatory ♂♂, 30 juveniles (selected reference material: 6 marsupial ♀♀, 6 adult ♂♂, USNM 274183). 1 Jun 1992, 1 marsupial ♀, 1 preparatory ♀, 3 juveniles. 21 Sep 1992, 6 marsupial ♀♀, 3 preparatory ♀♀, 1 preparatory ♂, 1 juvenile. St. Andrew Bay, Carl Gray Park, Florida: 0–0.5 m, 11 Dec 1991, 15 marsupial ♀♀, 21 preparatory ♀♀, 6 adult ♂♂, 15 preparatory ♂♂, 36 juveniles (selected reference material: 5 marsupial ♀♀, 5 adult ♂♂, USNM 274185). Tampa Bay, Florida (precise location not available): 0.5–1 m, grass bed; 13 Dec 1992, 59 marsupial ♀♀, 72 preparatory ♀♀, 93 adult ♂♂, 46 preparatory ♂♂ (selected reference material: 20 marsupial ♀♀, 20 adult ♂♂, USNM 274186). Courtney Campbell Causeway, Tampa Bay, Florida: 1–1.5 m, 23 Jun 1992, 41 marsupial ♀♀, 50 preparatory ♀♀, 22 adult ♂♂, 26 preparatory ♂♂ (selected reference material: 20 marsupial ♀♀, 10 adult ♂♂, USNM 274184). Westinghouse, Tampa Bay, Florida: 0.7–1 m, 22 Jul 1981, 1 preparatory ♀, 1 juvenile. Fort de Soto, Tampa Bay, Florida: 1–1.5 m, 31 Oct 1976, 4 marsupial ♀♀, 4 preparatory ♀♀, 1 adult ♂, 1 juvenile. Anna Maria Island, Tampa Bay, Florida: 1–1.5 m, 6 Aug 1981, 1 juvenile.

Description of the marsupial female.—Length: 4.8 mm to 9.3 mm.

Carapace (Figs. 1, 2, 35, 36): Width exceeding depth and approximately 0.70 times length. Dorsal outline of carapace moderately arched, with a small posterior elevation. Ocular lobe usually with several irregular lenses. Frontal lobe with a very feeble transverse line at midpoint, with almost imperceptible elevation on each side posteriorly (to reveal these features it is usually necessary to use transmitted light and/or rotate the specimen). Carapace with 2 oblique carinae, anterior carina with a pronounced angular projection (geniculation), sometimes produced into a tooth (Fig. 2a); posterior carina usually less prominent than anterior, with upper end not reaching cardiac area and lower end disappearing just before meeting anterior oblique carina. Distance between left and right teeth or projections less than twice maximum width of frontal lobe. Posterior end of carapace with a marginal carina. Cardiac area variably depressed, not confined by longitudinal carinae. Pseudorostral lobe with a carina beginning near anterior margin of carapace, turning toward frontal lobe, and ending on frontal lobe suture. A connecting carina runs from the pseudorostral carina to the angular projection of anterior oblique carina. Both pseudorostral carina and connecting carina may be faintly indicated or absent (examination of the specimen under transmitted light and in different positions facilitates the detection of these carinae when they are poorly defined). Antennal notch widely open, antero-lateral angle obsolete.

Thorax approximately ¾ carapace length. First segment visible as a narrow band dorsally and laterally. Fifth segment shorter than fourth at dorsal mid-line, with postero-lateral corners rounded.

Abdomen equal to or slightly shorter than cephalothorax.

Telson (Fig. 14): 1.5–1.7 times as long as last abdominal segment; post-anal part longer than pre-anal part, lined with weak spines on each side.

First antenna (Fig. 3): first article of peduncle 0.4 times, or slightly more, length of remaining two peduncular articles and main flagellum combined; plumose seta on inner distal angle shorter than article. Main and accessory flagella with 5 and 3 articles, respectively.

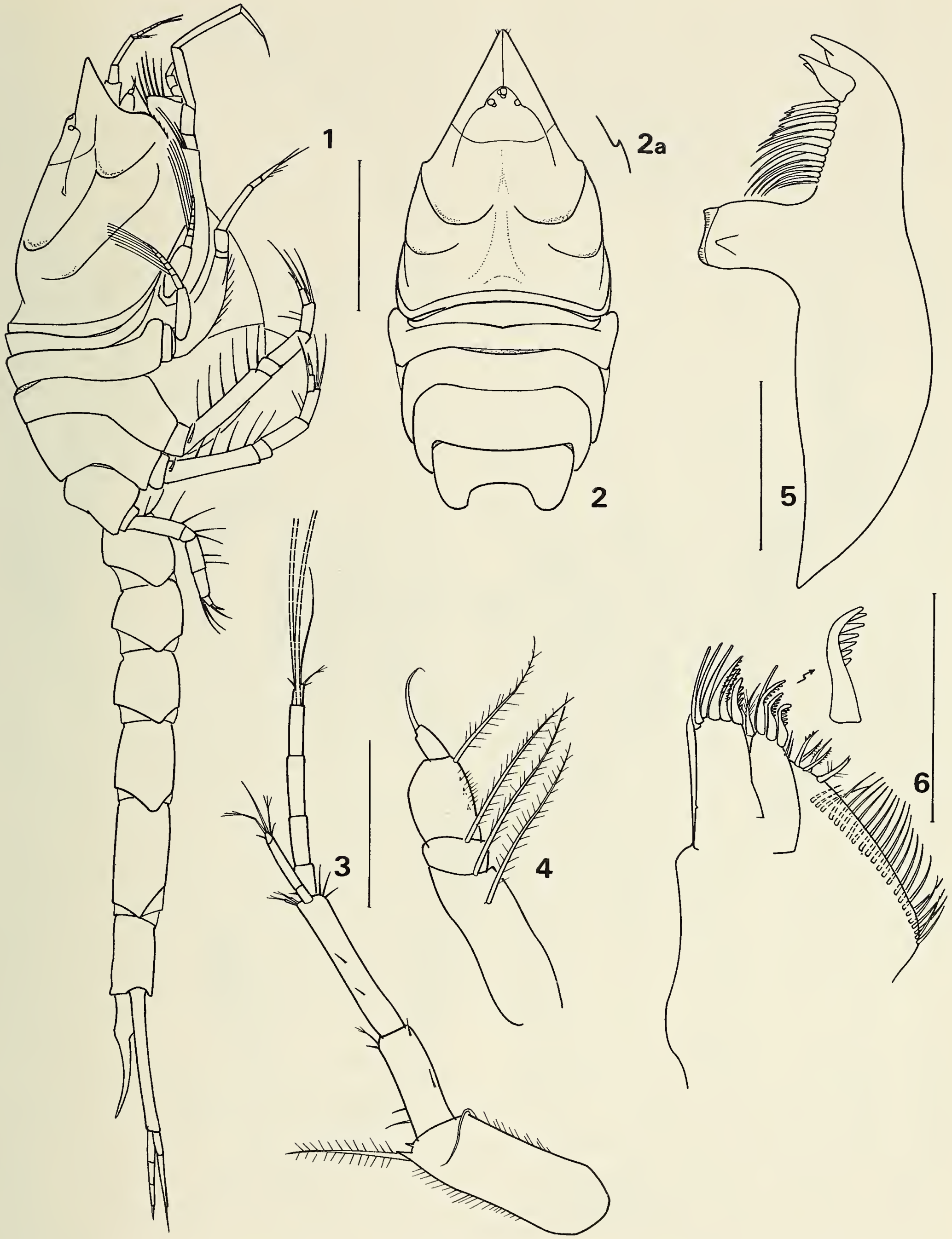
Second antenna (Fig. 4): first, second and third articles having 2, 1, and 1 strong plumose setae, respectively; fourth article small, with a distal simple seta.

Mandible (Fig. 5): bearing 11–14 setae between incisor and molar processes; some setae with bifurcate tips.

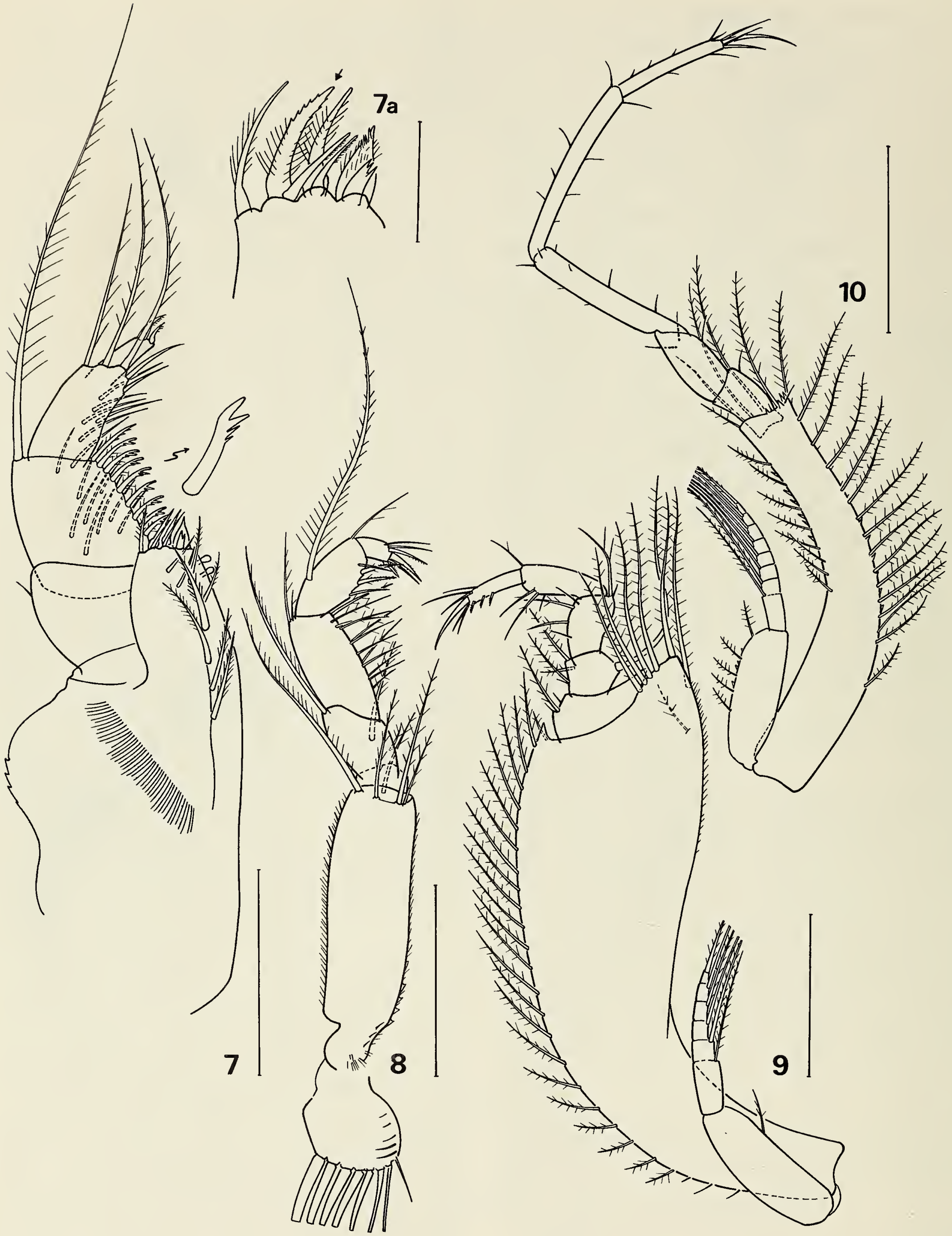
First maxilla: palp bearing two setae.

Second maxilla (Fig. 6): endites with 3 pectinate spines each.

First maxilliped (Figs. 7, 7a): basis, outer



Figs. 1–6. *Oxyurostylis smithi* Calman, 1912. Marsupial ♀: 1, habitus. 2, dorsal view of carapace and thorax. 2a, angle of anterior oblique carina produced into a tooth. 3, first antenna. 4, second antenna. 5, left mandible. 6, second maxilla. Scales: Figs. 1, 2: 1 mm (same scale); Figs. 3, 4: 0.3 mm (same scale); Figs. 5, 6: 0.2 mm.



Figs. 7–10. *Oxyurostylis smithi* Calman, 1912. Marsupial ♀: 7, first maxilliped (branchial apparatus and siphon omitted). 7a, detail of the endite of first maxilliped (arrow: second seta). 8, second maxilliped. 9, third maxilliped. 10, first peraeopod. Scales: Fig. 7: 0.2 mm; Fig. 7a: 0.05 mm; Figs. 8, 9: 0.3 mm; Fig. 10: 0.5 mm.

margin with a serrated rounded lobe; endite, distal end with 6 setae (second seta serrate) and 1 tooth with several cusps. Carpus with a row of marginal spines similar to that shown in detail (not all the ventral surface setae drawn).

Second maxilliped (Fig. 8): propodus with 8–9 setae, some pectinate, on inner margin (only some drawn).

Third maxilliped (Fig. 9): basis, inner margin with plumose setae and 1 strong distal tooth; outer process reaching approximately as far as middle of merus, with 6–8 large plumose setae distally, and 1 short plumose seta on dorsal surface. Ischium, outer margin produced into a well-developed lobe, inner margin with 1 plumose seta. Merus with 3 plumose setae on inner margin (one shorter than other two) and 1 strong plumose seta on outer margin. Remaining articles with simple or sparsely plumose setae. Carpus with 3–4 setae on inner margin and 1 distal seta on outer margin. Propodus with 3 setae on inner margin and 1 distal seta on outer margin. Dactylus with 3–4 small pectinate spines on inner margin and several setae distally.

First peraeopod (Fig. 10): basis approximately ⅔ as long as remaining articles combined, with plumose setae on both margins and distally; longest distal plumose seta not reaching carpus-propodus articulation. Ischium, merus and carpus combined slightly shorter than propodus and dactylus combined. Dactylus 0.60–0.65 times as long as propodus.

Second peraeopod (Fig. 11): basis with a row of teeth on outer margin and numerous plumose setae. Merus with 3–4 plumose setae. Carpus, outer margin with a row of teeth, appearing strongly serrate when seen laterally, and several small setae (distal setae largest).

Third and fourth peraeopods (Figs. 12, 13) with a rudimentary, 2-articulate exopod; fifth peraeopod without exopod.

Uropod (Fig. 14): peduncle extending beyond apex of telson, bearing 7–16 spines with sensory tips on inner margin. Rami subequal, equal to or slightly longer than half of peduncle. Endopod, first article longer than remaining two, second article equal to or slightly longer than third; first, second and third articles bearing 3–5, 2–4, and 2–3 spines with sensory tips on inner margin, and 1 weak distal spine on outer margin, respectively; terminal spine approximately as long as third article. Exopod: distal article with several weak spines on outer margin (only more dorsal spines drawn), 1 weak subterminal spine on inner margin, and 2 strong unequal spines distally (shorter spine less than ½ length of longer one).

Description of the adult male.—In addition to the sexual differences in the development of the second antennae, exopods, and pleopods, the adult male differs from the adult female in the following characters:

Length 4.8 mm to 7.6 mm.

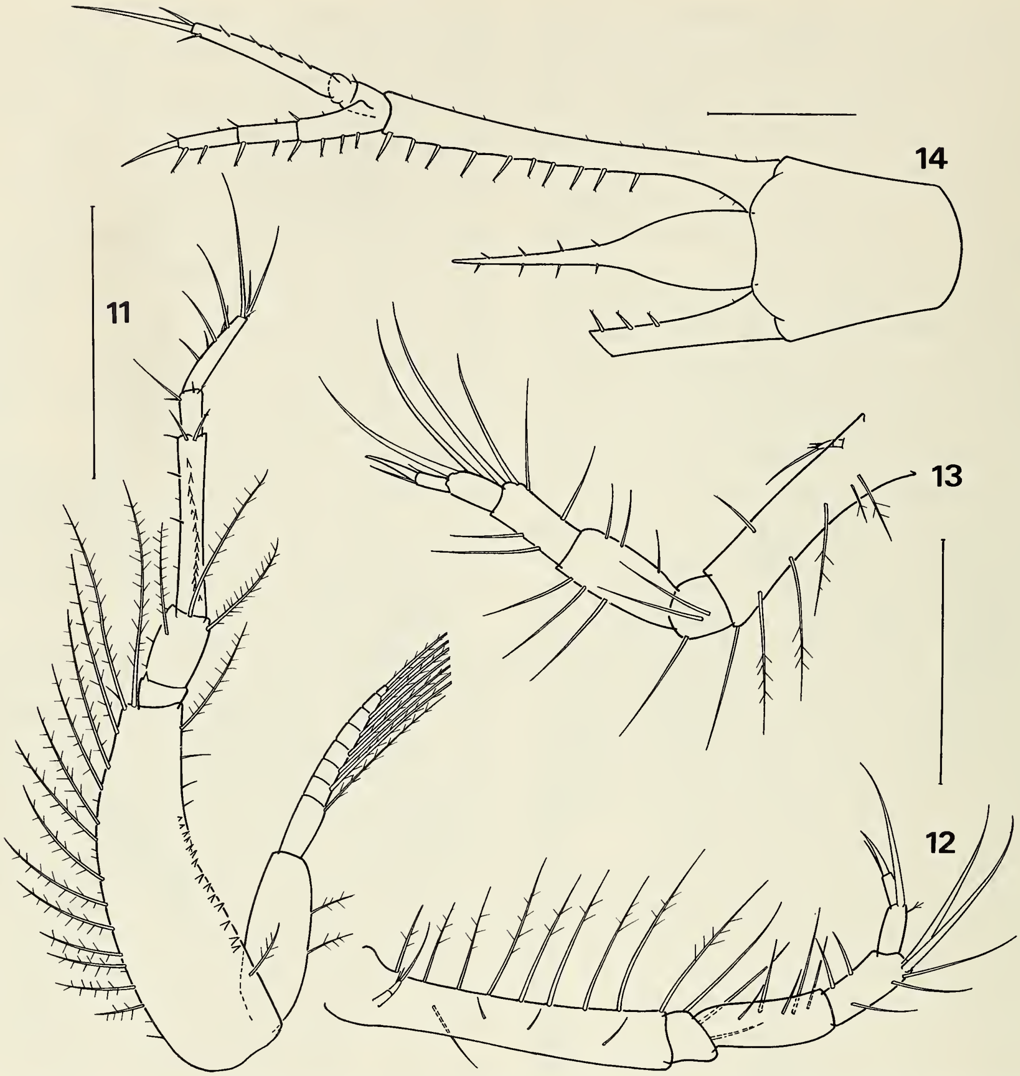
Carapace (Figs. 15, 17): dorsal outline almost straight; carinae described for female less noticeable or absent. Side of carapace with an acute horizontal carina running from posterior margin to intersect posterior oblique carina (these two carinae meet approximately at midpoint of carapace length; the oblique carina is barely traceable and frequently disappears before reaching the horizontal carina); in a few specimens the horizontal carina extends, as a fine line, to anterior oblique carina. Angular projection of anterior oblique carina never developed into tooth. Antero-lateral margin with 2–3 strong teeth.

Thorax: first segment only visible dorsally. Third segment with a rounded mid-ventral protuberance (hyposphenium, Fig. 17) bearing small setae distally. Fourth segment slightly produced mid-ventrally. Fifth segment, postero-lateral corners strongly produced and acute, almost reaching end of first abdominal segment.

Abdomen approximately 0.9 times as long as cephalothorax.

Telson (Fig. 22): 1.7–2.0 times as long as last abdominal segment, with a mid-dorsal depression bordered by a sharp carina.

First antenna (Figs. 18, 18a): main fla-



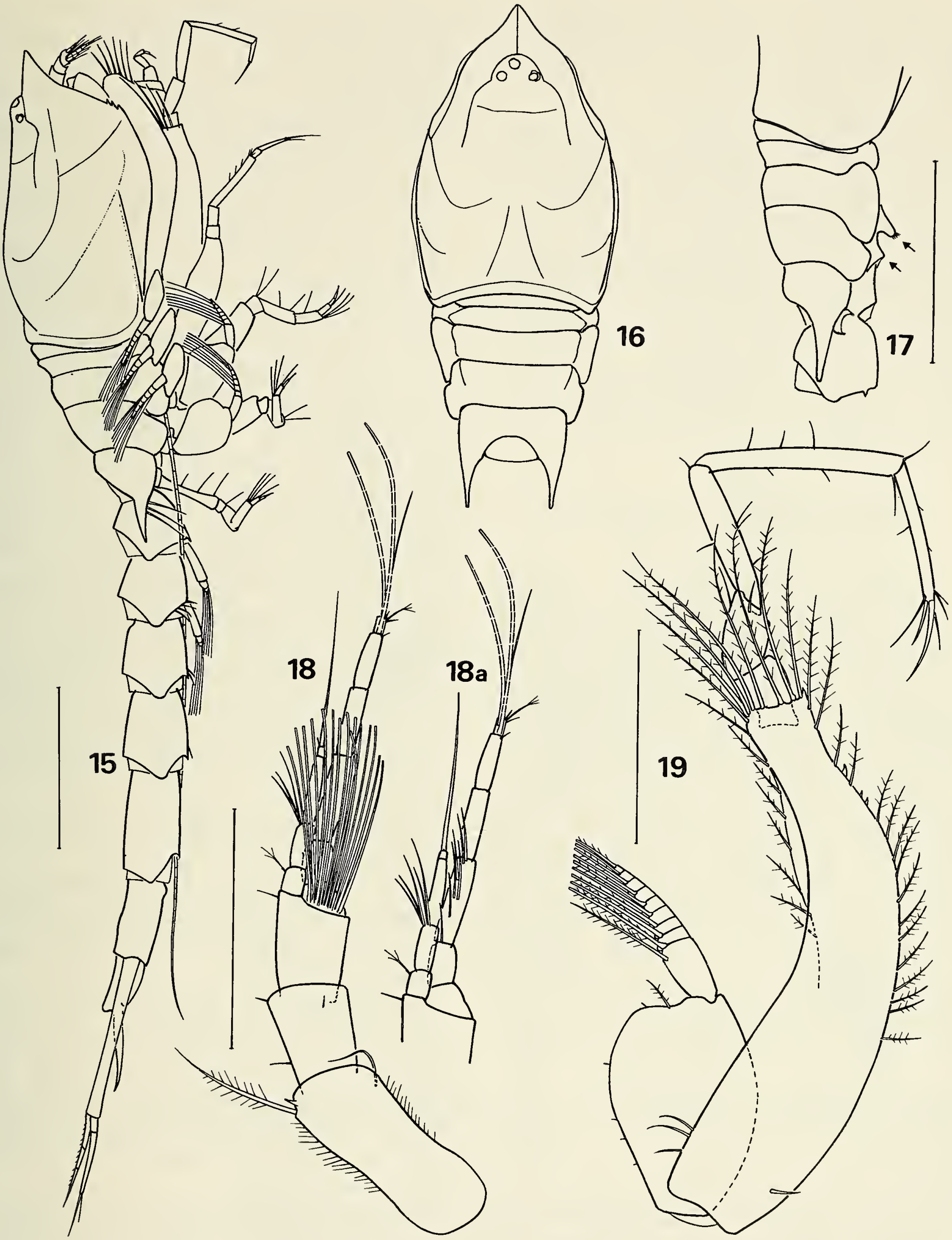
Figs. 11–14. *Oxyurostylis smithi* Calman, 1912. Marsupial ♀: 11–13, second, third and fourth peraeopods. 14, uropod and telson. Scales: Figs. 11–14: 0.5 mm (Figs. 12, 13 same scale).

gellum 6-articulate, first article with numerous aesthetascs. Accessory flagellum 4-articulate.

Third maxilliped: propodus with 4–5 setae on inner margin.

First peraeopod (Fig. 19): basis stronger than in female, slightly shorter than remaining articles combined. Ischium, merus, and carpus combined approximately 0.8 times as long as propodus and dactylus combined. Dactylus approximately 0.7 times as long as propodus. Exopod more robust than in female.

Second peraeopod (Fig. 20): basis stronger than in female, outer serration absent. Carpus, strong serration absent, with 3–5 well developed setae on inner margin, 4–6 unequal weak spines (shorter spines with sensory tips) distally, and 1 seta or weak spine with sensory tip approximately ⅔ distance along article (sometimes absent). Exopod more robust than in female.



Figs. 15–19. *Oxyurostylis smithi* Calman, 1912. Adult ♂: 15, habitus. 16, dorsal view of carapace and thorax. 17, lateral view of thorax (legs omitted) showing hyposphenia (arrows). 18, first antenna. 18a, detail of flagella (aesthetascs omitted). 19, first peraeopod. Scales: Figs. 15–17: 1 mm (Figs. 15, 16 same scale); Figs. 18, 18a: 0.3 mm (same scale); Fig. 19: 0.5 mm.

Third (Fig. 21) and fourth peraeopods with stronger basis than in females, with well developed exopods; fifth peraeopod, basis weaker than in female.

Uropod (Fig. 22): inner margin of peduncle with 12–20 bipectinate spines with sensory tips. Endopod, first, second and third articles with 6–9, 4–7, and 3–5 bipectinate spines with sensory tips, respectively.

Distribution.—From Bay of Fundy (Canada) to northern coasts of the Gulf of Mexico (0–30 m). The additional records reported here are from south Florida to Texas, Gulf of Mexico, in lagoons and other shallow protected areas (0–1.5 m).

Oxyurostylis lecroyae, new species
(Figs. 23–34, 37, 38)

Holotype.—Marsupial ♀ (USNM 274187). Type locality: Biloxi, Mississippi, approximately 1 m depth, 28 Aug 1991.

Paratypes.—From the same locality: 28 Aug 1991: 3 marsupial ♀♀, 2 adult ♂♂ (USNM 274188). 30 Dec 1991, 15 marsupial ♀♀, 2 adult ♂♂ (USNM 274189).

Additional material examined.—Bird Island, Galveston Bay, Texas: 3–3.5 m, 18 Sep 1991, 1 preparatory ♀. Cameron, Louisiana, 7 mi off shore: 29°39′52″N, 93°28′35″W, 10 m, Jun 1981, 8 marsupial ♀♀, 2 preparatory ♀♀ (USNM 189196). Bay Marchand Lease Area, Louisiana: 29°02′50″N, 90°09′46″W, 12 m, 13 Jan 1979, 2000 m east of platform, 4 marsupial ♀♀, 2 adult ♂♂ (USNM 187408). 500 m north of platform, 3 marsupial ♀♀, 1 preparatory ♀ (USNM 187413). 500 m south of platform, 5 marsupial ♀♀ (USNM 187424). Biloxi, Mississippi; approx. 1 m depth: 28 Aug 1991, 8 marsupial ♀♀, 7 preparatory ♀♀, 6 adult ♂♂. 25 Sep 1991, 2 marsupial ♀♀, 9 preparatory ♀♀, 5 adult ♂♂. 14 Oct 1991, 5 marsupial ♀♀, 2 preparatory ♀♀, 3 adult ♂♂. 30 Dec 1991, 29 marsupial ♀♀, 2 preparatory ♀♀, 2 adult ♂♂. 29 May 1992, 1 marsupial ♀. Courtney Campbell Causeway, Tampa Bay, Florida: 1–1.5 m, ? 1991, 5 marsupial ♀♀, 11 preparatory ♀♀, 28 adult ♂♂. Lido Beach, Sarasota, Florida: 1–1.5 m, 3 Dec 1992, 1 marsupial ♀, 1 preparatory ♀, 1 adult ♂. Marco Island, Florida: 25°57.94′N, 81°45.30′W, 7 ft, 9 Sep 1991, 10 marsupial ♀♀, 9 preparatory ♀♀, 4 adult ♂♂.

Description of the marsupial female.—Length: 2.9 mm to 5.9 mm.

Carapace (Figs. 23–25, 37, 38): width exceeding depth, 0.73–0.85 times length. Carinae variably developed, acute and distinct or blunt and perceptible only by rotating the specimen; arrangement as in the *O. smithi* specimens described above, except for the following: transverse frontal lobe carina absent or perceivable as a very feeble line never extended to pseudorostral lobes (observable only using transmitted light); posterior oblique carina absent; side of carapace with a horizontal carina running from posterior margin of carapace to intersect anterior oblique carina. Angular projection of oblique carina not developed into a tooth. Other aspects of carapace as in the *O. smithi* specimens described above.

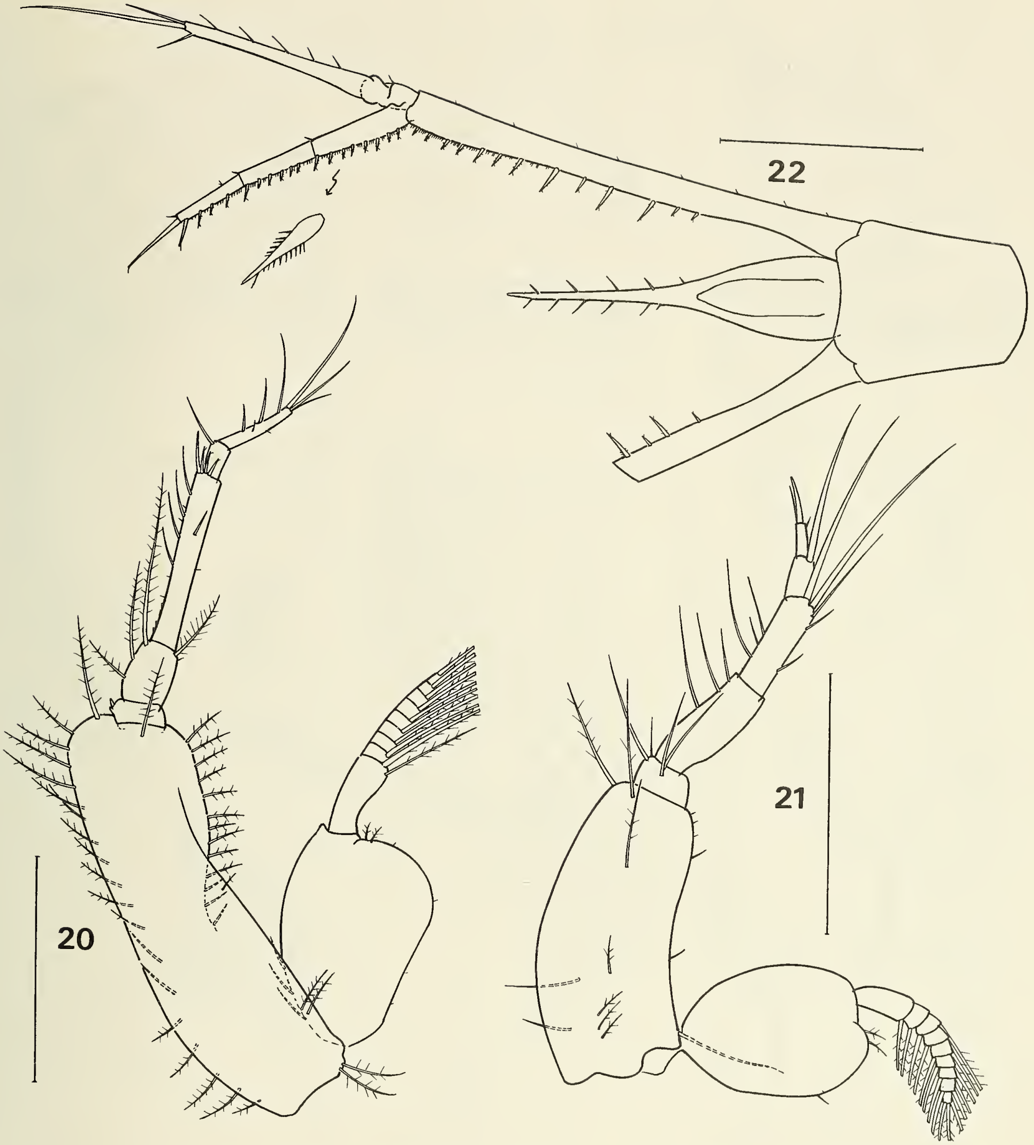
Thorax as in the *O. smithi* specimens described above.

Abdomen approximately 0.8 as long as cephalothorax.

Telson (Fig. 30): 1.8–2.0 times as long as last abdominal segment; post-anal part longer than pre-anal part, lined with weak spines on each side.

First antenna (Fig. 26): first article of peduncle approximately ⅓ as long as remaining two peduncular articles and main flagellum combined, plumose seta on distal inner angle approximately as long as article. Main and accessory flagella with 5 and 3 articles, respectively.

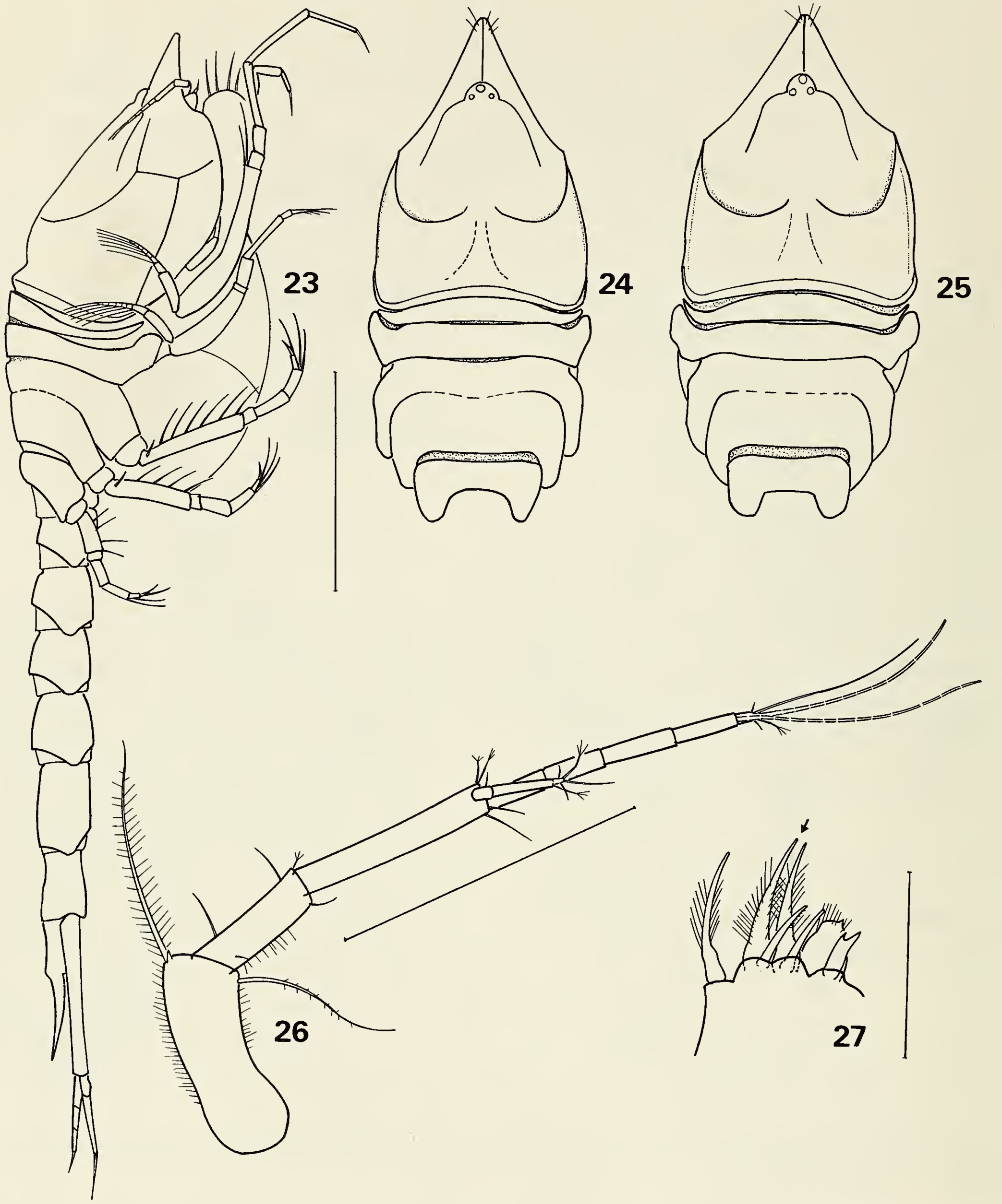
First peraeopod (Fig. 29): basis approximately 0.7 times as long as remaining articles combined, with plumose setae on both margins and distally; longest distal seta extends slightly beyond carpus-propodus articulation. Ischium, merus and carpus combined approximately 0.80 times as long as propodus and dactylus combined. Dactylus 0.70–0.75 times as long as propodus.



Figs. 20–22. *Oxyurostylis smithi* Calman, 1912. Adult ♂: 20, second peraeopod. 21, third peraeopod. 22, uropod and telson. Scales: 0.5 mm.

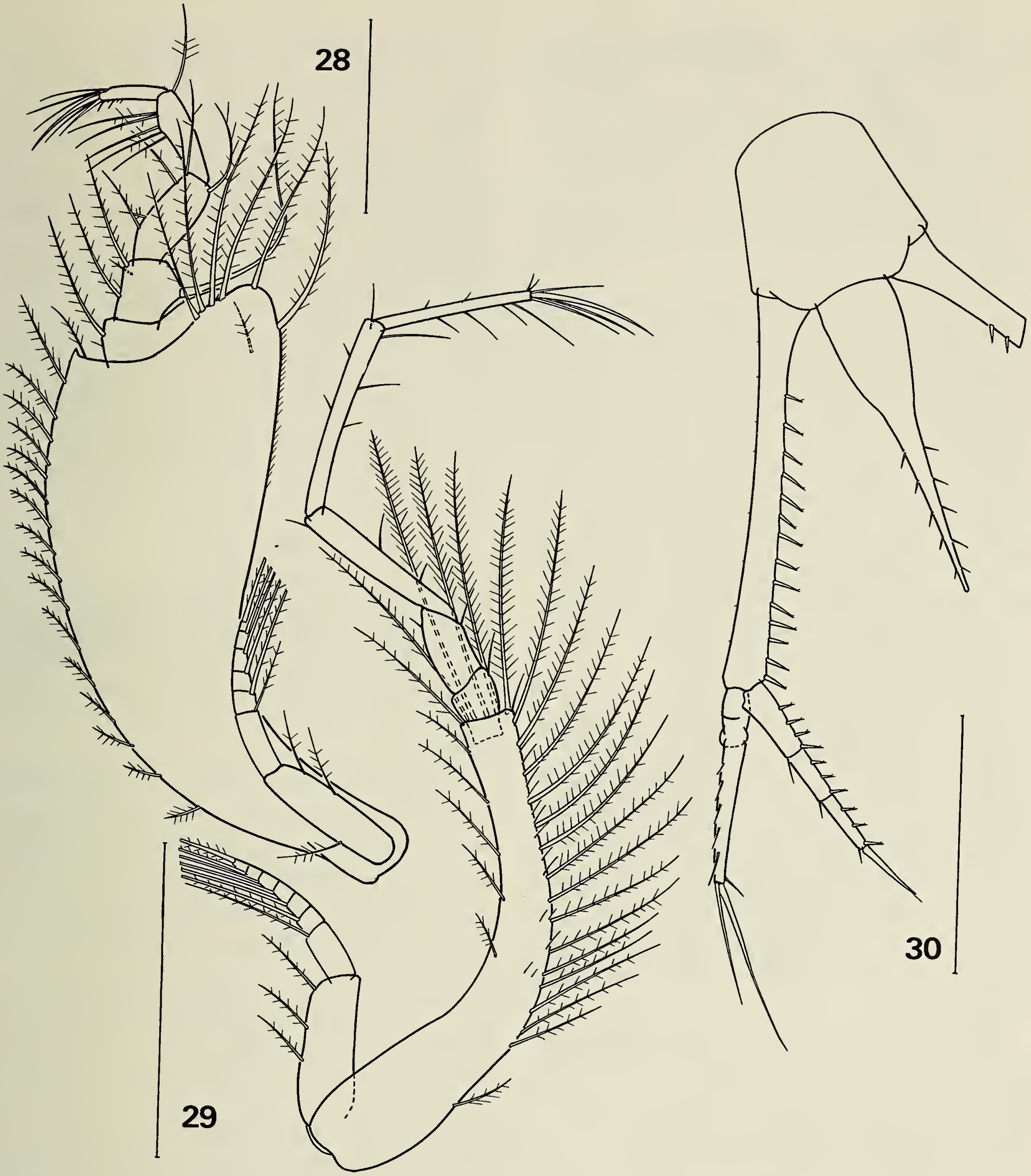
Uropod (Fig. 30): peduncle extending as far as or beyond apex of telson, inner margin with 9–15 spines with sensory tips. Endopod equal to or slightly longer than exopod; approximately ½ as long as peduncle; first article longer than remaining two; second article slightly shorter than third; first, second and third articles with 3–6, 2–3, and 2–3 spines with sensory tips on inner margin, and 1 weak distal spine on outer margin, respectively; terminal spine approximately as long as third article. Exopod, distal article with several weak spines on outer margin (only more dorsal spines drawn), 1 subterminal weak spine on inner margin, and 2 unequal larger spines distally (shorter spine more than ½ length of longer one).

Remaining appendages differing very



Figs. 23–27. *Oxyurostylis lecroyae,* new species. Marsupial ♀: 23, habitus. 24, dorsal view of carapace and thorax. 25, idem, from another ♀ showing a slight different width/length carapace propotion. 26, first antenna. 27, detail of the endite of first maxilliped (arrow, second seta). Scales: Figs. 23–25: 1 mm (same scale); Fig. 26: 0.3 mm; Fig. 27: 0.05 mm.

slightly from those of the *O. smithi* specimens described above. The main differences are as follows: mandible with 10–12 setae between incisor and molar processes. First maxilliped (Fig. 27): endite, second seta not serrate. Second maxilliped, inner marginal setae of propodus approximately twice as abundant as in the *O. smithi* spec-



Figs. 28–30. *Oxyurostylis lecroyae,* new species. Marsupial ♀: 28, Third maxilliped. 29, first peraeopod. 30, uropod and telson. Scales: Fig. 28: 0.3 mm; Figs. 29, 30: 0.5 mm.

imens described above. Third maxilliped (Fig. 28), basis: outer process with 6 plumose setae distally; merus with 3 inner marginal setae as in the *O. smithi* specimens described above, but shortest seta weak, simple or sparsely plumose; propodus with 4–5 setae on inner margin; dactylus with 1–2 pectinate spines on inner margin. Second peraeopod, serration on carpus less developed.

Description of the adult male.—In addition to the sexual differences in the development of the second antennae, exopods and pleopods, the adult male differs from the adult female in the following characters:

Length: 4.7 mm to 5.7 mm.

Carapace (Fig. 31): width 0.66–0.78 times length, dorsal outline almost straight. Oblique carina weak, blunt, perceptible only by rotating the specimen. Horizontal carina always prominent, extending from posterior margin of carapace to oblique carina. Antero–lateral margin without teeth (not as in the *O. smithi* specimens described above.)

Thorax: first segment only visible dorsally. Fifth segment, postero-lateral corners strongly produced, acute, almost reaching end of first abdominal segment; last three segments with mid-ventral protuberances (hyposphenia, Fig. 32), viz., third segment with a hooked protuberance bearing small setae distally, fourth and fifth segments with a triangular sharp protuberance, more developed on fourth than on fifth segment.

Abdomen: first segment usually with a small mid-ventral tooth.

Telson (Fig. 34): 2.1–2.4 times as long as last abdominal segment, with a mid-dorsal depression bordered by a sharp carina.

First antenna as in the *O. smithi* specimens described above, except for the following: first article of peduncle 0.36–0.38 times as long as remaining two peduncular articles and main flagellum combined; plumose seta on inner distal angle of first peduncular article is shorter than article (not as in female).

Third maxilliped: basis, inner distal tooth larger than in female; propodus with 5–7 setae on inner margin; dactylus with 2–3 pectinate spines on inner margin.

First peraeopod (Fig. 33): basis stronger than in female, equal to or slightly shorter than remaining articles combined. Ischium, merus and carpus combined approximately 0.7 times as long as propodus and dactylus combined. Dactylus 0.75–0.80 times as long as propodus. Exopod more robust than in female.

Second peraeopod as in the *O. smithi* specimens described above except carpus with 3–4 setae on inner margin and 4–5 spines with sensory tips distally.

Uropod (Fig. 34): peduncle extending beyond apex of telson; inner margin with 22–27 bipectinate spines with sensory tips. Endopod slightly longer than exopod; first, second and third articles with 5–8, 4–7, and 4–6 bipectinate spines with sensory tips, respectively. All of these spines are similar to that shown in detail for *O. smithi* in Fig. 22.

Distribution.—Gulf of Mexico, from Texas to Florida, 1–12 m depth.

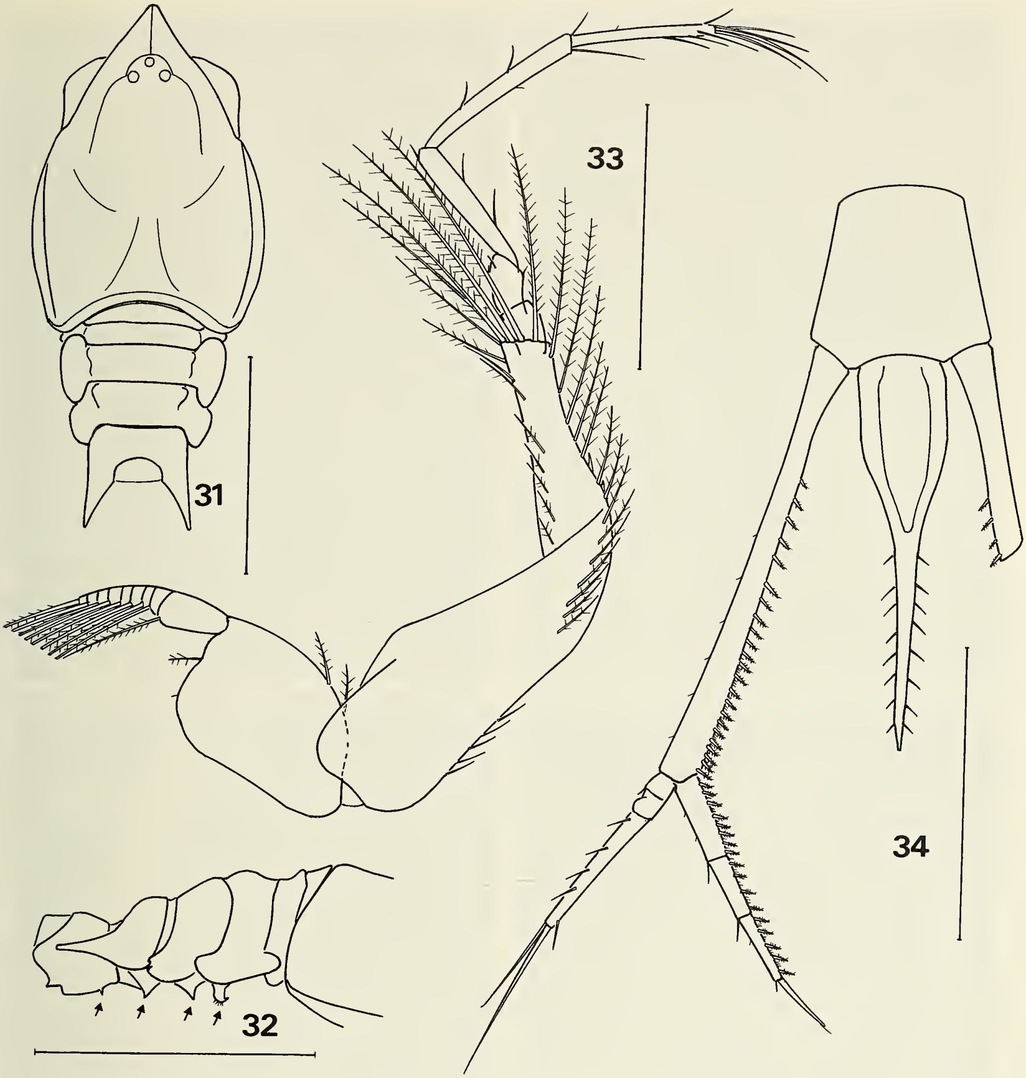
Derivation of the specific epithet.—This species is named for our colleague Sara LeCroy, in recognition for the sound advice and encouragement received during the preparation of this and many other papers.

Discussion

The genus *Oxyurostylis* includes six known species, all collected in the Americas at depths between 0 and 30 m (Calman 1912, Zimmer 1936, 1943; Brum 1966, Radhadevi & Kurian 1981, Petrescu et al. 1993).

Calman (1912) described *O. smithi* based on specimens from the Woods Hole area, but he also listed one specimen from Punta Rassa (Florida) and another from Calcasieu Pass (Louisiana) in the material examined. Unfortunately, these two specimens are severely damaged.

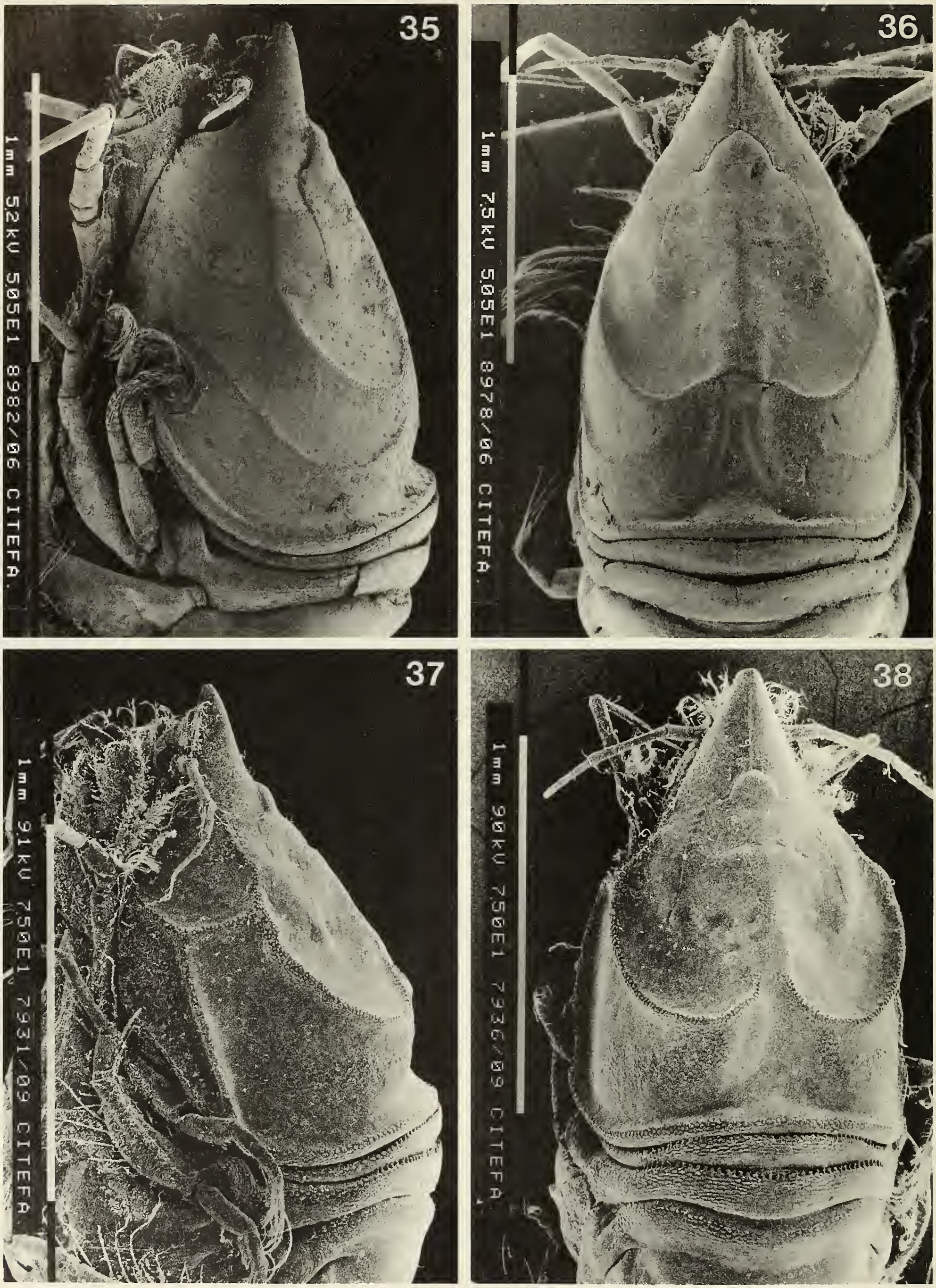
Zimmer (1980) examined additional specimens from the Woods Hole area, Chesapeake Bay, Cape Hatteras, and South Carolina, and he found some specimens with a carina connecting the pseudorostral and the first oblique carinae, and an angular projection (geniculation) on the first oblique carina. The authors also found these two above mentioned features in some of the specimens from South Carolina studied by Zimmer, whereas in all the specimens from the Woods Hole and New Jersey areas that the authors examined, the connecting carina is incipient, not reaching the anterior oblique carina, and the angular projection is not observed. Zimmer concluded that these differences show a certain geographical variation which, however, is not sufficiently



Figs. 31–34. *Oxyurostylis lecroyae,* new species. Adult ♂: 31, dorsal view of carapace and thorax. 32, lateral view of thorax (legs omitted) showing hyposphenia (arrows). 33, first peraeopod. 34, uropod and telson. Scales: Figs. 31, 32: 1 mm; Figs. 33, 34: 0.5 mm.

pronounced for the establishment of a geographical race.

All the specimens the authors examined from Massachusetts and New Jersey conform to Calman's original description and differ from the specimens from the Gulf of Mexico, described herein, in the following: (1) pseudorostral and both oblique carinae prominent, acute, separated from each other by conspicuous depressed areas, (2) frontal lobe crossed by two transverse carinae, the posterior one always well developed, (3) connecting carina incipient, not reaching the anterior oblique carina, (4) anterior oblique carina without angular projection or tooth, (5) oblique carinae meeting dorsally to form the lateral side of the cardiac area, (6) fifth thoracic segment approximately as long as fourth at dorsal mid-line, posterolateral corners bluntly pointed (this differ-



Figs. 35–38. SEM photographs. *Oxyurostylis smithi* Calman, 1912 Marsupial ♀: 35, lateral view of carapace. 36, dorsal view of carapace. *Oxyurostylis lecroyae,* new species. Marsupial ♀ with well developed carinae: 37, lateral view of carapace. 38, dorsal view of carapace. Scales: 1 mm.

ence applies only to females, in males the fifth thoracic corners are always strongly produced and acute).

The phenotypic differences between the populations from the northeastern Gulf of Mexico and the type locality area may deserve subspecific recognition. However, the authors prefer to avoid the introduction of a new name until more specimens from protected and exposed beaches, as well as from the sublittoral areas, are available.

Brum (1966) described *Oxyurostylis salinoi* from Brazil. The adult female of this species and that of *O. smithi* described herein differs mainly in the following: (1) pseudorostral carina serrated, (2) carapace plateau provided with mid-dorsal denticles, (3) first thoracic segment visible only dorsally, (4) main flagellum of first antenna composed of four articles, (5) first peraeopod elongated, basis about half as long as the remaining distal articles together. The females of *O. salinoi* have a small exopod on the third and fourth peraeopods, not observed by Brum (1966). All of these characteristics were confirmed by examining some of the paratypes.

Oxyurostylis lecroyae, new species, is unique in the genus in that the adult female has a horizontal carina on the carapace.

Radhadevi & Kurian (1981) described *O. atlantica* from the Gulf of Mexico and the Caribbean Sea. Regrettably, this description is insufficient and based only on a few juveniles. The authors consider *O. atlantica* a species inquirenda until it is more thoroughly investigated.

Although the descriptions of *O. smithi* and *O. lecroyae* presented herein clarify some taxonomic aspects of the genus, our knowledge of the *Oxyurostylis* from the Gulf of Mexico is still incomplete. The authors examined additional subtidal Gulf material closely related to *O. smithi* and *O. lecroyae,* but unfortunately these specimens were few and badly preserved, and therefore not included in the present taxonomic study.

Acknowledgments

The authors are very grateful to N. S. Jones and S. LeCroy for their helpful comments and corrections of an earlier version of the manuscript. We are also indebted to J. Foster, S. Grabe, A. Humes, M. Patillo, W. Price, M. Schotte, and P. Young for supplying us with specimens. Appreciation is due D. Giménez for his technical assistance with the scanning electron microscope. This study was partially supported by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and the United States Environmental Protection Agency (EPA).

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):613–616. 1995

Leucothoe laurensi, a new species of leucothoid amphipod from Cuban waters (Crustacea: Amphipoda: Leucothoidae)

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Abstract.—*Leucothoe laurensi* is described from the south coast of Cuba. It is distinguished from other leucothoids by a transverse palm and blade-like extension of article 6 in male and female gnathopod 2. *Leucothoe laurensi* ranges from Ascension Island to the central Caribbean, including the Carolinas to the Florida Keys.

Leucothoe Leach, 1814

Leucothoe Leach, 1814b:432.—Leach, 1814a:403.—J. L. Barnard, 1974:79.—Ledoyer, 1978:291.—Lincoln 1979: 172.—Barnard & Karaman, 1991:410–411.

Leucothoe laurensi, new species
Figs. 1–2

Diagnosis.—Male and female gnathopod 2 with nearly transverse palm and terminal blade-like process on article 6; maxilliped, inner plates triangular, separate, outer plates with sclerotized medial margin, reaching one-third along palp article 1; palp of maxilla 1, 2-articulate, inner plate with terminal seta; lower lips lacking inner lobes; posteroventral corner of epimera 3 rounded; telson elongate, triangular.

Description.—Female, 2.1 mm, USNM 266424. Article 3 of antenna 1 about one-half as long as article 1; rostrum small; anteroventral margin of head rounded; eye with 19 compact ommatidia; coxa 1 slightly smaller than 2–4, broadly rounded anteriorly, coxae 2–3 subtruncate, ventral margins with few short setae, posteroventral margin of coxa 4 produced into broad lobe, excavate dorsally, coxae 5–6 bi-lobed, 5 larger than 6, posterior lobe of 6 the deepest, coxa 7 small, evenly rounded.

Mandibles, right and left raker row with 8 spines, incisors broad, untoothed, left lacinia mobilis a stout spine, palp article 1 short. Lower lip lacking inner lobes, mandibular lobes well developed. Inner plate of maxilla 2 small, bearing a single apical seta, outer plate with 9 spines, palp 2-articulate. Maxilla 2 shortened, inner plate with 5 apical and 1 subapical setae; outer plate with 3 apical setae. Inner plates of maxilliped small, separate, each plate with 1 apical and 2 lateral stubby spines; outer plates moderately developed, reaching one-third along inner margin of palp article 1, inner margin sclerotized and sinuous, with a single large apical spine and seta; palp of normal proportions, 4-articulate.

Gnathopod 1 of stout form, posterior margin of article 6 finely serrate, dactyl long, curved, reaching point on carpus near insertion of long seta. Article 6 of gnathopod 2 with blade-like distal process; palm transverse, posterior margin of palm reaching a point 82 percent along anterior margin of propodus, bearing a series of embedded, truncate spines; propodus, medial margin with row of feeding setae that extend into the blade-like extension; inner margin of dactyl finely serrate; carpus reaching end of palm, distal margin with series of rounded cusps.

Pereopods 3–4 similar, bases linear. Pereopod 5 missing. Pereopods 6–7, bases expanded posteriorly, pereopod 7 with small

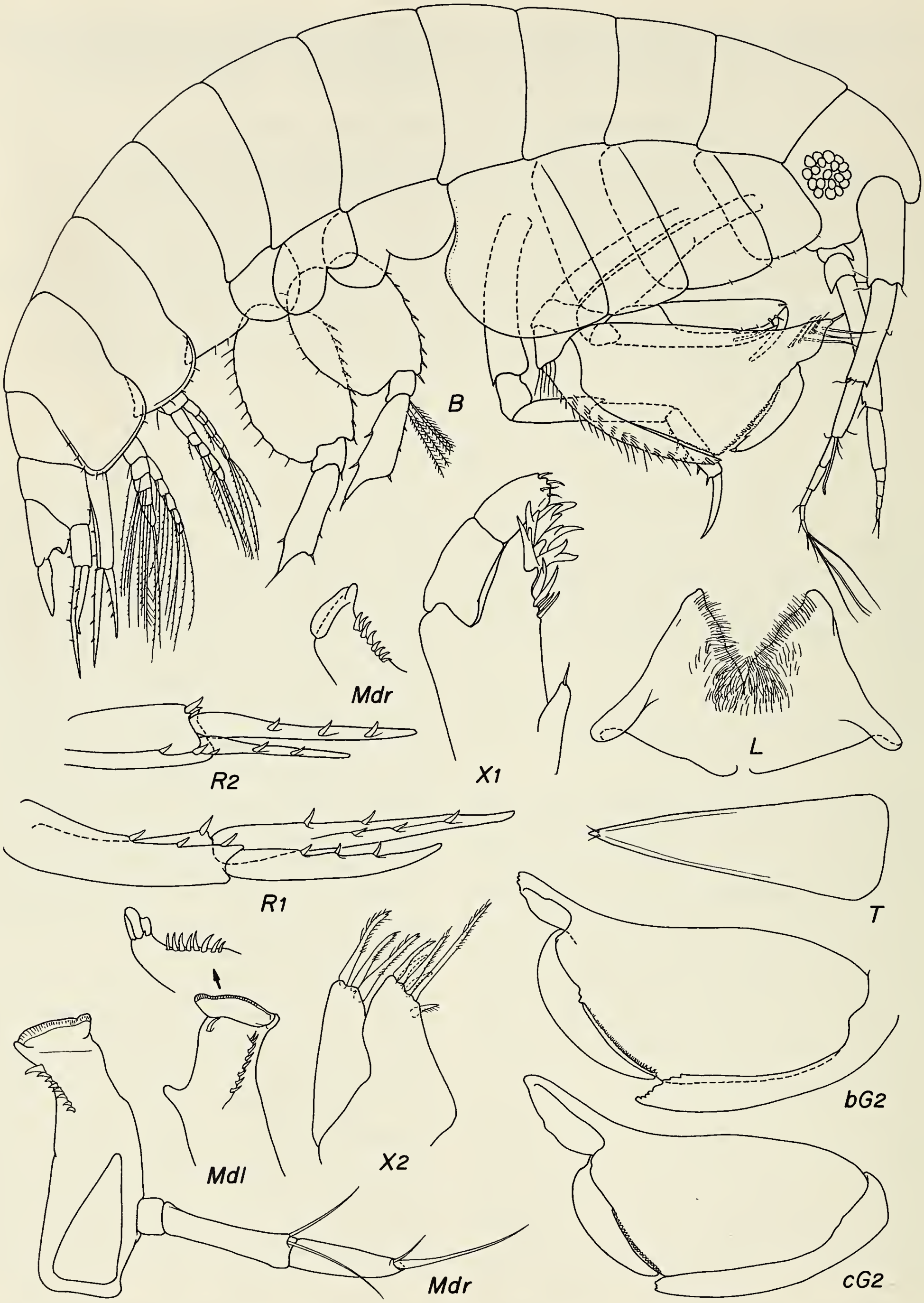

Fig. 1. *Leucothoe laurensi* n. sp., figures without lower case letter to left of each caption = holotype female "a", 2.1 mm; Capital letters in figures refer to the following parts; B = body, G = gnathopod, L = lower lip, M = mandible, P = pereopod, R = uropod, T = telson, X = maxillae, XP = maxilliped. Lower case letters to the left of capital letters refer to specimens cited in legends and voucher material in the text. ("b" = female, "c" = male) Lower case letters to the right of capital letters refer to the following adjectives, r = right, l = left, y = enlarged.

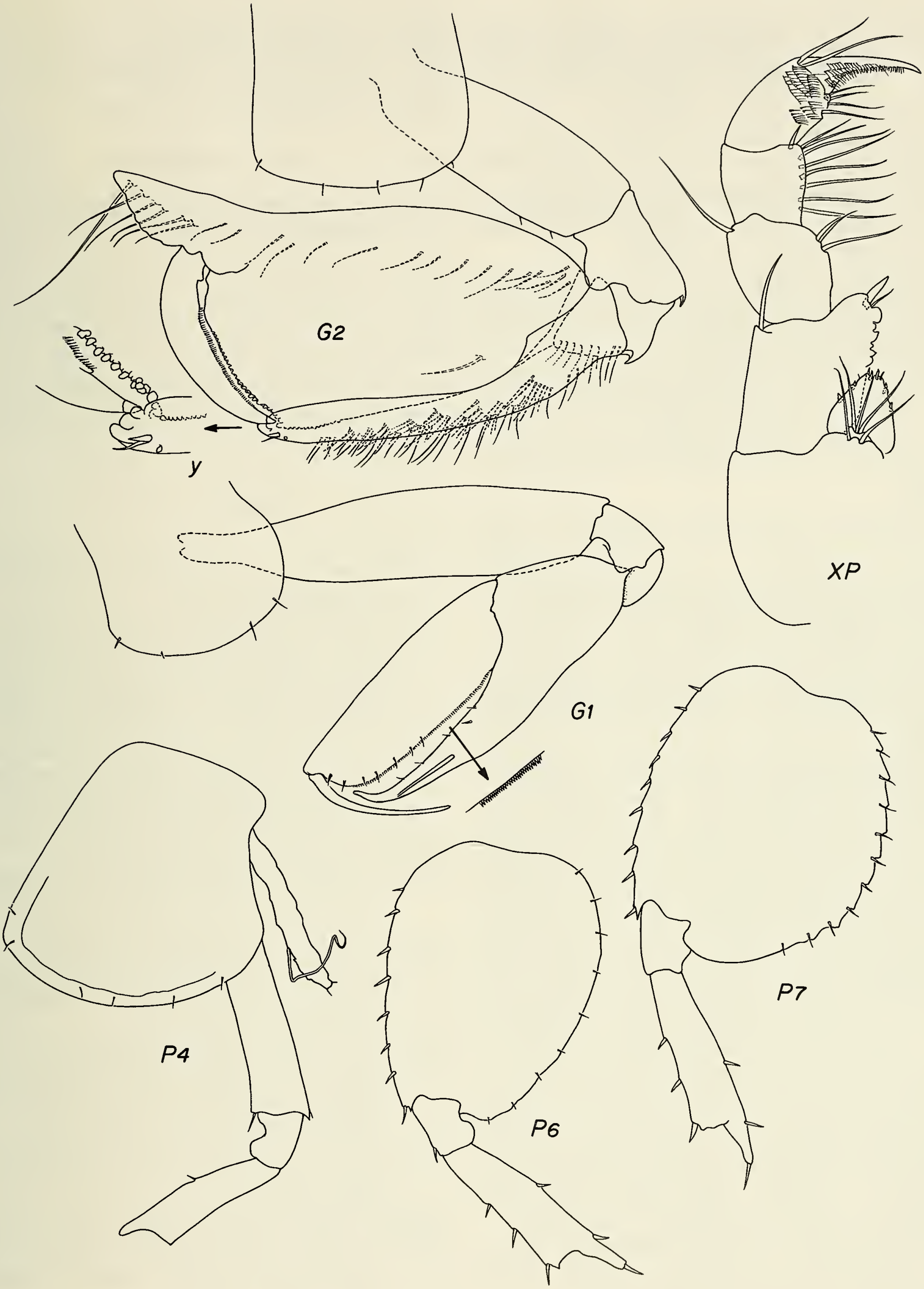

Fig. 2. *Leucothoe laurensi* n. sp., holotype female. Abbreviations as for Fig. 1.

ventral lobe. Uropods 1–2, outer ramus slightly shorter than inner, uropod 3 missing. Telson triangular, elongate. Gills simple, ovate. Oostegites narrow.

Description of male.—Similar to female except for article 6 of gnathopod 2, palm slightly more oblique, reaching only 64 percent along anterior margin of propodus (versus 82 percent in female).

Holotype.—Female "a", 2.1 mm, United States National Museum, USNM 266424; paratype USNM 266436.

Type locality.—Punta Pedernales, Isla de la Juventud, Cuba, fine sand, 50 m, M. Ortiz, collector, 24 April 1984.

Material.—Two specimens from type locality.

Additional material.—Female "b" 4.2 mm, and male "c" 4.1 mm, USNM 266425; Florida Keys, Looe Key Reef, coral overhangs on fore-reef, 5 m, J. Thomas, collector, 22 May 1982.

Etymology.—Named for the preeminent amphipodologist J. Laurens Barnard, 1928–1991.

Relationship.—This species is close to *Leucothoe euryonyx* (=*L. quadrimana* Ruffo, 1946, Ruffo Schickel 1967; and *L. dentitelson* Chevreux, 1925) in having a transverse palm and terminal process on article 6 of female gnathopod 2. *L. laurensi* is distinguished by having a nearly transverse palm and terminal, blade-like process on article 6 in both male and female gnathopod 2; in having a rounded posteroventral margin in epimera 3; and in having a non-dentate apical margin in the telson. The shape of the process on article 6, gnathopod 2 also differs, being hollow and cap-shaped in female *L. euryonyx,* versus thin and blade-shaped in male and female *L. laurensi.*

Distribution.—Tropical Western Atlantic: Cuba, Florida Keys, to 50 m.

Remarks.—*Leucothoe laurensi* is unusual among leucothoids in showing minimal sexual dimorphism in gnathopod 2. Males of *L. euryonyx* have three distinct knobs on the palm of gnathopod 2, and shortened carpal lobe. The first author has examined material attributable to *L. laurensi,* from Ascension Island and the Carolinas.

Acknowledgments

Specimens from the Florida Keys were collected under National Science Foundation grant DEB-8121128 to the first author. The second author was supported by a grant from the MacArthur Foundation, part of the Cuban-U.S. Biodiversity Program. Linda Lutz, Vicksburg, MS, inked the plates. Elizabeth Harrison-Nelson provided assistance in the lab.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):617–628. 1995

A new species of the genus *Discorsopagurus* (Crustacea: Decapoda: Paguridae) from Japan, previously known as *D. schmitti* (Stevens)

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Abstract.—A new species of polychaete tube-living hermit crab, *Discorsopagurus maclaughlinae,* is described and illustrated from Hokkaido, northern Japan. This species has been previously confounded with *Discorsopagurus schmitti* (Stevens, 1925), a species herein considered restricted to the west coast of North America. To include a second species, the generic diagnosis of *Discorsopagurus* McLaughlin, 1974, is emended. Differences between the two species are discussed.

The genus *Discorsopagurus* was proposed by McLaughlin (1974) for *Pylopagurus schmitti* Stevens, 1925, a species described from the state of Washington, west coast of North America. A suite of characters including the symmetrical uropods, flexed abdomen, partial fusion of abdominal tergites, and telson with lateral and posterior margins entire, set *Discorsopagurus* apart from all other pagurid genera lacking paired pleopods in either sex.

During a systematic study of the decapod Crustacea of Hokkaido, northern Japan, I obtained some specimens of a hermit crab living in unidentified polychaete worm tubes, apparently resembling specimens identified as *D. schmitti,* from Wakkanai, Okushiri Island, and Usujiri. Despite being reported as *Orthopagurus schmitti* or *Discorsopagurus schmitti* from the Russian Far East and northern Japan by several authors (Derjugin & Kobjakova 1935; Makarov 1937, 1938a, 1938b; Vinogradov 1950; Kobjakova 1956, 1958a, 1958b; Takeda & Miyauchi 1992), there are no records from other localities. Thus, I was prompted to determine whether or not the Asian specimens were, in fact, conspecific with the American *D. schmitti.*

A comparison of the Japanese specimens, including those reported by Takeda & Miyauchi (1992) as *D. schmitti,* with American representatives of *D. schmitti,* has proved that the former specimens are quite distinct; these are now described and illustrated as a new species. The addition of the new species to *Discorsopagurus* requires minor emendations to McLaughlin's (1974) generic diagnosis. Examination of the literature strongly suggests that *D. schmitti* reported by Russian authors actually refers to the new species. Therefore, *D. schmitti* sensu stricto is considered to be restricted to the west coast of North America.

The holotype and paratypes of *D. maclaughlinae* are deposited in the Natural History Museum and Institute, Chiba (CBM), and additional paratypes are in the Laboratory of Marine Zoology, Faculty of Fisheries, Hokkaido University (HUMZ), National Science Museum, Tokyo (NSMT), and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Terminology used in the description follows McLaughlin (1974), in general, and Morgan & Forest (1991) for the carapace sulci. The shield length (SL), measured from the tip of the rostrum to the midpoint of the posterior margin of the shield, is used to indicate size of specimens.

For comparative purpose, the following specimens have been examined:

Discorsopagurus schmitti (Stevens, 1925): USNM 265172, 3 males (SL 2.3–2.8 mm), 3 females (SL 2.5–2.8 mm), Burrows Channel, Fidelgo Island, Anacortes, Washington State, 1 Jan 1993, coll. P. Cassidy.

Orthopagurus minimus (Holmes, 1900): USNM 103772, 1 male (SL 5.6 mm), Corona Del Mar, California, Mar 1954; USNM 170404, 2 males (SL 2.7, 2.9 mm), 2.9 miles off south-east of Dirble Point, Santa Cruz Islands, R/V Velero IV, 34°05′N, 119°43′W, 29–88 m, 27 Apr 1976, trawl, coll. M. K. Wicksten.

Discorsopagurus McLaughlin, 1974

Diagnosis (emended).—Eleven pairs of phyllobranchiae. Shield calcified; posterior carapace membranous. Third segment of antenna with or without spine at ventromesial distal angle. Maxillule with endopodal external lobe moderately well developed, not recurved. First maxilliped with exopodal flagellum well developed. Third maxillipeds widely separated basally; basisischium fusion incomplete; crista dentata well developed, with 1 accessory tooth. Chelipeds unequal, right larger than left, not operculate. Fourth pereopods subchelate; propodal rasp well developed; dactyl apparently lacking preungual process at base of claw. Males with paired gonopores; coxae of fifth pereopods equal; no sexual tubes. Females with paired gonopores. No paired pleopods in either sex. Abdomen well developed, straight or slightly flexed, not twisted; tergites of third and fourth somites paired, incompletely fused chitinous plates; fifth tergite strongly calcified, with median suture; sixth tergite strongly calcified. Uropods symmetrical. Telson with or without slight lateral constrictions; posterior margin entire, straight or concave.

Remarks.—As McLaughlin (1974) noted, *Discorsopagurus* appears closest to the monotypic genus *Orthopagurus* Stevens, 1927, represented by *O. minimus* (Holmes, 1900). *Discorsopagurus,* as here emended, is best distinguishable from the latter by the absence of distinct lateral constrictions from the telson, non-operculate right cheliped, and the possession of a median suture on the fifth abdominal tergite.

Discorsopagurus maclaughlinae, new species

Figs. 1–4

Orthopagurus schmitti: Derjugin & Kobjakova, 1935:142; Makarov, 1937:65, fig. 19; Makarov, 1938a:420; Makarov, 1938b:228, pl. 2 fig. 1; Makarov, 1962: 217, pl. 2, fig. 1. Not *Pylopagurus schmitti* Stevens, 1925 (see remarks).

?*Orthopagurus schmitti:* Vinogradov, 1950: 230 (key), fig. 129; Kobjakova, 1956:51; Kobjakova, 1958a:233; Kobjakova, 1958b:252.

Discorsopagurus schmitti: McLaughlin, 1974:354 (in part); Takeda & Miyauchi, 1992:144, fig. 2.

Material examined.—Holotype: CBM-ZC 603, male (SL 5.6 mm), Usujiri, Pacific coast of southern Hokkaido, Japan, 25–30 m deep, 13 Nov 1992, dredge, coll. T. Komai. Paratypes: HUMZ-C 976, 1 male (SL 5.0 mm), 1 ovig. female (SL 4.3 mm), off Nosappu-misaki, Wakkanai, northern Hokkaido, depth unknown, 28 Mar 1991, gill net; HUMZ-C 1114, 1 female (SL 3.8 mm), Usujiri, 30–40 m deep, 10 Sep 1989, dredge, coll. T. Komai; HUMZ-C 1129, 1 female (SL 4.0 mm), Usujiri, 10–20 m deep, 15 Nov 1989, dredge, coll. T. Komai; USNM 270044, 1 male (SL 4.8 mm), Okushiri Island, Sea of Japan off Hokkaido, depth unknown, 27 Apr 1991, gill nets, coll. T. Komai; USNM 270045, 1 female (SL 3.8 mm), data as for USNM 270044; NSMT-Cr 1811, 5 males (SL 5.0–6.5 mm), 3 ovig. females (SL 5.1–5.8 mm), Soya Strait, 1991, coll. T. Miyauchi.

Description.—Shield (Fig. 1A) some-

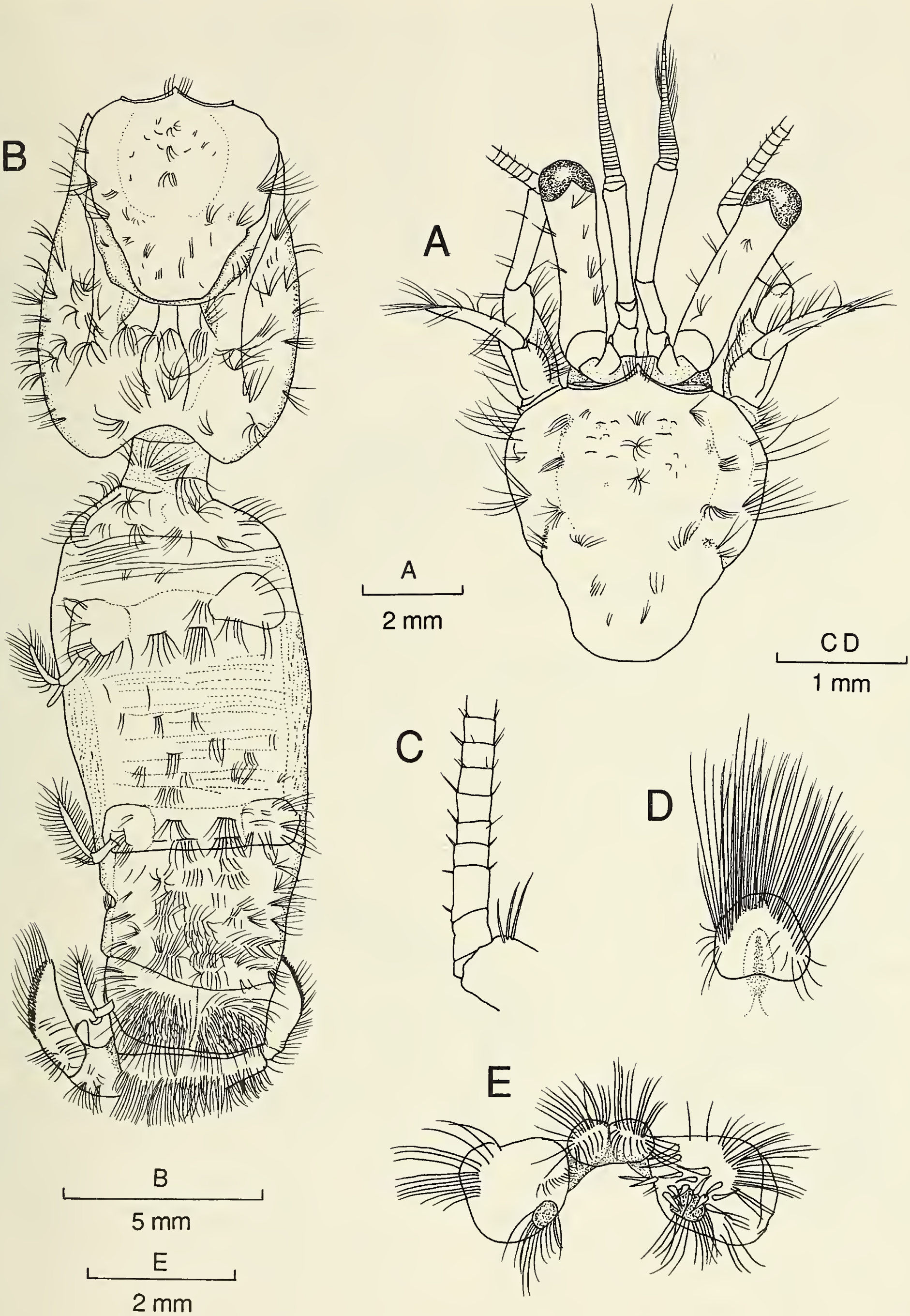

Fig. 1. *Discorsopagurus maclaughlinae,* new species. Holotype, male (CBM-ZC 603, SL 5.6 mm). A, shield and cephalic appendages, dorsal; B, carapace and abdomen, dorsal (sixth somite partially visible); C, proximal part of left antennal flagellum, dorsal; D, anterior lobe of sternite of third pereopods, ventral; E, coxae and sternal lobes of fifth pereopods, ventral.

what longer than broad; anterolateral margins sloping; anterior margins between rostrum and lateral projections moderately concave; posterior margin roundly truncate; dorsal surface with scattered tufts of setae laterally; anterolateral angle rounded. Rostrum moderately prominent, obtusely triangular with acute or subacute apex, distinctly overreaching lateral projections, partially obscured by tufts of setae. Lateral projections obtusely triangular, with prominent submarginal spine.

Posterior carapace (Fig. 1B) membranous except for somewhat calcified cardiac region, with scattered tufts of moderately long stiff setae; cardiac sulci sinuous, slightly falling short of posteromedian margin of carapace; sulci cardiobranchialis very short, somewhat diverging posteriorly; lineae anomurica curved, not reaching posterolateral margin of carapace.

Ocular peduncles (Fig. 1A) moderately long, 0.7–0.8 times as long as shield, 4.2 times as long as breadth of cornea, slightly inflated basally; cornea slightly dilated; dorsal or dorsomesial surface with row of tufts of moderately short setae. Ocular acicles subtriangular, terminating acutely with strong submarginal spine; mesial margin somewhat expanded, lateral margin slightly convex, dorsal surface lacking setae.

Antennular peduncles (Fig. 1A) moderately short, exceeding ocular peduncles by ⅓ to ¼ length of ultimate segment. Ultimate segment approximately half length of shield. Basal segment unarmed.

Antennal peduncles (Fig. 1A) moderately short, reaching or slightly overreaching ocular peduncles; with supernumerary segmentation. Fifth, fourth and third segments with few tufts of short or moderately short setae; third segment with ventromesial distal spine. Second segment with dorsolateral distal angle produced, terminating in bifid spine, mesial margin sometimes with 1 additional spine distally; dorsomesial distal angle with small spine obscured by tuft of setae, mesial margin with tufts of setae. First segment with lateral face unarmed or occasionally with spinule, ventral margin produced, with few spinules. Antennal acicle falling short of fifth segment of peduncle, terminating in small spine partially obscured by tufts of stiff setae. Antennal flagellum long, far overreaching tip of right cheliped; each article with short bristles (Fig. 1C).

Mandible (Fig. 2A) with 3-segmented palp. Maxillule (Fig. 2B) with proximal endite subquadrate; endopod with 1 bristle on moderately produced inner lobe, outer lobe well developed, not recurved. Maxilla broken during dissection (not illustrated); endopod with lateral margin strongly expanded basally. First maxilliped (Fig. 2C) with endopod equaling distal endite in distal extension; exopod with lateral margin slightly expanded basally. Second maxilliped (Fig. 2D) with basis-ischium fusion incomplete. Third maxilliped (Fig. 2E) with basis-ischium fusion incomplete; basis with some spinulose tubercles or spines; ischium (Fig. 2F) with crista dentata well developed, proximal tooth not much stronger than remaining teeth, bearing 4 movable spinules at distomesial angle and 1 accessory tooth; merus with dorsodistal and ventromesial spines; carpus with dorsodistal spine. Sternite of third maxilliped with 1 acute spine on either side of midline.

Right cheliped (Fig. 3A, B) longer than left. Chela moderately broad, greatest breadth across level of mesial base of dactyl, 1.6–1.8 times as long as broad, 1.4 times as long as carpus. Dactyl moderately short, slightly shorter than palm, moderately deep; cutting edge with row of strong calcareous teeth almost over entire length, row of small corneous teeth distally, terminating in small corneous claw; dorsomesial margin with row of moderately strong to strong spines decreasing in size distally and few tufts of short stiff setae, dorsal surface with row of moderately strong spines or tubercles and few tufts of stiff setae, mesial face slightly spinulose, ventral surface with scattered tufts of long stiff setae. Palm slightly inflated; dorsomesial margin with

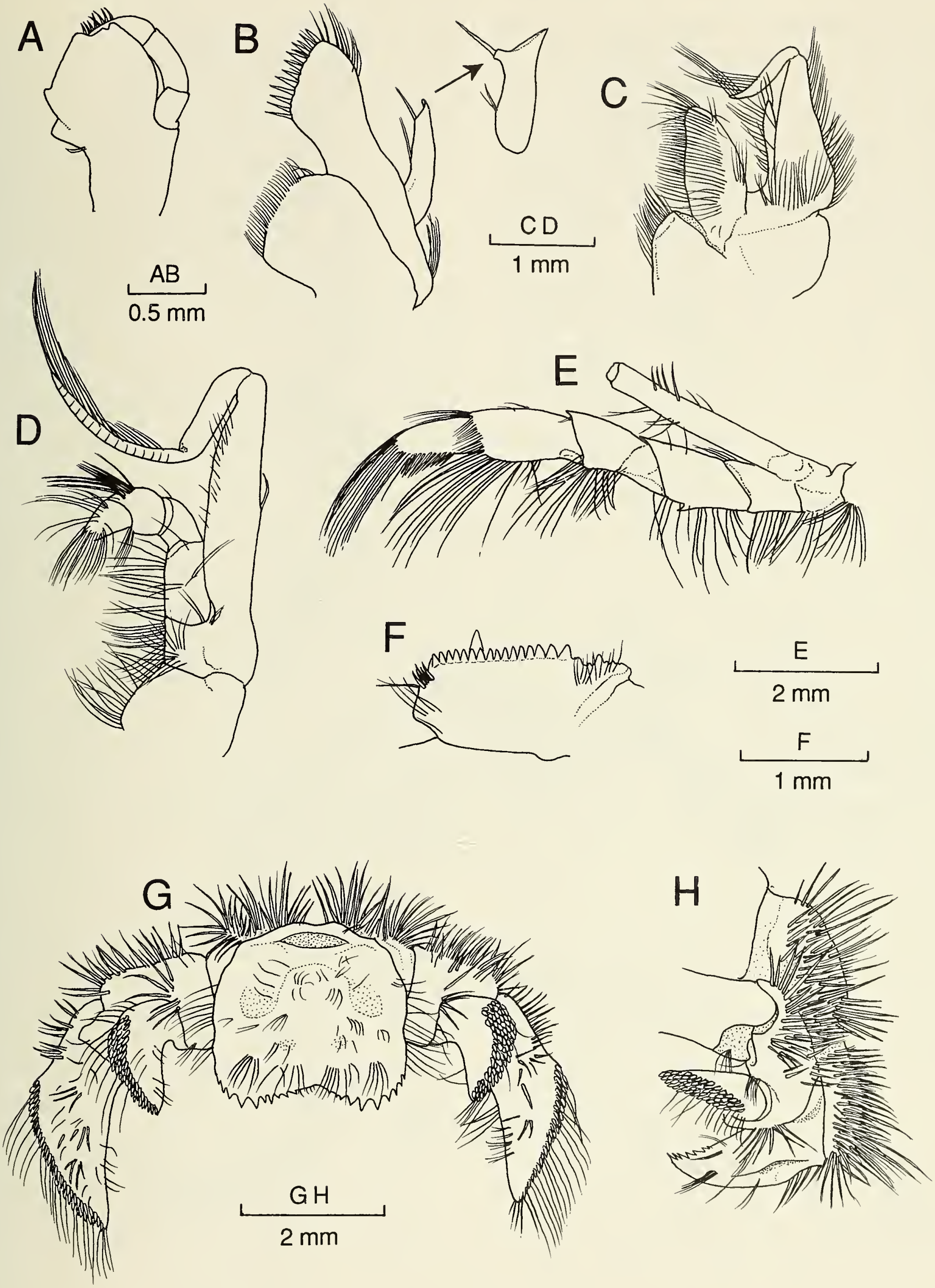

Fig. 2. *Discorsopagurus maclaughlinae,* new species. Holotype, male (CBM-ZC 603, SL 5.6 mm). Mouthparts, left, external view. A, mandible; B, maxillule (inset is endopod in lateral view); C, first maxilliped; D, second maxilliped; E, third maxilliped, lateral, exopod bent medially; F, ischium of same, internal; G, telson and uropods, dorsal; H, sixth abdominal somite, telson and uropods, lateral (distal part of uropodal exopod omitted).

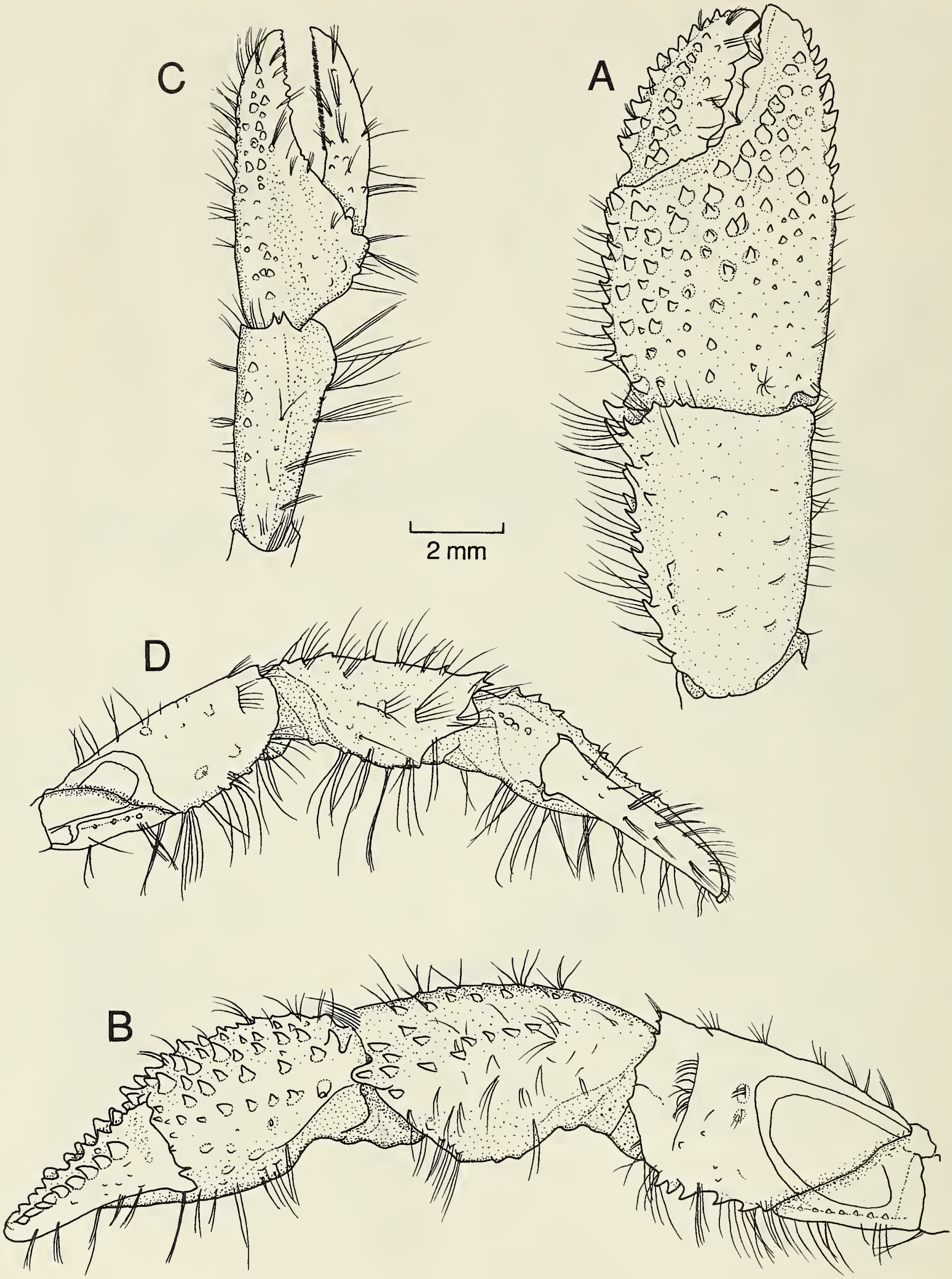

Fig. 3. *Discorsopagurus maclaughlinae,* new species. Holotype, male (CBM-ZC 603, SL 5.6 mm). A, right chela and carpus, dorsal; B, right cheliped, mesial; C, left chela and carpus, dorsal; D, left cheliped. mesial.

row of moderately strong conical spines and tufts of moderately long stiff setae; dorsal surface with several irregular rows of small or moderately strong spines extending to fixed finger; dorsolateral margin of fixed finger clearly delimited with row of moderately strong spines and dorsolateral margin of palm weakly delineated; lateral, mesial and ventral surfaces with scattered tufts of long stiff setae. Carpus slightly broadened distally, 1.4–1.5 times as long as distal breadth (excluding distolateral spines), almost as long as merus, somewhat inflated ventrally; dorsomesial margin with single or double row of moderately strong spines, increasing in size distally, and tufts of moderately strong stiff setae, dorsal surface sometimes with small spines medially or short transverse rows of moderately long stiff setae, distal margin with few small spines medially; dorsolateral margin not sharply delimited, lateral face with scattered tufts of short setae; ventrolateral margin with row of small tubercles and tufts of short stiff setae, lateral face with scattered tufts of short or moderately short setae; ventromesial margin with row of low tubercles and tufts of short to moderately long setae, mesial face with scattered tufts of short to moderately long setae; ventral surface with small spinulose tubercles. Merus subtriangular in cross section; dorsal surface with short transverse ridges bearing stiff setae, distal margin with 3 or 4 acute spines and stiff setae; mesial face sometimes with vertical ridge with stiff setae and scattered tufts of short stiff setae, ventromesial margin with single row of moderately strong spines and tufts of long stiff setae; lateral face with scattered tufts of short setae, ventrolateral margin with small spines or spinulose tubercles and tufts of long stiff setae. Ischium with row of small denticles on ventromesial margin. Coxa with tufts of long setae on distal margin.

Left cheliped (Fig. 3C, D) slightly overreaching base of dactyl of right. Chela distinctly longer than carpus; without torsion. Dactyl considerably elongated, approximately twice length of palm, slightly curved; with hiatus between fixed finger when closed; cutting edge with row of small corneous teeth, terminating in small corneous claw; dorsomesial margin with only few low tubercles and tufts of moderately long stiff setae; dorsal surface with few spinulose tubercles and row of tufts of moderately long stiff setae; mesial surface faintly tuberculate, with row of tufts of moderately long stiff setae; ventral face with few tufts of long stiff setae. Palm slightly inflated ventrally; dorsal and lateral surfaces with irregular rows of small spines and spinulose tubercles, and scattered tufts of stiff setae, dorsolateral margin not delimited; dorsomesial margin abruptly convergent posteriorly, weakly delineated, mesial face slightly tuberculate, with tufts of long stiff setae; ventral surface with tufts of long stiff setae. Carpus slightly shorter than merus; dorsal surface with 2 rows of moderately strong spines, distal margin with 2 or 3 acute spines and stiff setae laterally; mesial face with short obliquely vertical ridges bearing long stiff setae; lateral face with scattered tufts of short stiff setae; ventrodistal margin not denticulated; ventral face with tufts of long stiff setae. Merus subtriangular in cross section; dorsal surface with ridges bearing long tiff setae; mesial and lateral faces with few tufts of short setae; ventral surface with row of moderately strong spines medially, and tufts of long stiff setae. Ischium with row of small tubercles on ventromesial margin. Coxa similar to that of right cheliped.

Second and third pereopods (Fig. 4A, C) differing slightly in armature of dactyls and shape of ischia; moderately long, second pair slightly exceeding tip of right cheliped, third pair slightly shorter. Dactyls (Fig. 4B, D) relatively long and moderately slender, 1.2–1.3 times as long as propodi, not twisted; apex terminating in strong corneous claw; dorsal surfaces each with single or double row of long stiff setae; lateral faces each with scattered tufts of short setae, and with shallow longitudinal sulcus; mesial

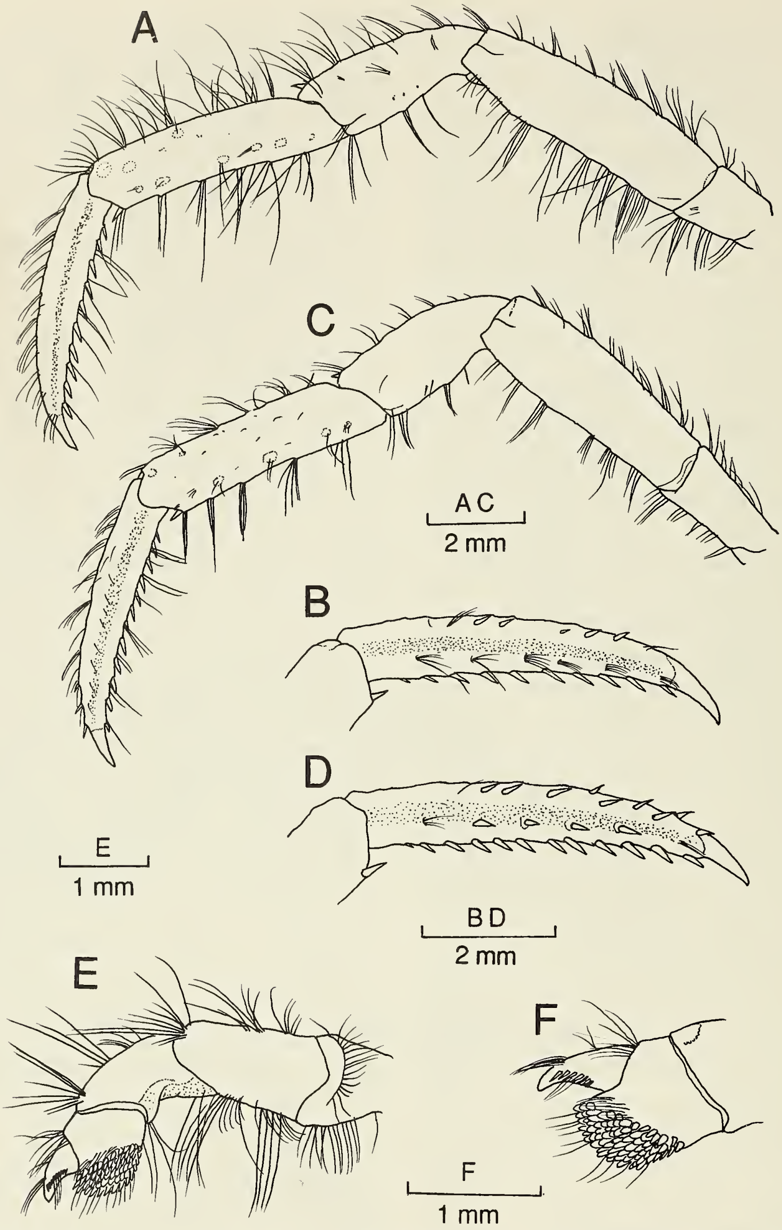

Fig. 4. *Discorsopagurus maclaughlinae,* new species. Holotype, male (CBM-ZC 603, SL 5.6 mm). Left pereopods: A, second, lateral; B, dactyl of same, mesial; C, third, lateral; D, dactyl of same, mesial; E, fourth pereopod, lateral; F, propodus and dactyl of same.

faces each with shallow longitudinal sulcus flanked by rows of tufts of short setae and rows of corneous spines in third, with row of corneous spines only along dorsal margin in second; ventral margins each with 10–12 strong corneous spines over entire length. Propodi distinctly longer than carpi; dorsal surfaces each with tufts of long stiff setae; lateral and mesial faces each with scattered tufts of short to moderately long setae; ventral margins each with row of tufts of long stiff setae and with few corneous spines distally. Carpi moderately short; dorsal surfaces unarmed in left second and third pair, with few small spines in right second, each with tufts of long stiff setae; lateral, mesial and ventral surfaces with scattered tufts of stiff setae. Meri laterally compressed; dorsal surfaces each with row of low spinulose protuberances and tufts of long setae; lateral and mesial faces nearly naked; ventral margins slightly protuberant, each with tufts of long stiff setae. Ischia with dorsal and ventral margin bearing tufts of stiff setae; ischium of third pair somewhat longer than that of second, with slightly sinuous ventral margin. Coxae of third pereopods with gonopore in females.

Sternite of third pereopods (Fig. 1D) semicircular, not skewed, with numerous long setae on anterior surface.

Fourth pereopods (Fig. 4E) subchelate, relatively stout, dorsal and ventral surfaces with tufts of long setae. Dactyls (Fig. 4F) strongly curved, without preungual process; cutting edge with relatively long corneous teeth laterally. Propodus (Fig. 4F) strongly inflated ventrally, rasp composed of 5 or 6 irregular rows of numerous scales.

Fifth pereopods chelate. Male coxae (Fig. 1E) each with gonopore obscured by stiff setae or pointed scales. Sternite (Fig. 1E) developed as paired rounded protuberances, obscured by long stiff setae.

Abdomen (Fig. 1B) well developed, straight or slightly flexed, not twisted. Fourth somite with tergite in form of paired, incompletely fused, chitinous plates. Fifth somite with tergite strongly calcified, possessing median suture, thickly covered with stiff setae except in midline. Sixth somite (Fig. 2H) with tergite strongly calcified, subrectangular in shape, separated into 2 sections by transverse groove at level of midlength; dorsal surface with dense stiff setae, margins sloping; posterior margin slightly concave, with moderately deep sinus followed by shallow sulcus either side of median concavity.

Pleopods of males (Fig. 1B) unpaired, third to fifth pleopods with exopod moderately well developed, endopod reduced. Pleopods in females unpaired, second to fourth pleopods with both rami moderately well developed; fifth pleopod with exopod moderately well developed, endopod reduced. Uropods (Fig. 2G) stout, symmetrical.

Telson (Fig. 2G) with weak median constriction; posterior lobes separated by shallow median notch, each terminal margin with 10 or more corneous spines increasing in size toward posterolateral angle.

Coloration in life.—Chelipeds and ambulatory pereopods generally brown; spines or tubercles on palm of right cheliped white. Shield mottled brown. Ocular peduncles and antennal flagella uniformly brown. In preservative, color fading to straw.

Habitat.—The specimens from Usujiri, Pacific coast of southern Hokkaido, were dredged from rubble bottom at depths of 10–40 m. This species was never encountered in the intertidal zone in the surveyed area. All of the specimens examined were found using detached tubes of serpulid polychaetes.

Distribution.—Northern part of the western Pacific: Russian coast of the Sea of Japan, Saghalien, southern Kurile Islands, Hokkaido; 6–220 m.

Etymology.—This interesting species is named in honor of Dr. Patsy A. McLaughlin, for her great contributions to systematics of the Paguridea.

Relationship.—Although this new species has been confounded with *Discorsopagurus schmitti,* the differences between them are numerous: Each article of the antennal flagellum possesses some short bristles in *D. maclaughlinae,* while in *D. schmitti* it bears long setae, giving a cast net-like appearance to the entire flagellum; in *D. maclaughlinae,* the third segment of the antennal peduncle is armed with a spine at the ventromesial distal angle. Such a spine is absent in *D. schmitti*; in the new species, the tergite of the fifth abdominal somite is not particularly sculptured; its dorsal surface is obscured by dense stiff setae. However, in *D. schmitti,* it is somewhat sculptured with upturned margins and elevated central region; its dorsal surface bears scattered long setae; the shape of the telson is remarkably different in the two species. In *D. maclaughlinae,* the lateral margins of the telson is slightly constricted, and the posterior margins are concave, each with a row of 10 or more spines. In *D. schmitti,* the lateral margins are not constricted, and the posterior margins are nearly straight or slightly convex, each with 3 or 4 spines; the merus of the third maxilliped is armed with the dorsodistal and ventromesial spines in *D. maclaughlinae,* but in *D. schmitti* it is unarmed; the articulation between the palm and the carpus of the left cheliped does not show a slight degree of clockwise torsion in *D. maclaughlinae*; the dactyl of the left chela is much longer in *D. maclaughlinae* than in *D. schmitti,* and; the dactyls of the second and third pereopods are relatively longer and slenderer in *D. maclaughlinae* than in *D. schmitti* (1.2–1.3 times as long as propodus in the former, 0.9–1.1 times as long in the latter). In the new species, the mesial surface of each dactyl bears a single or double row of corneous spines, which is absent in the American species.

Remarks.—Derjugin & Kobjakova (1935) included *Discorsopagurus schmitti* (as *Orthopagurus*) in their list of Decapoda from the Russian coast of the Sea of Japan. Makarov (1937, 1938b) first presented a somewhat detailed account of *Discorsopagurus schmitti* (as *Orthopagurus*) from Vladimir and Olga Bays. His description agrees in general with the present new species, though it lacks some important information, such as morphology of the telson. Vinogradov's (1950:307, pl. 22, fig. 129A, B) figure of *Orthopagurus schmitti,* showing the dorsal views of whole body of both sexes, is rather diagrammatic and uninformative. However, it is very likely that his illustration represents *D. maclaughlinae,* since the figure shows smooth antennal flagella. Although Kobjakova (1956, 1958a, 1958b) did not present detailed accounts of her materials, it is likely that her records from southern Saghalien and Kurile Islands by Kobjakova (1956, 1958a, 1958b) were actually this new species. As McLaughlin's (1974) distribution of *Discorsopagurus schmitti* was based on Russian literature, her report is considered partially to refer to the new species. In a recent report of anomuran Crustacea of Soya Strait, northern Hokkaido, Takeda & Miyauchi (1992) gave a brief account under the name of *Discorsopagurus schmitti,* together with photographs of a specimen living in a polychaete tube. I have reexamined their specimens (NSMT-Cr 1811; 5 males, 3 ovig. females) and confirmed its identity as *D. maclaughlinae.* At present, there is no evidence indicating the existence of the true *D. schmitti* in the western Pacific.

The minor emendations made to the generic diagnosis pertain to such intraspecifically variable characters as the presence or absence of a spine at the ventromesial distal angle of the third antennal segment, the sculpture of the sixth abdominal somite, and the shape of the telson. Although McLaughlin (1974) suggested some relationship between *Discorsopagurus* and the Parapaguridae in reference to the partially fused abdominal tergites and the telson with entire lateral and posterior margins, the presence of distinct posteromedian concavity of the telson in the new species seems to link *D. schmitti* to other pagurid genera. It is very likely that the similarity displayed by *Discorsopagurus* and parapagurids is superficial and the character states found in the former may be related to adaptation to worm tube usage. The difference in development of the posteromedian concavity of the telson may reflect degree of adaptation to the specialized habitats. The adaptation to worm tube usage seems to be more highly advanced in *D. schmitti* than in *D. maclaughlinae. Discorsopagurus schmitti* nearly exclusively inhabits attached tubes of the honeycomb worm *Sabellaria cementarium* Moore (Gherardi & Cassidy 1994); the antennal flagellum, of which each article carries long setae, suggests that feeding is accomplished, at least partially, by antennal filtering in *D. schmitti,* as is also the case in members of *Paguritta* (McLaughlin & Lemaitre, 1993). As previously mentioned, *D. maclaughlinae* uses detached polychaete tubes. Observation of specimens kept alive in aquarium has shown that the new species is a deposit feeder, as in usual pagurid.

Acknowledgment

My thanks are due to Mr. K. Nomura, the technical staff of the Usujiri Marine Biological Laboratory, Hokkaido University, for helping to collect material at Usujiri. I wish to express my sincere gratitude to Drs. R. B. Manning and R. Lemaitre of the National Museum of Natural History, Smithsonian Institution, for making available specimens of *Discorsopagurus schmitti* and *Orthopagurus minimus* for comparison. I am deeply indebted to Drs. P. A. McLaughlin, R. Lemaitre, K. Baba of Kumamoto University, and one anonymous reviewer for critically reviewing the manuscript and offering many helpful comments. Prof. Dr. L. B. Holthuis of the National Natuurhistorisch Museum, Leiden, kindly provided me with copies of several Russian literature.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):629–636. 1995

Redescription of *Sudanonautes faradjensis* (Rathbun, 1921), a fresh-water crab from Central Africa (Brachyura: Potamoidea: Potamonautidae)

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Abstract.—The fresh-water crab *Sudanonautes faradjensis* (Rathbun, 1921), previously considered to be a subspecies of *S. africanus* (A. Milne Edwards, 1869), is recognized here as a valid species. The species is redescribed from the holotype and from a large series of specimens from four countries in Central Africa. *Sudanonautes faradjensis* is identified by a combination of characters of the carapace, chelipeds, and gonopod 1. The distribution of *S. faradjensis* includes the northern part of the rain forest region of Central Africa, from south Cameroon to Zaire.

The Central African fresh-water crab *Sudanonautes faradjensis* (Rathbun, 1921) was first described from material collected by the American Museum of Natural History Congo expedition of 1911–1915, led by H. Lang and R. Chapin. Although *S. faradjensis* was subsequently recognized as a valid species by a number of authors (Balss 1929, 1936; Chace 1942; Capart 1954), more recently others (Bott 1955, Monod 1977) have considered this taxon to be a synonym of *S.* (*S.*) *africanus chaperi* (A. Milne Edwards, 1887). The latter taxon was redescribed by Cumberlidge (1985), who assigned it to the genus *Liberonautes,* and also indicated that *Potamon* (*Potamonautes*) *faradjensis* Rathbun, 1921 was most likely a valid species. Based on the examination of the types of both *L. chaperi* and *S. faradjensis* the two species have indeed been found not only to be distinct, but also to belong to different genera. Rathbun's (1921) original description did not include adequate descriptions of gonopods 1 and 2, and of a number of other characters which are now thought to be necessary for the proper identification of the species in this genus, and so the species has been redescribed here from the holotype from Faradje, Zaire.

Materials and Methods

The left mandible and left gonopods 1 and 2 were illustrated following removal from the specimen (Fig. 2a–g). Carapace length (CL), carapace width (CW), carapace height (CH), and front width (FW), were recorded from each specimen using digital calipers. Carapace proportions were calculated according to carapace length, and the resulting data pooled and used for descriptions of growth (Fig. 3a, b). Statistical comparisons between species were made between sexually mature adults only. Since many literature records are not reliable, the distribution of *S. faradjensis* described here is based on data from the direct examination of specimens from 20 different localities in four countries.

The following abbreviations are used: AMNH, American Museum of Natural History, New York; MNHN, Muséum National d'Histoire Naturelle, Paris; NHM, The Natural History Museum, London, UK; NNH, National Natuurhistorisch Museum, Leiden, The Netherlands; NMU, Northern Michigan University, Marquette; RCM, Royal Congo Museum, Tervuren, Belgium; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC; ZMB, Museum für Naturkunde der Humboldt-Universitat, Berlin, Germany; CW = carapace width at widest point; CL = carapace length, measured along median line; CH = cephalothorax height, maximum height of cephalothorax; FW = front width, width of front measured along anterior margin, M = male, F = female, juv = juvenile.

Family Potamonautidae Bott, 1970
Sudanonautes faradjensis (Rathbun, 1921)
Figs. 1–3

Potamon (*Acanthothelphusa*) *faradjensis* Rathbun, 1921:428–430, pl. 31, fig. 13 (type locality: Faradje, Zaire).

Potamon (*Potamonautes*) *faradjensis*.—Balss, 1929:126, fig. 8; 1936:166–7, fig. 1.

Potamon faradjensis.—Chace, 1942:211.—Capart, 1954:833, figs. 8, 20.

Sudanonautes (*Sudanonautes*) *africanus chaperi*.—Bott, 1955:298–299 (part), pl. XXVII, figs. 1a–c, 2, 62, 96a, b.—Monod, 1977:1216 (part). Not *Parathelphusa chaperi* A. Milne Edwards, 1887.

Types.—AMNH 3346, Holotype, Faradje, Zaire, adult M (CW 71.5, CL 51.0), Dec 1912, coll. H. Lang & R. Chapin. AMNH 3351, paratypes, Faradje, 1 M, 2 F, coll. H. Lang & R. Chapin (photographed and illustrated by Rathbun, 1921). RCM 836, paratype, van Kerkhovenville, coll. Apr 1912, H. Lang & R. Chapin, AMNH.

Material examined.—Cameroon: NHM 25.1.1937/8, Papita section, dense forest country, Lomie District, 1 M, 2 F, coll. 1936, Mr. Merfield (from Powell-Cotton Museum). RCM 53.283, Dokwa, 1 M, 3 Jul 1970, coll. Thijs van den Audenaerde. RCM 54.171, Dja Posten, River Dja, 1 M, CW 75.9 mm, 8 Mar 1975, coll. Thijs van den Audenaerde. RCM 54.197, Meri, 26 Jan 1976, 2 M, CW 58.5, 59.7 mm, coll. F. Puylaert. GABON.–NNH 24761, Tussen Turindo en Makakou, 1 adult, 7 Mar 1962, coll. B. Condé (donated by J. Gery). SMF 7296, Ivindo u. Mariyots, Makokon, 1 F, CW 66.5 mm, 9 Dec 1975, coll. unknown. Central African Republic: MNHN B5078, Bangui. NMU 1.IV.1991, river Oubangi, at Bangui, 1 M, 1 F, (found with 1 *Potamonautes langi*), 1 Apr 1991, coll. L. M. Bourgault. RCM 55.400, Landjia river Oubangui, 1 M, 1 F, 3 Feb 1982, coll. L. de Vos & Kempeneers. RCM 56.349, Kembé, above the falls on the river Kotto, 29 Mar 1984, 2 adults, coll. J. P. Marquet. Zaire: NMU VII.1993, Kinshasa, Zaire river, 4 M, 8 Jul 1993, coll. L. M. Bourgault. USNM 54300, Faradje, 1 M, 1 F, 7 Mar 1915. SMF 2382, Lisala, 1 M, CW 48.7 mm, coll. S. Deheyn (RCM 32071). RCM 71, river Ubangi, Banzyville, 1 juv, 1901, coll. G. T. Royaux. RCM 202, Equaterville, 1 F juv, 1921, coll. Verlaine. RCM 258, Leopoldville (= Kinshasa), 1 specimen, 1933, coll. M. A. Cinant. RCM 50.379, Stanleypool (= Kisangani), 1 F, 17 Jul 1957, coll. P. Brien, M. Poll, & J. Bouillion. RCM 50.380, Stanleypool (= Kisangani), 1 M, Apr 1957, coll. P. Brien, M. Poll, & J. Bouillion. RCM 54.043, Stanleypool (= Kisangani), 2 specimens, 1 Mar 1953, coll. J. Mandeville. ZMB 13494, Dumé, 1 F, coll. 29 Jun 1909, O. Freyer.

Diagnosis.—Postfrontal crest spanning entire carapace, crest deeply notched before meeting sharp, forward-pointing epibranchial tooth; shallow notch in crest behind exo-orbital tooth; series of 7 to 8 sharp teeth on anterolateral margin posterior to epibranchial tooth. Posterior lateral surface of carapace with fields of raised short lines; cervical, semi-circular, cardiac, urogastric grooves very deep. Epibranchial, intermediate and exorbital teeth all large, sharp, pointed forward. Terminal segment of gonopod 1 long, thin and needle-like, subterminal segment of gonopod 1 slender. Carapace very flat (CH/CL = 0.41).

Redescription.—Carapace (Fig. 1a–c) ovoid, widest on anterior third (CW/CL 1.36), very flat (CH/CL 0.41), cervical, semi-circular, urogastric, cardiac grooves very deep; transverse branchial grooves present but weak. Front bilobed, indented, anterior margin curving down, relatively

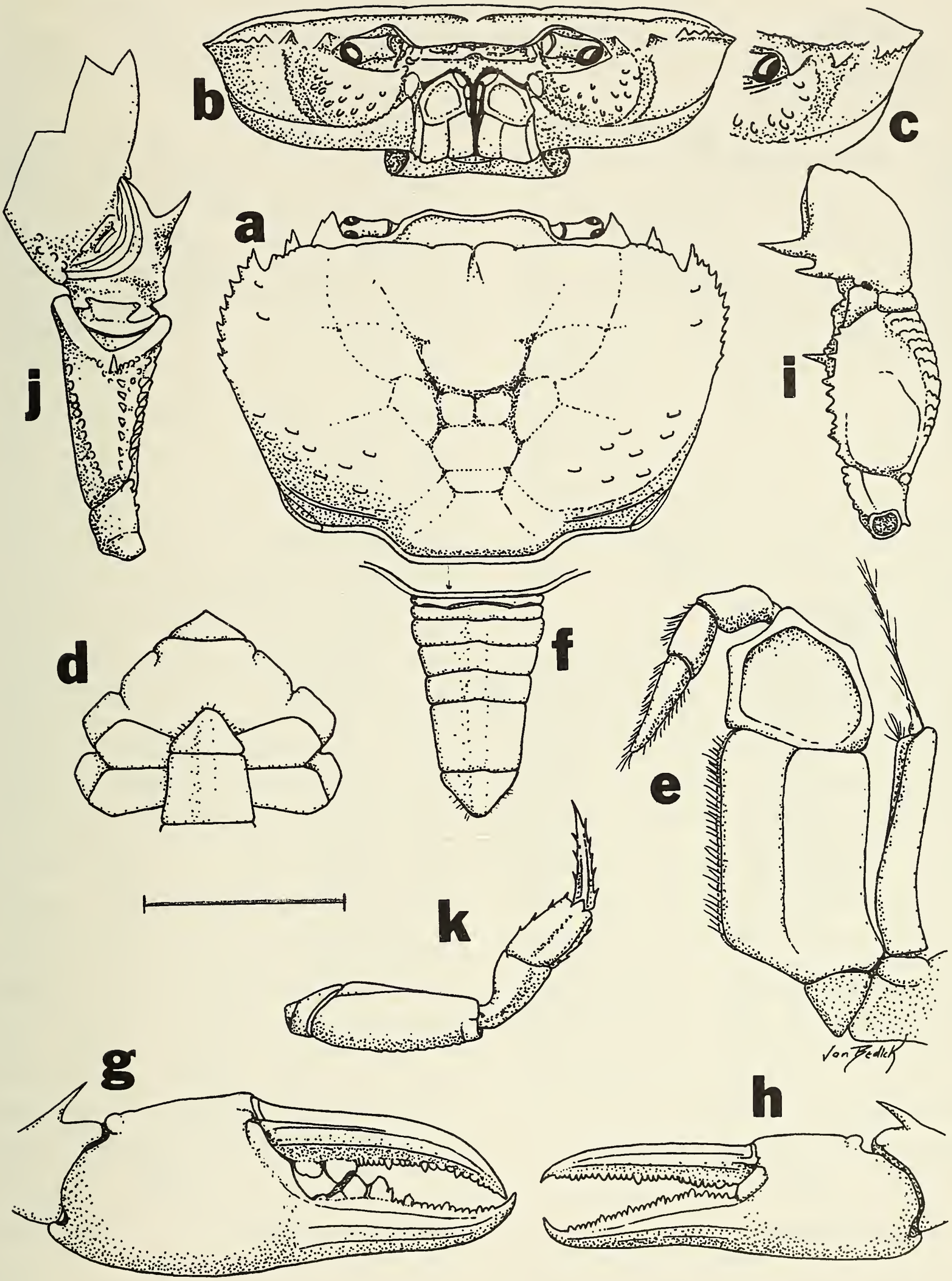

Fig. 1. *Sudanonautes faradjensis* (Rathbun, 1921), adult male holotype, (CW 71.5 mm) from Faradje, Zaire (AMNH 3346). a, whole animal, dorsal aspect; b, carapace, frontal aspect; c, carapace showing detail of epibranchial corner; d, sternum; e, left third maxilliped; f, abdomen; g, right cheliped, frontal view; h, left cheliped, frontal view; i, carpus, and merus of right cheliped, superior view; j, carpus, and merus of right cheliped, inferior view; k, left pereiopod 2. Scale bar equals 30 mm (a, b, c, d, f), 15 mm (g–k), 10 mm (e).

narrow, less than ⅓ carapace width (FW/CW = 0.30). Posterior lateral surface of carapace with fields of raised short lines, anterolateral surface with faint raised granules. Postfrontal crest spanning entire carapace, consisting of fused epigastric, postorbital crests, almost straight in epigastric regions, curving forward behind orbits to meet anterolateral margins at the epibranchial teeth; crest smooth in middle, slight crenulations at lateral ends. Postfrontal crest deeply notched before meeting sharp, forward-pointing epibranchial tooth; shallow notches in crest behind exo-orbital tooth and behind front; mid-groove on postfrontal crest short, forked at posterior end. Series of 7 to 8 small sharp teeth on anterolateral margin posterior to epibranchial tooth; anterolateral margin continuous with posterolateral margin. Posterior margin about ⅔ as wide as carapace width.

Fields of conspicuous granules in suborbital regions. Suborbital, subhepatic, and pterygostomial regions with 2 sutures, 1 longitudinal, 1 vertical, dividing area into 3 parts (Fig. 1b, c). Longitudinal suture dividing suborbital, subhepatic regions from pterygostomial region, beginning medially at lower margin of orbit, curving backward across entire region. Vertical suture short, v-shaped, dividing suborbital region from subhepatic region marked by row of small rounded granules (Fig. 1b, c); suture origins between exo-orbital and intermediate teeth, curving down to meet longitudinal suture. Third maxillipeds filling entire oral field, except for transversely oval efferent respiratory openings at superior lateral corners; long, plumose flagellum on exopod of third maxilliped (Fig. 1e); ischium of third maxilliped smooth, with clear vertical groove (Fig. 1e). Mandibular palp 2-segmented; terminal segment single, undivided, fringed with hairs, longest at junction between segments (Fig. 2a–c). First transverse groove on sternum (between sternal segments 2 and 3) complete; second groove (between sternal segments 3 and 4) consisting of 2 small notches at sides of sternum (Fig. 1d). Segments 1–6 of abdomen four sided, last segment triangular, sides indented, rounded at distal margin (Fig. 1f); segment 3 broadest, segments 4–7 tapering inwards (Fig. 1f).

Gonopod 1 with very slender terminal segment, long (⅘ as long as subterminal segment), almost straight continuation of subterminal segment, only gently curved outward, tapering to pointed tip, longitudinal groove visible from caudal and superior views (Fig. 2d, f), not visible from cephalic view (Fig. 2e). Subterminal segment of gonopod 1 very slim (Fig. 2d, e), with raised flap extending halfway across segment, margin vertical, edged with small spines, flap forming roof of chamber for gonopod 2; subterminal segment beneath flap forming lower floor of chamber for gonopod 2 (Fig. 2d). Gonopod 2 (Fig. 2g) shorter than gonopod 1 (reaching only to junction between last 2 segments of gonopod 1). Terminal segment of gonopod 2 extremely short, only ⅑ as long as subterminal segment, sides folded inwards and spoon-shaped, tip rounded. Subterminal segment gonopod 2 widest at base, tapering sharply inward, forming long, thin, pointed, upright process which supports short terminal segment; rounded collar at junction between terminal segment and subterminal segment.

Chelipeds (Fig. 1g–j) unequal, right longer, higher than left. Dactylus of right cheliped long, slender, grooved, not arched; palm of propodus swollen; proximal region of fingers of digits of right cheliped each with 2 large teeth, opposing teeth meeting, forming small space at base, cut off from the longer interspace distal to these teeth. Both fingers with 3 intermediate sized pointed teeth, interspersed with a series of smaller pointed teeth along their lengths (Fig. 1g, h). Teeth of smaller cheliped all very small, fingers almost meeting when closed. Inferior margins of merus with rows of small teeth, cluster of granules surrounding larger pointed tooth at distal end. Inner margin of carpus of cheliped with 2 large, slender, pointed teeth, second half size of

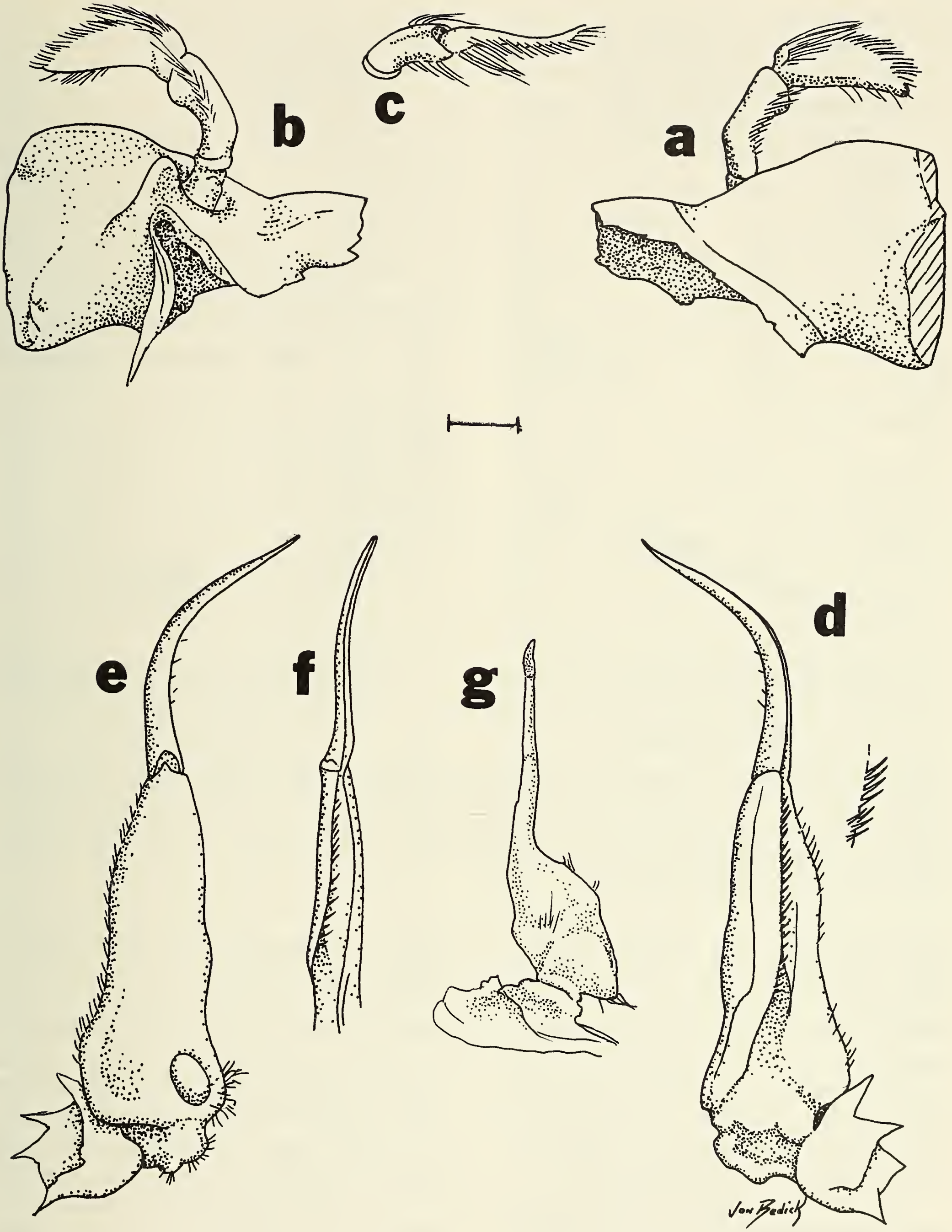

Fig. 2. *Sudanonautes faradjensis* (Rathbun, 1921). a, left mandible anterior view; b, left mandible posterior view; c, left mandibular palp, superior view; d, left gonopod 1, caudal view; e, left gonopod 1, cephalic view; f, terminal segment of left gonopod 1, superior view; g, left gonopod 2, caudal view. Scale bar equals 3 mm (a–c), 2 mm (d–g). (a–f, adult male holotype (CW 71.5 mm) from Faradje, Zaire, AMNH 3346; g, adult male (CW 66 mm) from Kinshasa, Zaire, NMU VII.1993.)

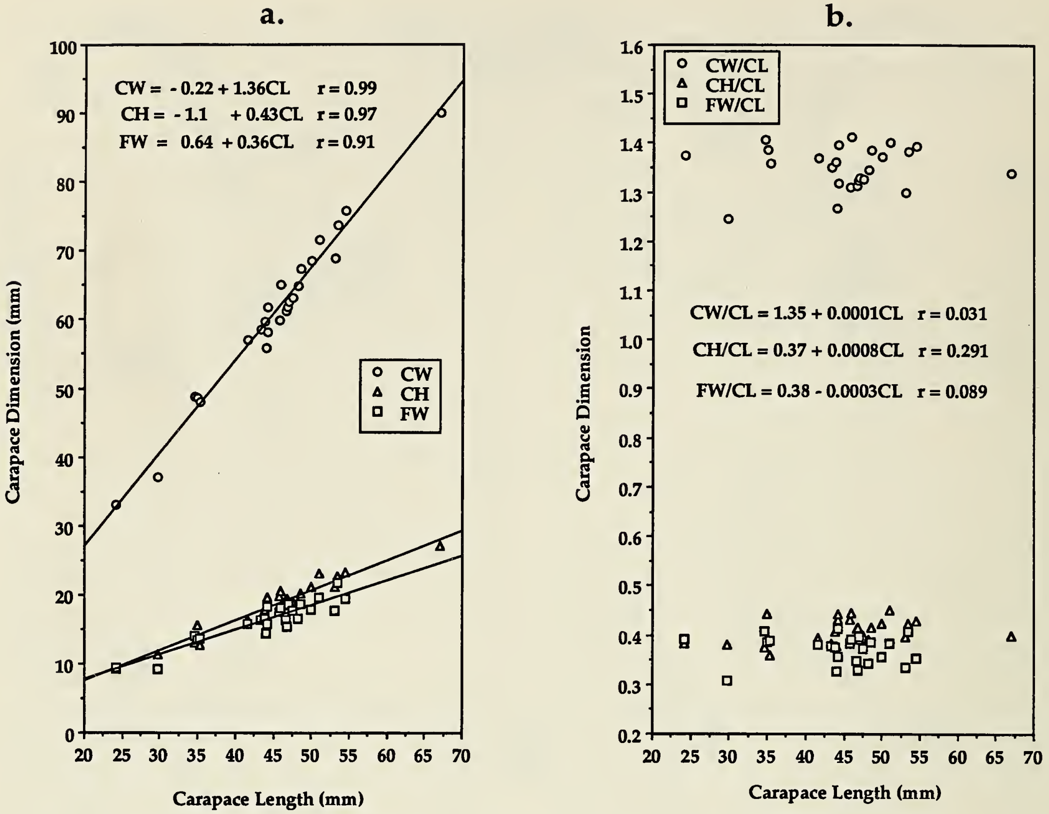

Fig. 3. Comparisons of 24 specimens of *Sudanonautes faradjensis* (Rathbun, 1921). a, dimensions of the carapace (CW, CH, FW) compared to body size (CL), *r* values (all at $df = 23$) indicate a highly significant correlation ($P < 0.001$) between size classes; b, relative proportions of carapace width (CW/CL), carapace height (CH/CL), and front width (FW/CL), compared to body size (CL), *r* values (all at $df = 23$) indicate no significant correlation ($P > 0.05$) between size classes.

first (Fig. 1i, j). Left cheliped similar to right, but smaller (Fig. 1h). Walking legs (pereiopods 2–5) slender (Fig. 1k), fourth longest, fifth shortest. Posterior margin of propodi serrated, dactyli tapering to point, each bearing rows of downward-pointing sharp bristles; dactylus of fifth shortest of the walking legs. Stridulating apparatus associated with coxae of pereiopod 2.

Adult female.—Right and left chelipeds similar proportions to male of similar size, unequal in both length and height. Mature female abdomen very wide, reaching coxae of pereiopods 2–5. Segments of female abdomen 4-sided, becoming gradually longer distally, segments 1–5 becoming gradually wider (widest at groove separating segments 4, 5); segment 6 and telson together forming near semicircle.

Growth (Fig. 3a, b).—Carapace dimensions and relative proportions as shown in Fig. 3a, b. Sexual maturity judged by development of female abdomen: abdomen of mature females overlapping bases of coxae of walking legs, pleopods broad, hair-fringed. Pubertal molt occurring between CW 35–45 mm. Largest known specimen (male from Cameroon) CW 90 mm. Relative width of carapace (in relation to carapace length, CW/CL) not changing with age: CW/CL of adults not significantly wider ($P > 0.05$) than that of juvenile and pubescent animals (Fig. 3b). Width of frontal margin (FW/CL) not changing with age:

FW/CL of adults not significantly wider ($P > 0.05$) than that of juvenile and pubescent animals (Fig. 3b). Relative height of carapace (CH/CL) not changing with age: that of adult *S. faradjensis* not significantly different ($P < 0.05$) than CH/CL of juvenile and pubescent animals. Shape of gonopod 1 and chelipeds changing as crabs grow older. Terminal segment of gonopod 1 of juveniles almost straight; right and left chelipeds of juveniles (CW 25–40 mm) are even sized, palms not inflated, cutting edges meeting, not enclosing a space.

Color.—(Based on living adult from Kinshasa, Zaire). Dorsal carapace and postfrontal crest dark brown-black, flanks paler brown; eyestalk brown, cornea black; sternum, abdomen light brown. Arthrodial membranes between joints of chelipeds and pereiopods light brown; chelipeds, pereiopods light brown.

Distribution.—Rain forest regions of Cameroon, Central African Republic, Gabon, Zaire. Middle reaches of the Zaire river basin, and in the rivers Ubangui and Uele, tributaries of the Zaire river. Distribution in Zaire described by Rathbun (1921) and Balss (1936), and in Cameroon by Balss (1929).

Ecological Notes.—*Sudanonautes faradjensis* is restricted to the more humid areas of the rain forest from south Cameroon to Zaire. This species occurs in permanent aquatic habitats from large rivers to small streams. The following notes are based on Herbert Lang's observations (leader of U.S.A. Congo Expedition) as reported by Rathbun (1921). *Sudanonautes faradjensis* is one of the largest river-living crabs of the Uele district in the Zaire basin. The species is found under stones in quiet portions of the river near rapids, where it is reportedly preyed upon by small crocodiles and carnivorous fish. *Sudanonautes faradjensis* moves quickly and can usually escape from its predators.

Remarks.—The short terminal segment of gonopod 2 (Fig. 2g), the long, slender, outward-curving terminal segment of gonopod 1 (Fig. 2d), and the intermediate tooth on the anterolateral margin between the exo-orbital and epibranchial teeth (Fig. 1a–c) place this species in *Sudanonautes*. Identification of *S. faradjensis* to species can be made by noting the following characters: a very flat carapace (CH/CL = 0.41) with fields of raised short lines on the posterior lateral surface; large, sharp, forward-pointing epibranchial, intermediate and exorbital teeth; a series of 7 to 8 sharp teeth on the anterolateral margin posterior to the epibranchial tooth; a deep notch on the postfrontal crest before it meets the epibranchial tooth; and a long, thin and needle-like, terminal segment of gonopod 1.

Comparisons.—*Sudanonautes faradjensis* is most likely to be confused with other large species of fresh-water crabs occurring in the rain forest zones of Central Africa, such as *S. chavanesii* (A. Milne Edwards, 1886) and *S. africanus* (A. Milne Edwards, 1869). Since the terminal segment of gonopod 1 of all three species is similar (but not identical), other characters should be used to distinguish between species. For example, *S. faradjensis* can be distinguished from both *S. africanus* and *S. chavanesii* by examination of the anterolateral margin: that of *S. faradjensis* possesses rows of sharp teeth behind the epibranchial tooth (Fig. 1a), whereas the anterolateral margins of *S. africanus* and *S. chavanesii* are both smooth. In addition, the epibranchial tooth of *S. faradjensis* is sharp and pointed (Fig. 1a), whereas that of *S. africanus* is small and low. Furthermore, the epibranchial tooth of *S. faradjensis* is in line with the mid-point of the postfrontal crest (Fig. 1a), whereas that of *S. chavanesii* is set back posteriorly, well behind the line of the mid-point of the postfrontal crest.

In addition to the above differences, there are a number of characters that distinguish *S. faradjensis* from the other species in the genus. For example, the carapace of *S. faradjensis* is significantly flatter ($P < 0.001$) than most other species in the genus, and the carapace of *S. faradjensis* is rough-textured with patches of raised blisters and ridges in the posterior region, and deep urogastric and cardiac grooves (Fig. 1a).

The spiny river crab, *Liberonautes chaperi* (A. Milne Edwards, 1887), redescribed by Cumberlidge (1985) and Cumberlidge & Sachs (1989), is superficially similar to *S. faradjensis.* However, the two species can be easily distinguished by the terminal segment of gonopod 2: that of *L. chaperi* is long, like a flagellum, whereas that of *S. faradjensis* is short and stubby (Fig. 2g). In addition, the terminal segment of gonopod 1 of *L. chaperi* curves inward, not outward as in *S. faradjensis* (Fig. 2d). Finally, *L. chaperi* is found only in West Africa from Côte d'Ivoire to Guinea, whereas *S. faradjensis* is restricted to the forests of Central Africa.

Acknowledgments

Christopher B. Boyko, Department of Invertebrates (AMNH) is thanked for the loan of the holotype and paratypes of *S. faradjensis.* The following are thanked for hosting visits: H. Feinberg (AMNH); Paul Clark (NHM); D. Guinot and J. Forest (MNHN); L. Holthuis and C. Fransen, NNH, Leiden, The Netherlands; R. Joqué (RCM); R. Manning (USNM); and H. Gruner (ZMB). I especially thank artist Jon C. Bedick of Northern Michigan University, for all of the illustrations used in this paper. Part of this work was supported by a Faculty Grant from NMU, Marquette.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):637–642. 1995

Lithoscaptus pardalotus, a new species of coral-dwelling gall crab (Crustacea: Brachyura: Cryptochiridae) from Belau

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Abstract.—A new species of coral-dwelling gall crab, *Lithoscaptus pardalotus,* was found inhabiting the faviid coral *Favia* cf. *helianthoides* at Ngemelachel, Belau. The new species can be distinguished from others in the genus by the combination of having the internal orbital angle exceeding the external orbital angle and having very slender carapace that is nearly twice as long as wide.

Among collections of gall crabs (Cryptochiridae) I made in Belau [Palau] in 1984, were several specimens that could not be assigned to any described species. These specimens, collected from colonies of *Favia* cf. *helianthoides,* are described as a new species of the genus *Lithoscaptus* Milne Edwards, 1862.

Type material has been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), the Bernice P. Bishop Museum, Honolulu, Hawaii (BPBM), the Queensland Museum, Brisbane, Australia (QM), and the Muséum National D'Histoire Naturelle, Paris (MNHN).

Abbreviations used are: cl, carapace length; cw, carapace width; coll., collector; ft, feet; m, meters; mm, millimeters; MXP, maxilliped, ovig., ovigerous; P, pereopod; and PLP, pleopod. PHAP numbers refer to the author's collection numbers. Place names in Belau follow orthography proposed by Motteler (1986). The former place name is presented in brackets.

Lithoscaptus pardalotus, new species
Figs. 1, 2

Type material.—Holotype: Belau, Ngemelachel [Malakal] Is., off causeway by park S of Micronesian Mariculture Demonstration Center; 1 m; 18 Jul 1984; on *Favia* cf. *helianthoides* (Wells); PHAP 131; ♀, USNM 274140. Paratypes: Belau; all same locality and host as holotype, 1–3.5 m; PHAP 058; 4 Jul 1984; 1 ♀, BPBM S11274; PHAP 109; 14 Jul 1984; 2 ♀, 2 ♂, USNM 274142; PHAP 114; 14 Jul 1984; 2 ♀ (ovig.), MNHN B. 25100; PHAP 127; 18 Jul 1984; 3 ♀ (2 ovig), MNHN B. 25101; PHAP 128; 18 Jul 1984; 1 ♂, USNM 274141; PHAP 220; 27 Jul 1984; 2 ♀ (1 ovig), QM W20647.

Measurements.—Holotype: cl, 4.0 mm, cw, 2.2 mm. Paratypes: largest male: cl, 2.9 mm, cw, 1.6 mm; largest female: cl, 4.4 mm, cw, 2.5 mm; smallest ovigerous female: cl, 3.0 mm, cw, 1.8 mm.

Description.—(Female) Carapace convex in both directions, about 1.8 times longer than wide, widest just anterior to midlength, narrowing slightly anteriorly; in lateral view anterior portion sloping from midlength toward front; dorsal surface with W-shaped depression, with many scattered conical and round tubercles. Lateral margins of carapace subparallel; anterolateral margins lined with erect conical tubercles. Intraorbital margin concave, with scattered simple setae, irregularly denticulate; internal orbital angle extending beyond external, each orbital angle marked with prominent spine; orbit broadly V-shaped, margin granular. Posterior carapace convex, with scattered round tubercles decreasing in size posteriorly; cardiac region marked by inverted U-shaped furrow; posterolateral margins rounded, with rounded tubercles and granules. Carapace bearing scattered simple setae on entire surface. Pterygostomial region fused to carapace.

Basal segment of antennule extending slightly beyond eye, subtriangular in dorsal view (excluding apical spine), mostly smooth but with few granules and scattered setae dorsally, margins with 8–9 spines, distal apex marked with prominent spine; ventrally bearing scattered granules, no setae, subtriangular in shape; outer margins subequal, inner margin concave, edge rounded.

Eyestalks fully exposed dorsally, slightly swollen proximally, with scattered setae, mesial margin bearing prominent spine distally, 2 smaller spines subdistally; smooth ventrally; eyestalk length about 1.9 times cornea length.

Ischium of MXP-3 about 1.5 times longer than wide, surface mostly smooth, granular near distal margin, inner margin straight, distal half crenulate, lined with simple setae; outer margin denticulate, bearing few simple setae; exopod about half length of outer margin of ischium, with few pappose setae on outer margin. Merus granulate toward outer margin, latter finely denticulate, bearing few simple setae along entire length, distal angle produced, tuberculate. Palp segments bearing few simple setae along outer margins.

Cheliped (P-1) slightly shorter than first walking leg (P-2). Merus compressed, length about 2.2 times height; inner surface concave, smooth; outer surface convex, smooth; anterior margin smooth, with few simple setae; outer posterior margin with few granules, inner posterior margin serrated. Carpus length about 1.6 times height; outer surface smooth, but with granules near anterior margin; anterior margin with few low conical tubercles directed distally, with few scattered setae. Manus length about 1.4 times height, smooth, but with few granules proximally near anterior margin. Cutting edges of fingers entire, without setae; dactyl length about 0.6 times total chela length.

Merus of P-2 compressed, length about 2.6 times height; inner surface concave, and outer surface slightly convex, both surfaces smooth; anterior margin straight, curving slightly downward distally, with few granules along length and erect conical tubercles distally, with scattered simple setae along most of length; posterior margin straight, lined with angled tubercles giving serrated appearance, with proximally-pappose setae; posterodistal angle with 3 blunt tubercles. Carpus length about 2.0 times height; subtriangular in cross-section; anterior surface slightly rounded, sloping mesially, with erect conical tubercles, few simple setae; inner surface smooth, with simple setae at anterior margin; outer surface flat, mostly smooth, with granules on upper half, some tubercles at anterior margin, latter with simple setae. Propodus about 2.8 times longer than high, subtriangular in cross-section; outer surface flat, with scattered granules decreasing in size toward posterior margin; anterior surface flat, with erect conical tubercles and scattered setae; inner surface smooth, margin with 4 erect conical tubercles. Dactyl curved distally, with 2 tubercles proximally on upper surface, with few simple setae.

Second walking leg (P-3) smaller than P-2; merus length about 2.0 times height; outer surface slightly convex, smooth except for few tubercles on upper distal corner; inner surface concave, smooth; anterior margin straight, distal third curves sharply downward; margin bearing scattered simple setae, with tubercles on distal third; posterior margin relatively straight, lined with proximally-pappose setae, with 1 prominent and 2 smaller tubercles subdistally; posterodistal angle rounded, entire. Carpus subtriangular in cross-section, length about 1.9 times height; inner surface flat, smooth; outer surface mostly smooth, with row of tubercles at upper third; anterior margin with row of erect conical tubercles, with

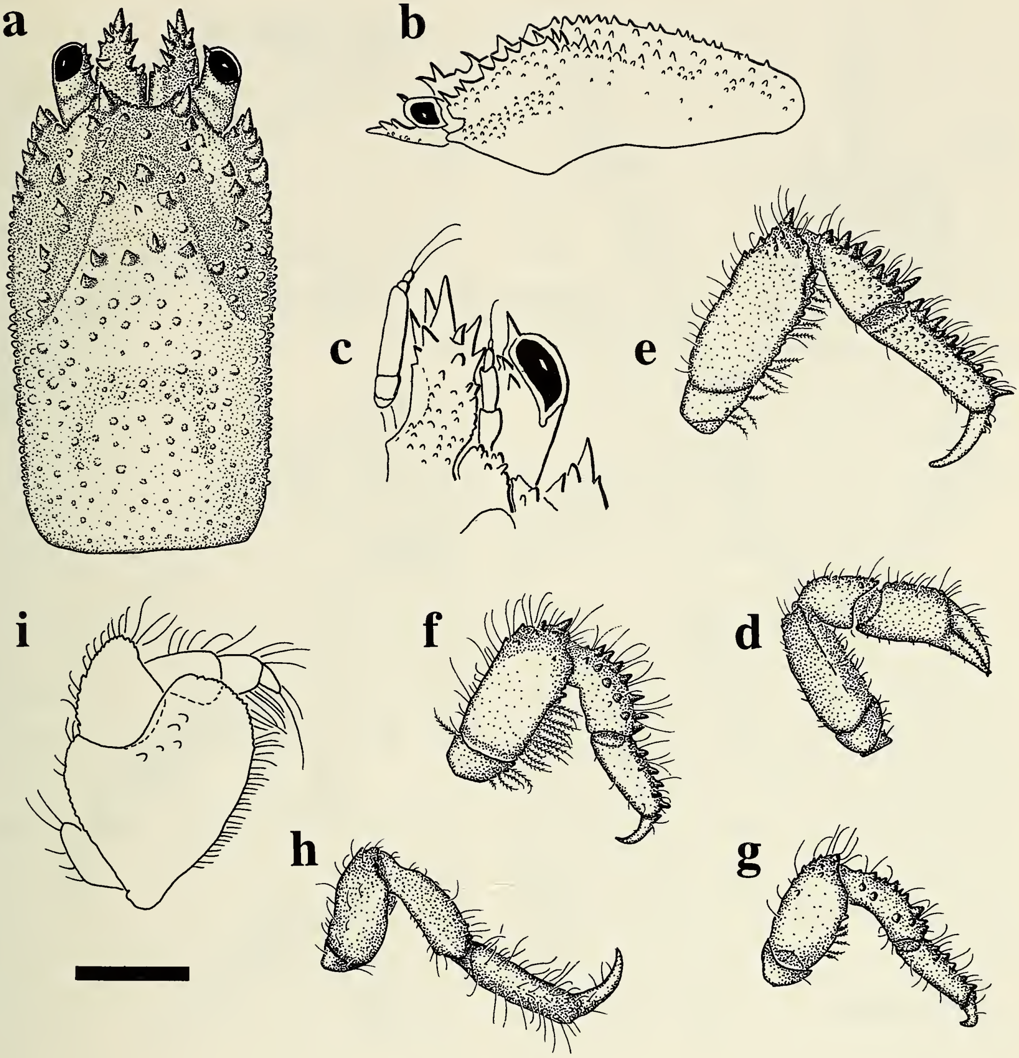

Fig. 1. *Lithoscaptus pardalotus,* new species, female holotype (carapace length 4.0 mm). a, Carapace (dorsal view); b, Carapace (lateral view); c, Left antennule, antenna, and eyestalk (ventral view); d–h, Right P1–P5; i, MXP-3. Scale: 1.0 mm (a–h); 0.46 mm (i).

few setae. Propodus slightly shorter than carpus, length about 2.3 times height; anterior margin with row of erect conical tubercles; outer surface mostly smooth, with few rounded tubercles toward anterior margin; inner surface smooth, with few setae. Dactyl curved distally, entire.

Third walking leg (P-4) slightly smaller than P-3; merus length about 1.7 times height; outer surface slightly convex, smooth, but with few rounded tubercles near anterodistal angle; inner surface convex, smooth, bearing few setae; posterior margin with 1 larger, 1 smaller tubercle subdistally; anterior margin slightly convex, with few simple setae, with angled tubercles giving serrated appearance on distal third. Carpus length 2.7 times height; outer surface convex, smooth, with few setae; posterior margin entire; anterior surface

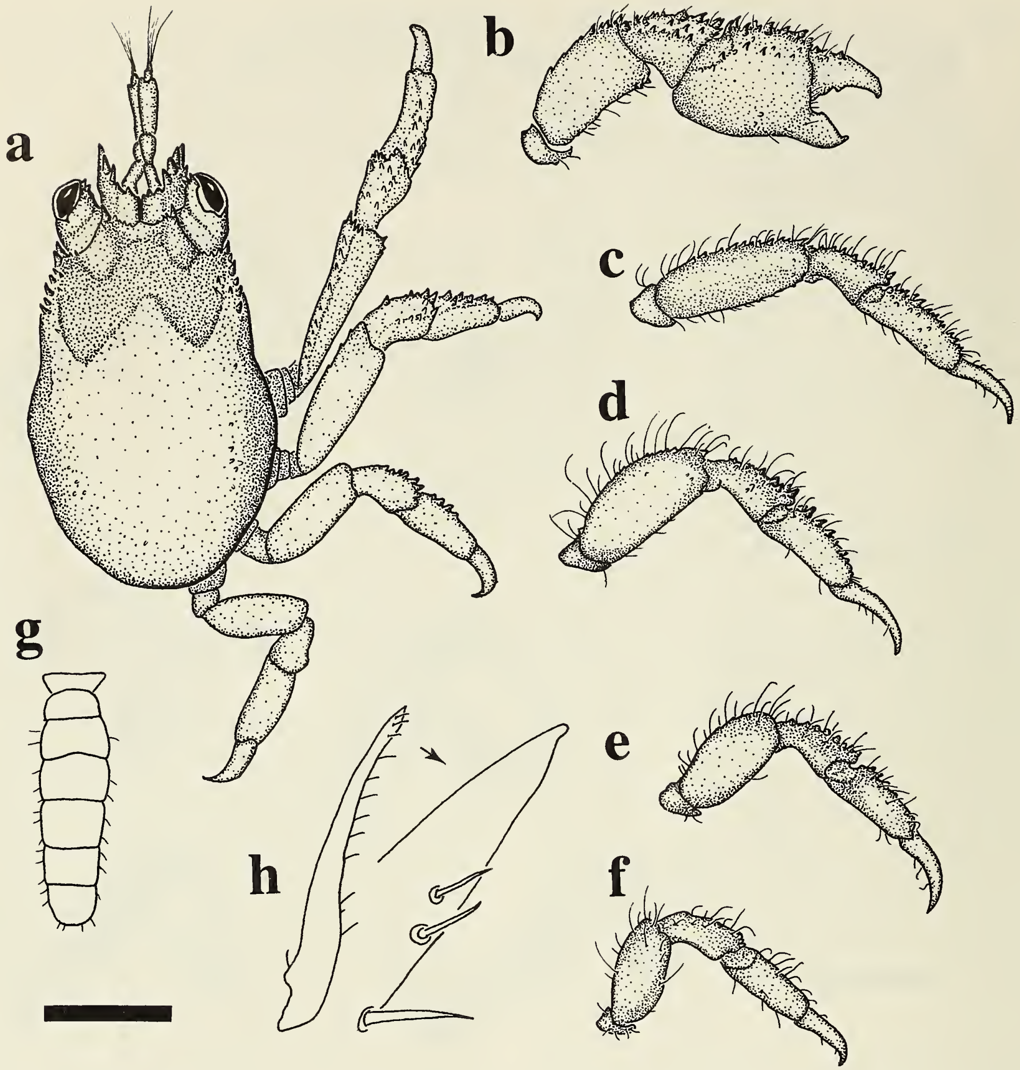

Fig. 2. *Lithoscaptus pardalotus,* new species, male paratype (carapace length 2.9 mm. a, Carapace and right P2–P5 (dorsal view); b–f, Right P1–P5 (lateral view); g, Abdomen; h, PLP-1 (with tip enlarged). Scale: 1.0 mm (a–g); 0.46 mm (h).

rounded, sloping toward outer surface, outer margin with 3 rounded tubercles, with few simple setae; inner surface slightly convex, smooth. Propodus rotated slightly mesially, length about 3.2 times height; outer surface slightly convex, smooth, with few simple setae; inner surface slightly convex, smooth, with few setae; posterior margin entire, with few setae; anterior margin straight, with 6 erect rounded tubercles, with scattered setae. Dactyl curved distally, rotated mesially, entire, with few scattered simple setae.

Fourth walking leg (P-5) more slender, longer than P-4; merus not compressed, length 1.9 times height; outer, inner surfaces convex, smooth, with scattered setae; posterior margin rounded, with tubercle near posterodistal angle; anterior margin rounded, convex, having few rounded tubercles distally, bearing few scattered simple setae. Carpus length 2.9 times height;

outer, inner surfaces slightly rounded, smooth, with scattered simple setae; posterior margin rounded, entire, having few simple setae; anterior margin rounded, with tubercles near distal margin, with few simple setae. Propodus rotated about 90° mesially, length 4.2 times height; outer, inner surfaces rounded, smooth, outer with scattered simple setae, inner having few rounded tubercles and few pappose setae. Dactyl curved distally, rotated slightly mesially, smooth, with many simple setae on inner surface, posterior margin.

Male smaller than female. Carapace pear-shaped in dorsal view, mostly smooth; anterolateral margin with many spines; anterior depression wider, smoother than that of female. Chelipeds more robust than in female; merus, carpus, and propodus with acute, angular tubercles along anterior margins. Dactyl with angular tubercles proximally; cutting surface of dactyl with tooth subproximally; fixed finger with low ridge running length of cutting surface. First pleopod as figured.

Coloration.—Carapace of female off-white, anterior part with many regularly-spaced black spots. Eyestalks mostly white with black wedge dorsally, red-orange stripe laterally; cornea dark red with white spot. Basal segment of antennule white with scattered black dots and larger black area proximally; palp clear, with white markings. Ventrum opaque, with scattered irregularly-shaped black spots; P-1 and P-2 bright white dorsally, last 3 segments of P-1 and dactyl of P-2 with rose hue. Male carapace clear, covered with reticulated black spots except on anterior depressions. Eyestalk as carapace, corneas dark red with silver spot. Ventrum opaque; MXP-3 with black spots. P-1 through P-5 off-white with scattered irregular black and blue-white spots.

Etymology.—From the Greek "*pardalotos*", spotted like a leopard, in reference to the black spots on the anterior part of the carapace.

Remarks.—Lithoscaptus pardalotus, new species, *L. tri* (Fize & Serène, 1956), and *L. nami* (Fize & Serène, 1957) can be distinguished from the other species presently included in the genus *Lithoscaptus* (Kropp 1990, 1994) by having the internal orbital angle extending beyond the external orbital angle. The slenderness of the new species, with a carapace length almost twice its width, distinguishes it from *L. tri* and *L. nami* in which the carapace length is about 1.3 times its width. The black-spotted pattern on the anterior carapace also differs from patterns found on other species.

Hosts.—Faviidae: *Lithoscaptus pardalotus* was collected on *Favia* cf. *helianthoides.* I can find no other references to gall crabs occurring on this species of coral.

Distribution.—Micronesia: Belau.

Acknowledgments

I thank the University of Guam Marine Laboratory, the University of Maryland, and the USNM for support during field work in Micronesia. Funding for field work was provided in part by a grant from the Biological Oceanography Section of the National Science Foundation to G. J. Vermeij. Field work in Belau was supported by the Micronesian Mariculture Demonstration Center. My laboratory work at the USNM was kindly supported by R. B. Manning. I thank R. H. Randall for identifying the host coral. This is University of Guam Marine Laboratory Contribution Number 365.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):643–648. 1995

Charybdis hellerii (Milne Edwards, 1867), a nonindigenous portunid crab (Crustacea: Decapoda: Brachyura) discovered in the Indian River lagoon system of Florida

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Abstract.—The portunid crab *Charybdis hellerii* (Milne Edwards, 1867), a species of Indo-Pacific origin, is reported from the Indian River lagoon system of Florida. Although this species was reported in 1987–1988 from Cuba, Colombia, and Venezuela, this is the first subsequent record in the western Atlantic, and the first in the continental United States. The specimens found in the Indian River include adults of both sexes (one female ovigerous), and juveniles, indicating that the population is reproducing and that this nonindigenous species has become established in the region. This species must now be considered present in the tropical western Atlantic at least across the entire Caribbean region. Recognition characters of *C. hellerii* are provided, as well as a summary of what is known about its distribution, biology, and probable method of arrival. Comments on other marine decapods introduced in eastern North America are included.

On 20 April 1995, two adult specimens, a male and an ovigerous female of *Charybdis hellerii* (Milne Edwards, 1867), a species of Indo-Pacific origin, were caught in baited traps in the Indian River lagoon system of Florida in the vicinity of the Ft. Pierce Inlet. The male, 74 × 49 mm of carapace width × carapace length, remained alive in an aquarium for over a month until it was sacrificed. The ovigerous female (54 × 39 mm), died the same day it was captured. Following an announcement at The Crustacean Society's summer meeting (Lemaitre 1995) of the discovery of these specimens, several researchers (see names in acknowledgments) working in the Indian River during the period May–August 1995, informed me that they had found additional adults and juveniles in the Sebastian and Fort Pierce Inlets.

Charybdis hellerii was first collected in the western Atlantic in 1987 (Fig. 1), in Cuba by Gómez & Martínez-Iglesias (1990), in Venezuela by Hernández & Bolaños (1995), and in Colombia by Campos & Türkay (1989) where it was also collected in 1988. Although there have been no subsequent published reports of this species, it has been found repeatedly since 1988 in the Santa Marta area of Colombia (N. H. Campos, pers. comm.). The present report of *C. hellerii* in eastern North America extends the range of this species in the western Atlantic across the Caribbean region, to include subtropical Florida.

Keys for the identification of species of *Charybdis* as well as illustrations of *C. hellerii,* are available in a number of publications (e.g., Chopra 1935, Leene 1938, Stephenson et al. 1957, Stephenson 1972, Gómez & Martínez-Iglesias 1990). However, for the benefit of researchers working in the New World who may not have easy access to the earlier, more detailed taxonomic references, it seems appropriate to include here the most important recognition characters of this newly introduced species. Such information may facilitate future discovery and monitoring of populations of this portunid crab.

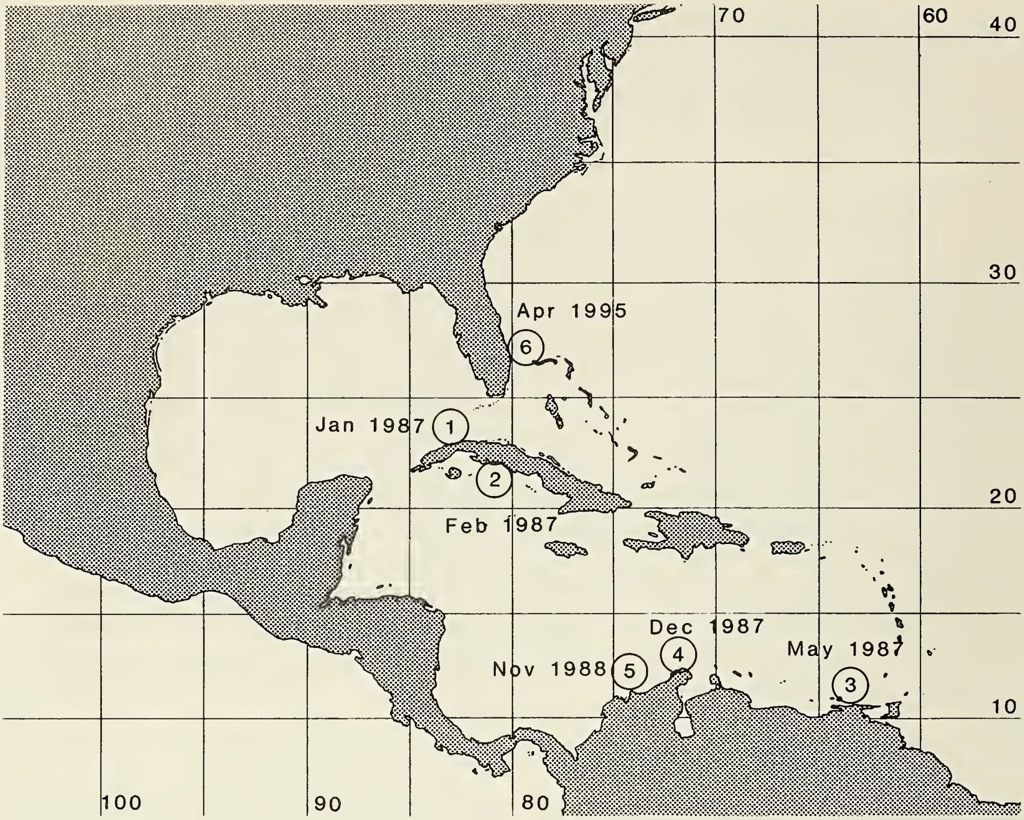

Fig. 1. Map showing collecting dates and locations of capture of *Charybdis hellerii* (Milne Edwards, 1867) in chronological order: 1, 2, Cuba: NE coast, Bahía Gibara (Provincia Holguín), and S coast, Bahía Cienfuegos (Provincia Cienfuegos) (Gómez & Martínez-Iglesias 1990); 3, NE Venezuela: Ensenada de Turpialito, Golfo de Cariaco (Estado Sucre) (Hernández & Bolaños 1995); 4, 5, Colombia: Bahía de Portete (Guajira), and Bahía Chengue (Magdalena) (Campos & Türkay 1989); 6, eastern USA: Indian River, Ft. Pierce, Florida (this report).

Method of capture.—The traps used were cylindrical, and consisted of 50 cm-long sections of PVC pipe of 20 cm diameter. The ends of each cylinder trap were fitted with cone entrances made of galvanized hardware cloth with a 1 cm mesh size. The cones were placed at each end with the narrow end facing the inside of the pipe. A small plastic bait basket was tied in the midsection of each trap. Bait used was mullet, purchased locally. Arrays of four traps were fixed to a long line, with a 20 kg lead weight on each end of the line. Two such arrays were left overnight in the vicinity of the Ft. Pierce Inlet: one in a channel south of Little Jim Island (in 1.5 m depth); and another in the Ft. Pierce turning basin just north of South Bridge (about 20 m from the mainland shoreline, in 4 m depth). After capture, the specimens were transported to the laboratories of the Smithsonian Marine Station at Link Port, Florida. The adult male and ovigerous female specimens have been deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., under catalogue number USNM 275907.

Family Portunidae
Charybdis hellerii (Milne Edwards, 1867)
Figs. 1, 2

Recognition characters.—Carapace with dorsal surface naked; anterolateral margin

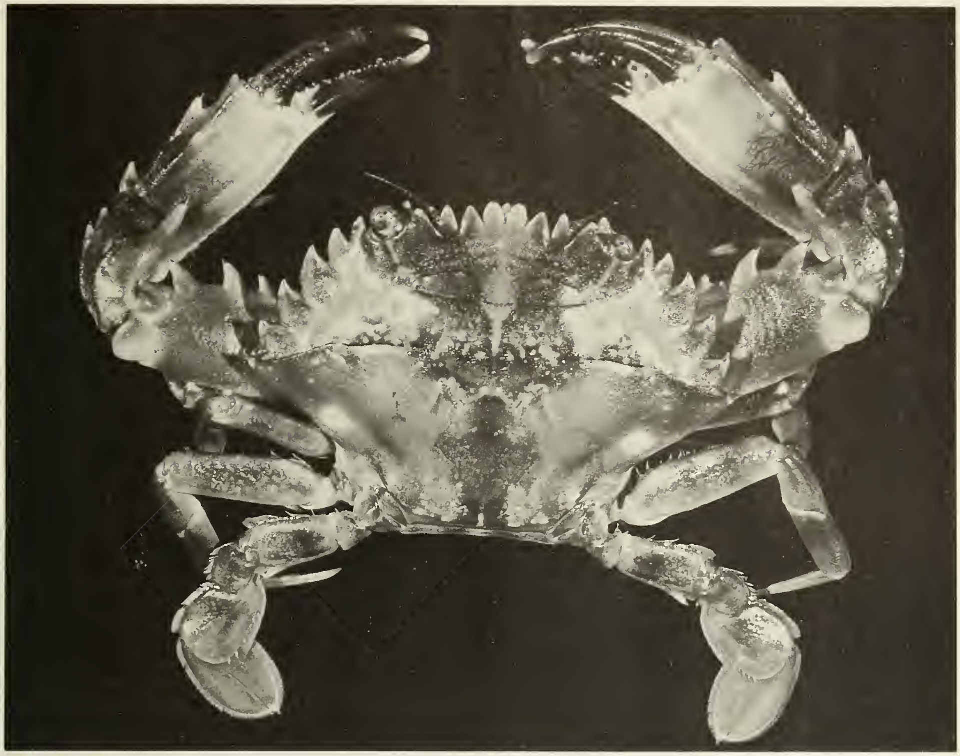

Fig. 2. *Charybdis hellerii* (Milne Edwards, 1867), male (74 × 49 mm), channel south of Little Jim Island, Ft. Pierce, Florida, USNM 275907.

with 6 sharp, black-tipped teeth (including outer orbital). Frontal region with 6 prominent teeth: 2 inner orbitals plus 4 blunt submedians, latter reaching slightly in advance of orbitals. Chela stout; palm with 5 strong black-tipped spines on dorsal face. Swimming leg with merus and carpus each armed with strong black-tipped spine on posterior margin distally; propodus with row of spines on posterior margin. Sixth abdominal segment of male about as broad as long, posterodistal margins rounded; telson bluntly triangular, basal width less than distal width of sixth abdominal segment. Male first gonopods, when viewed in situ, reaching approximately to suture between fifth and sixth thoracic somite, diverging in distal third; each with row of about 25 slender spines on lateral margin distally (spines diminishing in length distally).

Coloration.—Overall dark green except for light purple area on upper, inner surface of palm, and dark purple on dorsal surfaces of distal 4 segments of walking and swimming legs. Carapace with pale green or whitish areas on frontal, hepatic and epibranchial regions. Fingers of chelipeds dark purple.

Distribution.—Indo-Pacific: Japan, Philippines, New Caledonia, Australia, Hawaii, and throughout the Indian Ocean, including the Red Sea (Stephenson 1972, Kathirvel & Gopalakrishnan 1974, Vannini 1976, Javed & Mustaquim 1994). Eastern Mediterranean: Israel, and Egypt (Steinitz 1929, Galil 1992). Western Atlantic: eastern Florida, Cuba, Colombia, and Venezuela (Campos & Türkay 1989, Gómez & Martínez-Iglesias 1990, Hernández & Bolaños 1995, this report).

Biology.—This species is considered commercial in southeast Asia (Moosa 1981). Not much is known about its biology. The larvae of *C. hellerii,* for example, have not been described. Other species of *Charybdis* for which the complete larval development is known, have five to six zoeal stages and a megalopa (Greenwood & Fielder 1980). Fecundity of *C. hellerii,* as expressed by number of eggs, has been reported to range from 22,517 to 292,050 eggs per female (Siddiqui & Ahmed 1992). Other congeneric species (e.g., *C. cruciata, C. hoplites pusilla, C. natator, C. feriatus*) with biology probably similar to that of *C. hellerii,* are known to spawn year round but with peaks in early spring and fall, and have fecundities ranging from 181,230 to 3,200,000 million eggs per female (Pillai & Nair 1970, 1976; Campbell 1984; Sumpton 1990). *Charybdis hellerii* prefers soft bottom, although it is also found in rocky bottom and among live coral, and ranges from the intertidal to 51 m in depth (Stephenson et al. 1957, Galil 1992). Javed & Mustaquim (1994) recently reported specimens of *C. hellerii* from Pakistan that were carrying acorn barnacles (*Chelonibia patula*) on the carapace and chelipeds.

Timing and method of introduction.—Reports on the presence of *C. hellerii* in the Caribbean and Florida suggest that the arrival of this species in the region occurred in relatively recent times, probably in the late 1980's (see Fig. 1). Campos & Türkay (1989), and Gómez & Martínez-Iglesias (1990), observed that the presence of *C. hellerii* in Colombia and Cuba was correlated with increased ship traffic coming from the eastern Mediterranean where this species migrated via the Suez Canal and is now firmly established (Steinitz 1929, Galil 1992). Campos & Türkay (1989:122) indicated the possibility that the species arrived in ballast water or "clinging to the ships trunk". Transport in ballast water is the most probable explanation for the arrival of this species to the Caribbean and eastern Florida. It is unlikely that crabs could cling to the hull of any modern ship, although crabs could be transported by ships in fouled sea chests or fouled seawater intake pipes. As suggested by Gómez & Martínez-Iglesias (1990:71), it is also possible that this species was introduced in one or more sites and subsequently dispersed via larval stages to various other coastal environments in the region.

Presence in the Indian River of adults, including at least one ovigerous female, and juveniles, leaves little doubt that a reproducing population exists in this area and that the species is already established. The scant information available on the biology of *C. hellerii* indicates the potential of this species to successfully colonize marine ecosystems of South Florida and the Gulf of Mexico.

Marine decapods introduced in eastern North America.—*Charybdis hellerii* is the third marine decapod to be introduced and become established in the North American Atlantic coast. The other two being the western Pacific grapsid crab *Hemigrapsus sanguineus* (see Williams & McDermott 1990, McDermott 1991), and the European portunid crab *Carcinus maenas* (see Hedgpeth 1993, Carlton & Geller 1993, Cohen et al. 1995, Carlton & Cohen 1996). *Hemigrapsus sanguineus* is now known from Cape Cod to Chesapeake Bay (J. T. Carlton, G. Ruiz, A. H. Hines, Jr., pers. comms.). *Carcinus maenas* is the oldest decapod introduction to eastern North America. This species is known to have been present in eastern North America at least since the early 1800's, although it was then known under the name *Cancer granulatus* Say, 1817 [see Rathbun 1930:15, under *Carcinides maenas* (Linnaeus)]. By the late 1800's, *C. maenas* was well established from Cape Cod to New Jersey (Smith 1879), and currently is known to be established from Nova Scotia to New Jersey (Cohen et al. 1995). It has also been introduced to and is established in Australia, South Africa, Japan, and Pacific North America (Le Roux et al. 1990, Carlton & Cohen 1996). Curiously, the older published information on this species does not mention how it reached eastern North America. Recently, Cohen et al. (1995) have indicated that the global dispersal of *C. maenas* appears to be linked to the movement of fouled and bored wooden ships.

At least five other marine decapods have been considered in the literature as "introduced" in eastern North America but have not become established. Of these, two Indo-West Pacific penaeids (*Penaeus japonicus, P. monodon*) and two eastern Pacific penaeids (*P. stylirostris, P. vannamei*) are cultured extensively in South Carolina, Florida, and Texas, and while specimens of the latter three have been found in the wild as escapees from the shrimp farms, no reproducing populations have been reported (Wenner & Knott 1992). The Asian *Eriocheir sinensis* or "Chinese mitten crab", is believed to have arrived to eastern North America in ship ballast water (Nepszy & Leach 1973). Adults of *E. sinensis* have been steadily collected in the Great Lakes, most in Lake Erie, since the early 1970's to 1994 (J. T. Carlton, pers. comm.). However, since *E. sinensis* is catadromous, it cannot reproduce in the Great Lakes. One transient specimen of *Eriocheir sinensis* was found in Louisiana in 1987 but has not been found there since (D. L. Felder, pers. comm.). This species apparently has also been transported as a live food item sold in Asian-American markets (Horwath 1988, 1989).

Acknowledgments

I thank Woody Lee, Smithsonian Marine Station Link Port, Ft. Pierce, Florida, for his invaluable help in trap building, navigational guidance through the Indian River, and assistance during trips to the Station. For providing me with information on additional specimens of *Charybdis hellerii* found in the Indian River, I thank D. L. Felder (University of Southwestern Louisiana, Lafayette), and A. H. Hines, Jr., and R. B. Manning (both from the Smithsonian Institution, Washington, D.C.). I am particularly grateful to J. T. Carlton (Williams College-Mystic Seaport, Connecticut), and an anonymous reviewer for extensive comments and up-to-date information that considerably improved the manuscript. The following individuals also supplied useful information: Dave K. Camp (Florida Marine Research Institute, St. Petersburg, Florida), A. J. Provenzano, Jr. (Old Dominion University, Norfolk, Virginia), M. Tavares (Universidade Sta. Ursula, Rio de Janeiro, Brazil), E. L. Wenner (Marine Resources Research Institute, Charleston, South Carolina), A. B. Williams (National Marine Fisheries Service, Washington, D.C.), and J. D. Williams (National Biological Survey, Gainesville, Florida). This study was supported by the Smithsonian Marine Station at Link Port, Ft. Pierce, Florida, and is contribution no. 387 from that Station.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):649–655. 1995

Two new species of freshwater crabs of the genus *Hypolobocera* from Colombia (Crustacea: Decapoda: Pseudothelphusidae)

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Abstract.—Two new species of the genus *Hypolobocera* Ortmann, 1897, *H. kamsarum* and *H. emberarum,* from the Colombian Andes mountains, are described. The presence of a mesial lobe on the first gonopod of *H. kamsarum,* and a large triangular lateral lobe on the first gonopod of *H. emberarum,* distinguish these species from all others in the genus.

The genus *Hypolobocera* Ortmann, 1897, comprises a group of 28 species of freshwater crabs that inhabit a vast territory in Colombia, Venezuela, Ecuador and Perú. This is by far the most extended distribution in all the pseudothelphusid genera. The systematics and biogeography of the genus has been reviewed by Rodríguez (1982, 1992), and corrections to the diagnosis of several species have been published recently by Rodríguez (1994).

The morphology of the first male gonopod, a basic character for the diagnosis of the species, displays considerable variability in this group. To facilitate species identification, Rodríguez (1982) proposed the division of the genus into six groups, based on morphological and biogeographical characters. However, several transitional or aberrant species are still difficult to assign with complete certainty to any group. This is the case with one of the two new species described herein, *Hypolobocera kamsarum,* obtained during recent explorations of the Andean mountains of Colombia.

In the description of these two new species we have used the terminology established by Smalley (1964) for the different processes of the male first gonopods. The material is deposited at the Museo de Historia Natural, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN-MHN). The abbreviations cb and cl are used for carapace breadth and carapace length, respectively.

Family Pseudothelphusidae Rathbun, 1893
Tribe Hypolobocerini Pretzmann, 1971
Genus *Hypolobocera* Ortmann, 1897
Hypolobocera kamsarum, new species
Figs. 1, 2

Material examined.—Vereda Alto Campucana, Municipio Mocoa, Putumayo Department, Colombia, 1350 m alt., 2 Jun 1994, leg. O. V. Castaño: 1 male holotype, cl 14.0 mm, cb 23.7 mm (ICN-MHN-CR 1349); 1 male paratype, cl 13.4 mm, cb 21.8 mm, 1 female paratype, cl 14.6 mm, cb 24.8 mm (ICN-MHN-CR 1350).

Diagnosis.—First gonopod apex oval, with field of spines, mesial border strongly projected proximally, forming strong triangular mesial lobe; caudal ridge straight, strongly concave proximally in lateral view; lateral lobe small, transverse, evenly rounded in lateral view, ending far from apex of gonopod. Exognath of third maxilliped relatively long, approximately 0.6 length of ischium of third maxilliped.

Description of holotype.—Carapace narrow (cb/cl = 1.7). Cervical groove almost

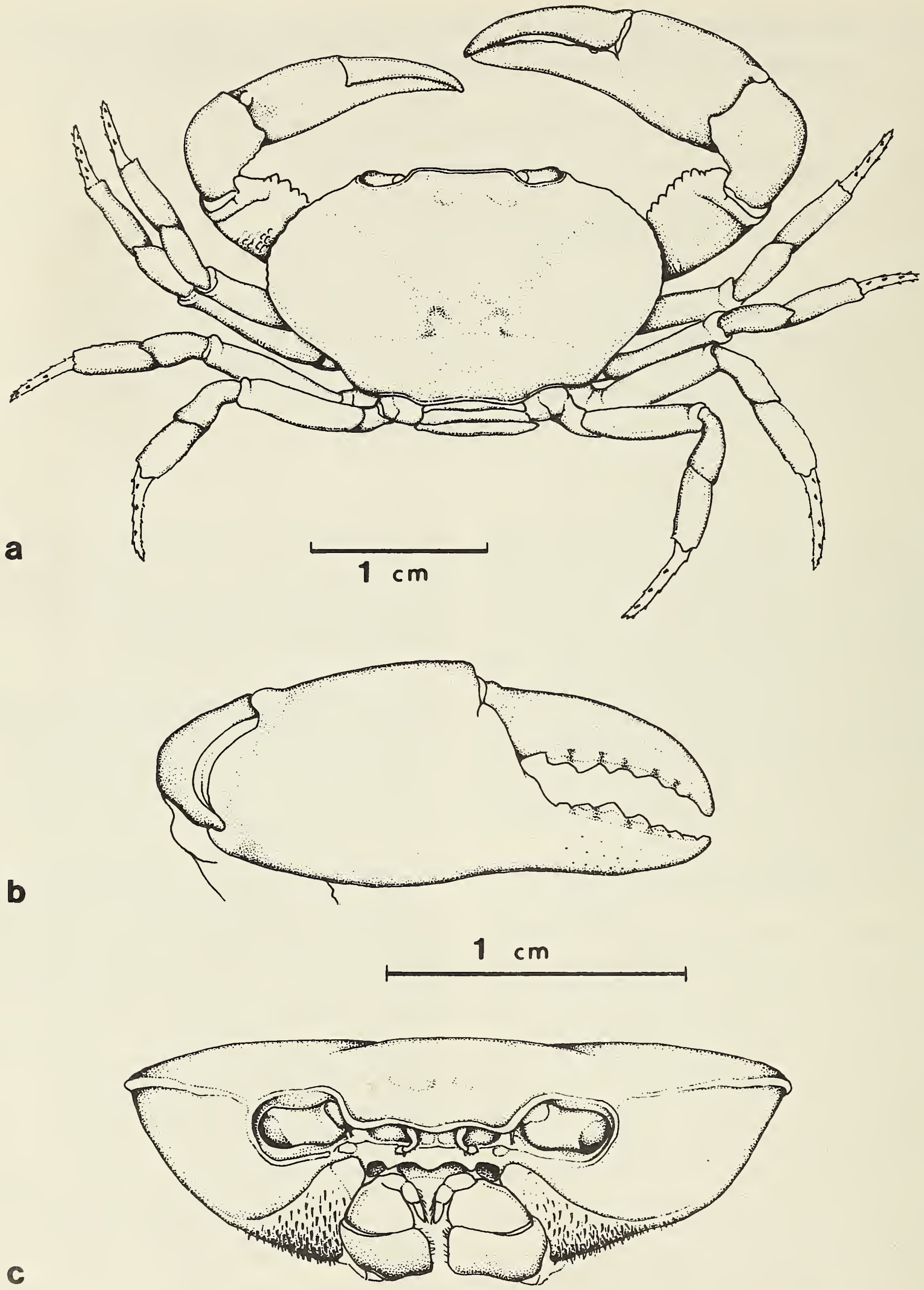

Fig. 1. *Hypolobocera kamsarum,* new species, holotype: a, dorsal view of carapace and pereiopods; b, chela of largest cheliped, external view; c, frontal view of carapace.

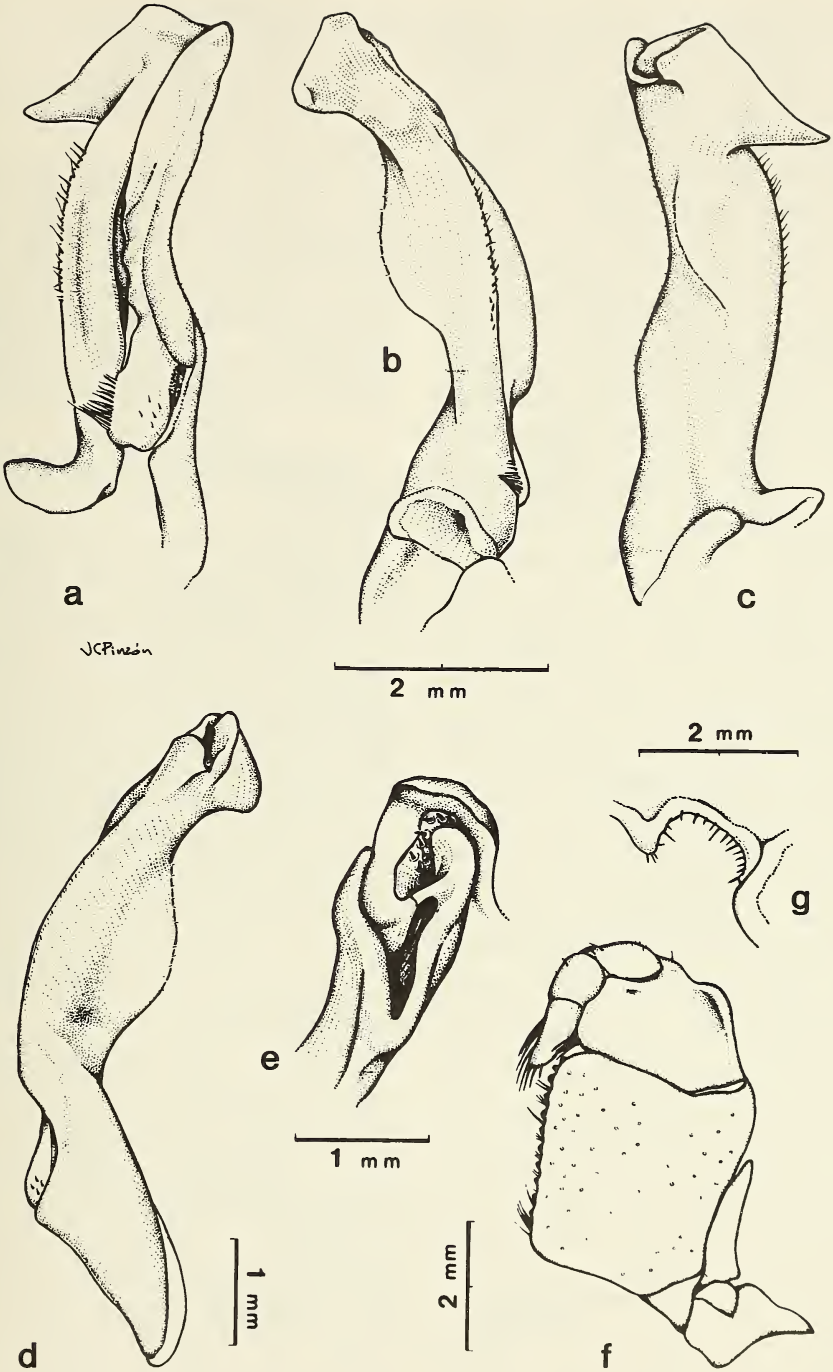

Fig. 2. *Hypolobocera kamsarum,* new species, holotype, left first gonopod: a, whole gonopod, caudal view; b, whole gonopod, mesial view; c, whole gonopod, cephalic view; d, distal portion of lateral view; e, detail of apex, cephalic view; f, left third maxilliped; g, aperture of left efferent channel, frontal view.

straight and deep, ending far from lateral margin. Anterolateral margin with papillae not well defined; posterior half smooth. Postfrontal lobes small, ovally shaped, low. Median groove absent. Surface of carapace between front and postfrontal lobes inclined anteriorly and towards mid-line. Upper border of front bilobed in dorsal view, without tubercles; lower margin strongly sinuous in frontal view; front between upper and lower margin low, vertical. Lower orbital margins each with row of tubercles. Surface of carapace smooth, covered by small papillae; limit between regions indistinct (Fig. 1a, c).

Palm of larger chela (right) strongly swollen, without proximal tubercle on fingers, fingers not gaping when closed (Fig. 1b). Palm of smaller chela moderately swollen, fingers not gaping when closed. Walking legs (pereiopods 2–5) slender, but not unusually elongated; pereiopods 2 and 3 longest of similar in length (length 1.16 times breadth of carapace). Dactylus of pereiopods 2–5 each with 5 rows of spines diminishing in size proximally; arrangement of spines on dactylus of left third pereiopod as follows: anterolateral row with 4 spines, anteroventral row with 5 spines plus 1 proximal papilla, external row with 4 spines plus 2 intercalated papillae and 1 pair of proximal papillae, posteroventral row with 3 spines, and posterolateral row with 3 spines plus 1 proximal papilla. Exognath of third maxilliped relatively long, approximately 0.6 length of ischium of third maxilliped; merus of third maxilliped with acute angle on distal half of external margin (Fig. 2f). Efferent branchial channel open (Fig. 2g).

First gonopod with caudal ridge straight, strongly concave proximally (lateral view); lateral lobe small, transverse, evenly rounded (lateral view), ending far from apex of gonopod (Fig. 2a, b, d); apex oval, with mesial border strongly projected proximally, forming strong triangular mesial lobe (Fig. 2e).

Color.—Specimens preserved in alcohol: carapace overall chestnut mottled with orange. Walking legs lighter than carapace with scattered orange specks.

Etymology.—The species is named for the Kamsá Indians, in whose territory the species was found.

Remarks.—Although the hypoloboceran traits are quite distorted in this species by the development of a triangular apical mesial lobe of the first gonopod, the lateral lobe is still characteristic of the genus. Based on Rodríguez (1982), *Hypolobocera kamsarum* can be considered a transitional species as mentioned in the introduction.

Hypolobocera emberarum, new species

Figs. 3, 4

Material examined.—Vereda El Veinte, Municipio El Carmen, near the Atrato River, Chocó Department, Colombia, 2800 m alt., 30 May 1994, leg. I. D. Vélez: 1 male holotype, cl 14.2 mm, cb 23.8 mm (ICN-MHN CR-1358); 2 male paratypes, cl 13.1 and 13.0 mm, cb 22.0 and 21.8 mm, 3 female paratypes cl 13.4, 13.2 and 12.7 mm, cb 22.6, 22.3 and 21.4 mm (ICN-MHN CR-1359). Valle de Pérdidas, Municipio Urrao, Antioquia Department, Colombia, 1800 m alt., 3 Sep 1994, leg P. Duque: 3 males, cl 14.1, 11.4 and 10.9 mm, cb 23.8, 19.1 and 18.3 mm, 3 females, cl 14.0, 12.8 and 12.7 mm, cb 23.5, 21.5 and 21.4 mm (ICN-MHN CR-1383).

Diagnosis.—First gonopod with caudal ridge long, straight; lateral lobe prominent, subtriangular, hatchet-shaped, wider proximally, spinulated, extending near apex of gonopod and forming deep notch distally, with longitudinal ridge at base; apex with oval field of spines, with cephalic side rounded, projected cephalad. Exognath of third maxilliped strongly reduced, approximately 0.20 length of ischium of endognath. Lateral sides of carapace conspicuously hairy in largest specimens.

Description of holotype.—Carapace narrow (cb/cl = 1.7). Cervical groove deep, wide, slightly sinuous, ending far from lateral margin. Anterolateral margin smooth.

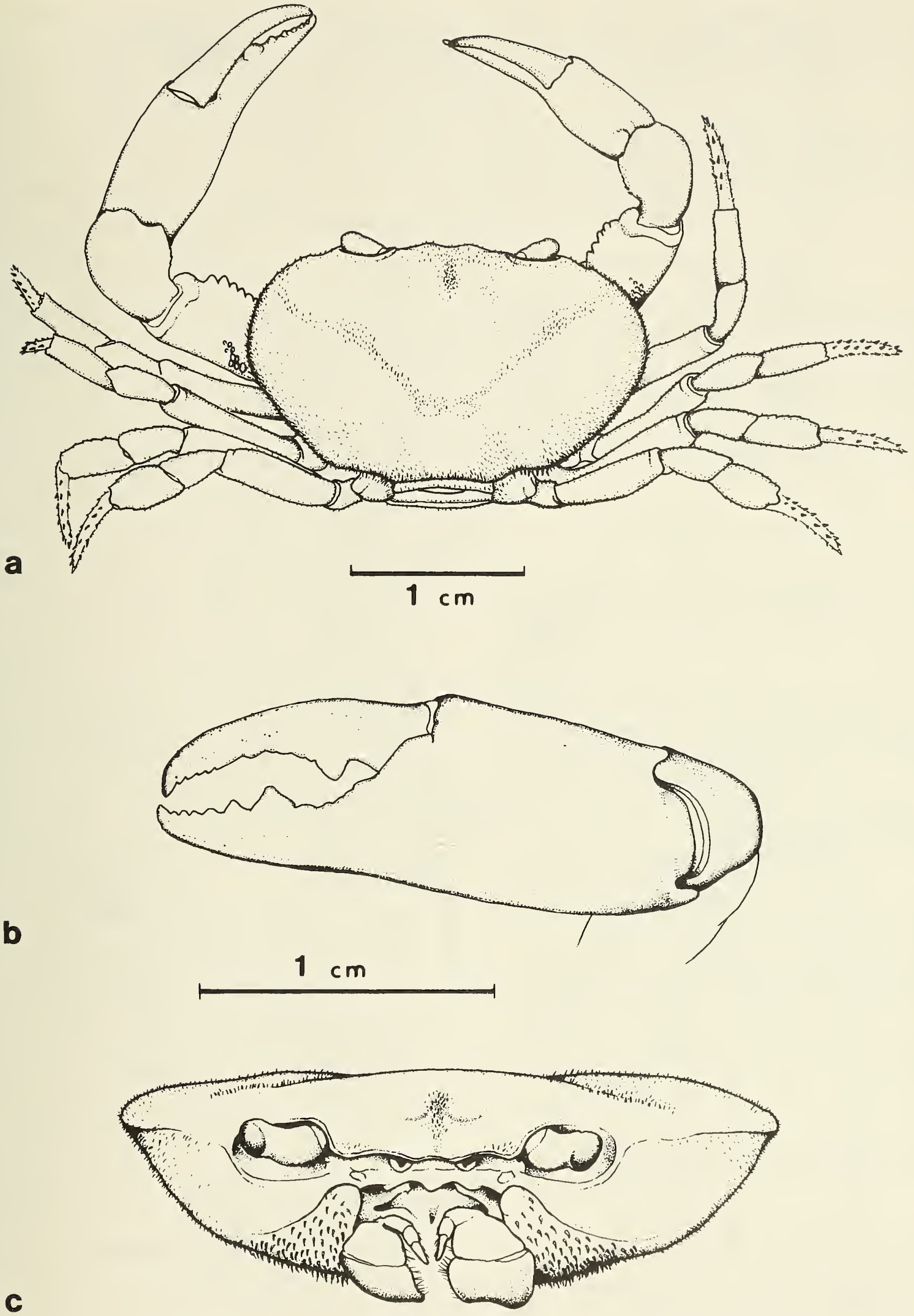

Fig. 3. *Hypolobocera emberarum,* new species, holotype: a, dorsal view of carapace and pereiopods; b, chela of largest cheliped, external view; c, frontal view of carapace.

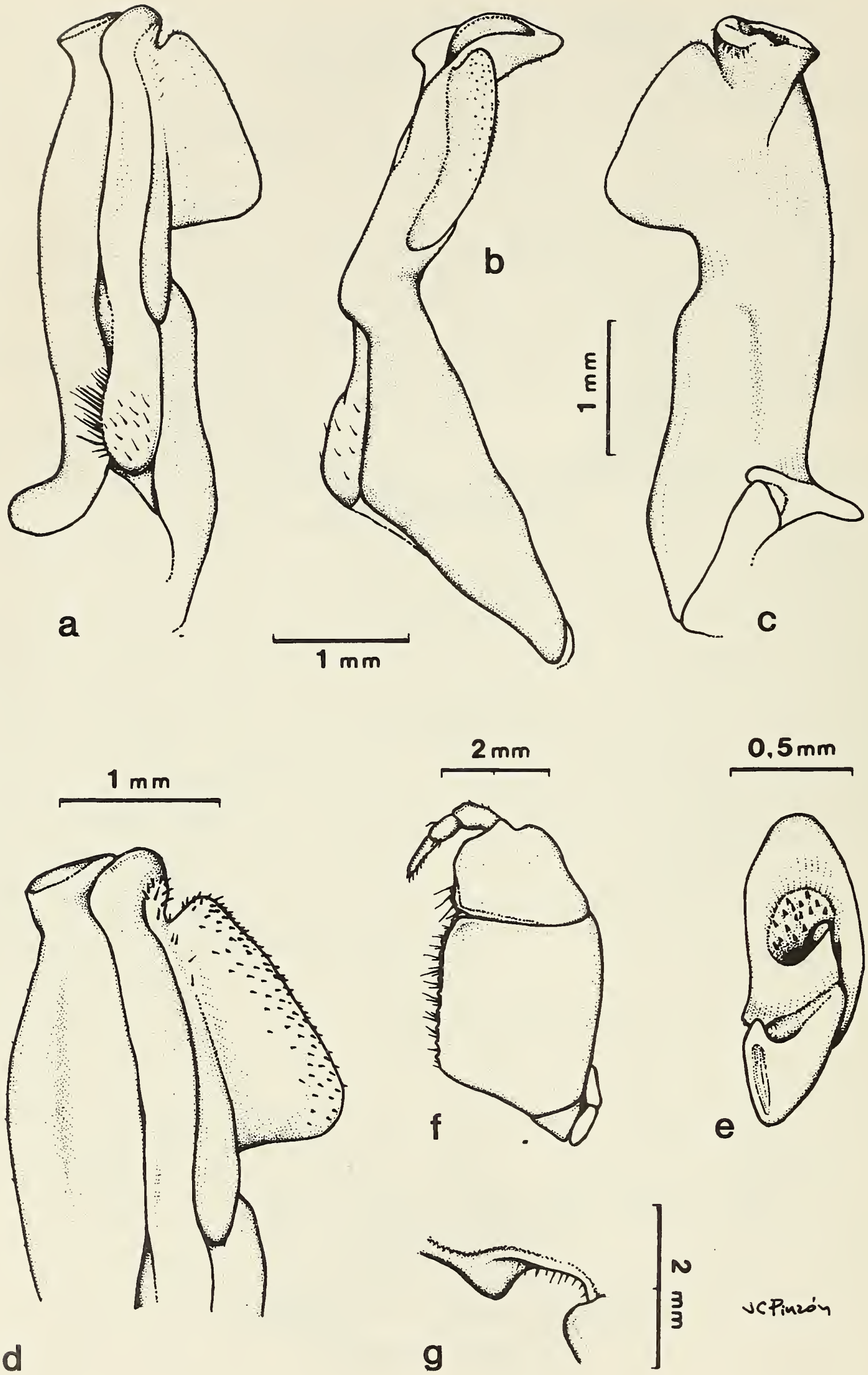

Fig. 4. *Hypolobocera emberarum,* new species, holotype, left first gonopod: a, whole gonopod, caudal view; b, whole gonopod, lateral view; c, whole gonopod, cephalic view; d, detail of apex, caudal view; e, detail of apex, superior view; f, left third maxilliped; g, aperture of left efferent channel, frontal view.

Postfrontal lobes ovally shaped, low. Median groove deep, narrow. Surface of carapace between front and postfrontal lobes inclined anteriorly. Upper border of front bilobed in dorsal view; lower margin sinuous in frontal view, with small tubercles. Surface of carapace smooth, covered by small papillae. Lateral sides of carapace conspicuously hairy in largest specimens (Fig. 3a, c).

Palm of larger chela (left) elongated, swollen, without proximal tubercle on fingers; fingers slender, slightly gaping when closed (Fig. 3b). Palm of smaller chela moderately swollen, fingers not gaping when closed, with tips crossing. Walking legs (pereiopods 2–5) slender, dactylus of pereiopods each with 5 rows of spines diminishing in size proximally; arrangement of spines on dactylus of right third pereiopod as follows: anterolateral row with 6 spines plus 3 proximal papillae, anteroventral row with 5 spines plus 3 proximal papillae, external row with 5 spines plus 2 papillae intercalated and 1 pair of proximal papillae, posteroventral and posterolateral rows with 4 spines. Exognath of third maxilliped 0.2 as long as ischium of third maxilliped; merus of third maxilliped with acute angle on distal half of external margin (Fig. 4f). Efferent branchial channel open (Fig. 4g).

First gonopod strongly bent in middle, caudal ridge long, straight, reaching to apex of gonopod; lateral lobe prominent, subtriangular, hatchet-shaped, wider proximally, extending near apex of gonopod and forming deep notch distally, caudal face covered with spinules (Fig. 4a, c, d); apex oval, with cephalic side rounded, projected cephalad (Fig. 4e).

Remarks.—This species resembles *Hypolobocera chocoensis* Rodríguez, 1980, in the shape of the lateral lobe of the first gonopod. However, the lateral lobe of *H. chocoensis* does not extend near the apex, and lacks a distal notch. Based on Rodríguez (1982), and on the general morphology and biogeography of *H. emberarum,* this species can be considered to belong to group IV.

Color.—Specimens preserved in alcohol: carapace and chelipeds overall dark brown-olive. Walking legs slightly lighter than carapace.

Etymology.—The species is named for the Embera Indians, in whose territory the species was found.

Acknowledgments

We thank Iván Dario Vélez, Patricia Duque and Olga Victoria Castaño, for collecting the specimens. We are also very grateful to Dr. Rafael Lemaitre and the referees for their valuable comments. The illustrations were prepared by Juan Carlos Pinzón.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):656–661. 1995

Redescription of a unique feather star (Echinodermata: Crinoidea: Comatulida: Comasteridae) with the diagnosis of a new genus

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Abstract.—A new genus, *Aphanocomaster,* is erected for *Comaster pulcher* A. H. Clark, which is known only from the holotype. The genus is similar to *Comaster* in having an apparent cryptosynarthry in the primibrach series, the first brachial syzygy chiefly between the first and second brachials on arms arising from the tertibrach series, and a central mouth. It differs in lacking a transverse initial comb tooth. The new genus differs from all other comasterid genera in having secundibrach series of four ossicles series in which both the first and second ossicles and the third and fourth are united by synarthrial articulations.

In the course of revising the Indo-Western Pacific genus *Comaster* L. Agassiz, a re-examination of *Comaster pulcher* A. H. Clark revealed that the single known specimen lacks a critical feature of the genus as currently diagnosed and exhibits another, previously unnoticed characteristic unique to the family. The combination requires removal of the species from *Comaster* and establishment of a new generic name for it. In addition, published descriptions are uniformly incomplete (A. H. Clark 1912, 1918, 1931).

Terms, abbreviations, measurements and symbols are as follows: Centrodorsal: central aboral plate. Cirri: aboral, segmented hooks attached to centrodorsal; Roman and Arabic numerals indicate numbers of cirri/individual and segments (cirrals)/cirrus, respectively (a range of values is usually given); LW of cirral: length to median width ratio when viewed laterally. Ray: one of five branched series of ossicles radiating from center of specimen. Radial: (n.) first ossicle of a ray or (adj.) a structure associated or oriented with a ray. Axil: ossicle at which a ray branches. Brachitaxis: series of ossicles following radial or axil and including the next axil; I–IVBr: first through fourth brachitaxes (written out primi-, secundi-, terti-, and tetrabrachitaxis, or tetrabrach series); Arabic numeral immediately following indicates number of ossicles in that brachitaxis (e.g., IIBr2). Arm: unbranched series of ossicles following distalmost axil; brachial (br; plural, brr): arm ossicle; subscript number indicates specific ray ossicle (brachitaxis or arm) counting from first ossicle after preceding axil or radial (e.g., $IIBr_2$, br_7); WL of ray ossicle: median width to midaboral length ratio when viewed aborally. Synarthry (—) (See "Note" below): articulation typically between first two ossicles of a brachitaxis or arm consisting of two ligament bundles separated by an aboral-oral fulcral ridge, sometimes with midaboral swelling. Cryptosynarthry: synarthry modified as a tight junction, visible externally as a fine line; the articular faces either smooth or with round or elongate, often concentric raised areas (Hoggett & Rowe 1986, fig. 2c). Syzygy (+): articulation between two successive ray ossicles consisting of radiating ridges and grooves and appearing externally as a perforated line (e.g., br_{3+4}); intersyzygial interval: number of articulations between successive syzygies. Pinnules (P): unbranched segmented appendages arising from alternate sides of successive brachials, and from exterior side of brachitaxes of more than two ossicles; on brachitaxes, subscript Roman numerals indicate brachitaxis from which pinnule arises (e.g., P_{II} on IIBr); on arms, subscripts count pinnules from the most proximal; Arabic numbers and letters refer to pinnules along exterior and interior side of an arm, respectively (that is, the sides away from and toward the extrapolated axis of the preceding axil) (e.g., P_4, P_c); LW of pinnule ossicles (pinnulars): length to median width ratio. Comb: modification of distal pinnulars of proximal (oral) pinnules producing comblike profile. Disk: central visceral mass or, specifically, its oral surface; anal interambulacral area: area on disk surrounded by food grooves and bearing anal papilla. For further discussions and examples of comatulid morphometrics, meristics, abbreviations and symbology, see A. M. Clark & Rowe (1971), Breimer (1978), Hoggett & Rowe (1986) and Messing & Dearborn (1990). In all illustrations, sparse uniform stippling indicates articulations between successive ossicles.

Note: The following descriptions include an exception to standard comatulid symbology. Synarthries are designated by one-em dashes (—), following the usage of Gislén (1934), so that, for example, IIBr4(1—2, 3—4) indicates a secundibrach series of four ossicles in which both the first and second and the third and fourth ossicles are united by synarthry. In comatulid crinoids, the first two ossicles following a radial or axil are joined either by synarthry (sometimes modified as a cryptosynarthry) or syzygy. Typically, only the latter is shown (as a + sign) in written symbology. When a syzygy is not present, a synarthry is assumed in this position (e.g., in IIIBr2, the two ossicles are joined by synarthry). Because the species discussed herein exhibits an unusual distribution of synarthries, they must be clearly indicated. However, even if additional specimens eventually demonstrate that the distribution of synarthries described below is an abnormality, the unique combination of other features exhibited by this specimen requires diagnosis of a new genus, as follows.

Aphanocomaster, new genus

Diagnosis.—A genus of Comasteridae with IBr2 ossicles apparently united by cryptosynarthry; IIBr2(1—2) and 4(1—2, 3—4); IIIBr2(1—2), 4(1—2, 3—4) and 4(1—2, 3 + 4) [possibly also 2(1 + 2)]; in brachitaxes of four ossicles, the second ossicle ($IIBr_2$ and $IIIBr_2$) laterally enlarged exteriorly to accommodate robust base of P_{II} and P_{III}, respectively; first brachial syzygies chiefly $br_{1+2,3+4}$ on arms arising from IIIBr; br_{3+4} alone on exterior arms arising from IIBr; comb teeth tall, triangular or spade-shaped, confluent with exterior lateral margin of pinnular; initial tooth sometimes slightly twisted, but not oriented transversely; mouth central; anal papilla midway between mouth and disk margin.

Type species.—*Comaster pulcher* A. H. Clark (1912), by monotypy.

Etymology.—From *aphanes* (*αφανεζ*), unseen, invisible, secret, obscure (Brown 1978), and the genus name *Comaster.* Gender is masculine.

Distribution.—Known only from a single station in the Kei Islands, Indonesia, 0–52 m (A. H. Clark 1931).

Remarks.—A. H. Clark (1921) and Gislén (1934) considered the few records in comatulids of four-ossicle brachitaxes consisting of two synarthrial pairs as abnormal. They recorded this pattern in only three species: *Cyllometra manca* (Carpenter) (Colobometridae) (originally as *C. anomala* A. H. Clark), *Heterometra quinduplicava* (Carpenter) (Himerometridae) and *Adelometra angustiradia* (Carpenter) (Antedonidae). A. H. Clark (in A. H. Clark & A. M. Clark 1967) suggested that the single known specimen of *A. angustiradia* might be a juvenile *Himerometra* or related genus, but placed it in the Antedonidae on the basis of its cirri and pinnules. Messing (1975) noted IIBr4 without IIBr$_{3+4}$ in several specimens of *Crinometra brevipinna* (Pourtalès) (Charitometridae), but did not otherwise identify the articulation between the third and fourth ossicles.

If, in specimens collected in the future, brachitaxes with two pairs of synarthries prove to be abnormally doubled forms of the much more widespread (among comatulids) brachitaxes of two ossicles united by synarthry, a new genus still must be erected for the type specimen of *Comaster pulcher*. No genus currently exists in the Comasteridae with the combination of features exhibited by this specimen: first brachial syzygy chiefly br$_{1+2,3+4}$, both IIIBr2(1—2), and IIIBr4(1—2, 3 + 4) present; no initial transverse comb tooth; mouth central. Only if the IIIBr4(1—2, 3 + 4) are also highly unusual and all brachitaxes are normally of two ossicles in future specimens would *pulcher* fall within a currently recognized genus: *Comissia* (Hoggett & Rowe 1986).

Aphanocomaster pulcher
(A. H. Clark, 1912)
Fig. 1

Comaster pulcher A. H. Clark, 1912:22.–1918:37, 40, 275, pl. 14, figs. 14, 15.–1931:443–444, pl. 50.—Gislén, 1919:14.

Holotype.—University of Amsterdam, Zoological Museum, U.Cri.-2114. Siboga Expedition Station 257, Du-roa Strait, Kei Islands, Indonesia, 0–52 m, 11 Dec 1899. 1 specimen.

Description.—Centrodorsal a thick, rounded pentagonal disk, 4.1 mm across (Fig. 1a). Aboral pole slightly depressed, with cirrus sockets encroaching on margin. Cirri XXXIV, 15–17, up to 11.2 mm long, in crowded double marginal row; first segment short, second with LW = 1.5–2.0; third segment longest, with LW 2.8; fourth and following segments decreasing in length, becoming compressed and slightly expanded distally; eighth segment with LW = 1.1–1.3; one or two segments preceding penultimate with LW = 1.0–1.1 (Fig. 1b, c). Fourth and following segments with low, aboral, subdistal, transverse swelling or ridge, sometimes finely spinulose, narrower on more distal segments, becoming low blunt and triangular on the four to five segments preceding penultimate (Fig. 1d, e). Fourth and following segments shiny. Opposing spine low and wide, sharp or blunt.

Arms 35, all in single plane, none complete. Radials very short, just visible. IBr2 ossicles joined by tight articulation, probably cryptosynarthry (see remarks). IBr$_1$ very short, WL = 4.5–5.0, completely separated or just touching at proximal corners, and slightly narrower distally so that adjacent IBr$_1$ are separated by V-shaped gap (Fig. 1a). One IIBr2(1—2) bearing IIIBr4(1—2, 3—4) exteriorly and IIIBr4(1—2, 3+4) interiorly; nine IIBr4(1—2, 3—4) bearing nine IIIBr2(1—2) [one of these with a close articulation; possibly IIIBr2(1 + 2)] and three IIIBr4(1—2, 3 + 4) [two of the latter arising from one IIBr4]. IIIBr developed in pairs or interiorly on IIBr. One interior IVBr2(1 + 2)?; the articulation uniting its ossicles a tight line similar to syzygy on proximal brr, but perforations not clearly visible. First ossicles of adjacent brachitaxes beyond the first (II–IVBr$_1$) joined interiorly for most or all of their length; adjacent IIBr and following brachitaxes separated interiorly by narrow U-shaped gaps; gaps becoming narrower between more distal brachitaxes, but remaining distinct between adjacent arm bases. Width at IIBr$_4$ axil 1.6 mm (1.3 at IIIBr axil).

Br$_1$ slightly longer exteriorly; adjacent br$_1$ joined interiorly; in arm bases with br$_{1-2}$ united by synarthry, br$_2$ cuneate and projecting exteriorly to accommodate base of large P$_1$. Proximal brachials otherwise oblong as far as br$_{6-8}$, WL = 1.7; triangular or almost so by about br$_{9-10}$, WL = 1.9. Middle brachials triangular, WL = 1.3–1.4. Distal brachials elon-

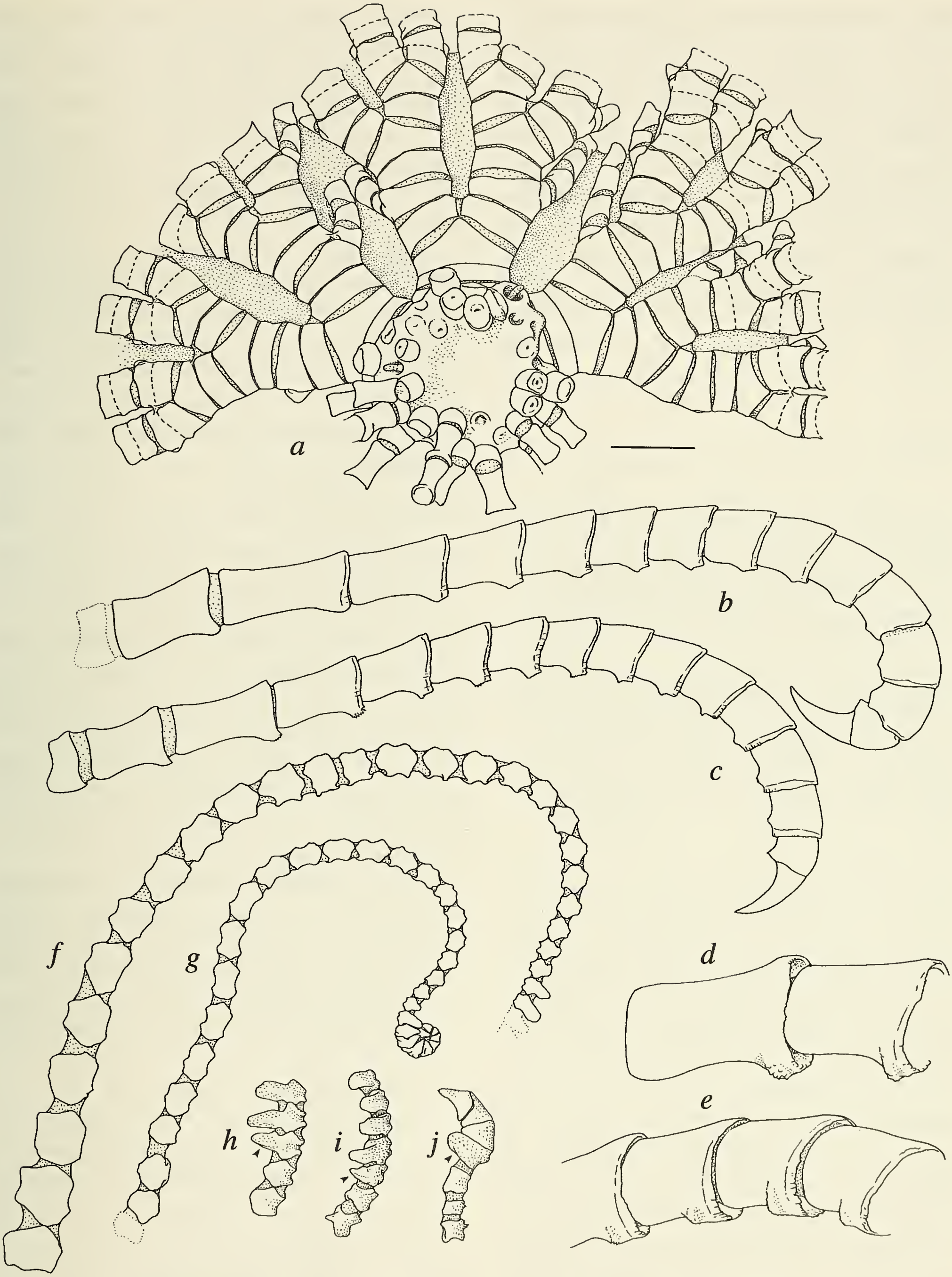

Fig. 1. a–i. *Aphanocomaster pulcher* (A. H. Clark), holotype. a. Aboral view showing centrodorsal, bases of cirri, bases of three rays, and basal few ossicles of proximal pinnules. b. Cirrus with weak aboral ornamentation. c. Cirrus with strong aboral ornamentation. d. Oblique view of fourth (left) and fifth cirrals showing finely spinulose transverse subdistal ridge. e. Oblique view of tenth (left) to thirteenth cirrals showing transverse aboral swelling narrowing to triangular process on more distal segments. f. P_{II} reconstructed from fragments; most of comb lost. g. P_2. h. Lateral view of proximal part of comb from a detached oral pinnule showing slightly twisted proximal tooth (arrow). i. Same, oblique view. j. *Comaster distinctus* (Carpenter), lateral view of proximal part of comb from a detached oral pinnule showing well-developed transversely-oriented proximal tooth (arrow). Scale bar: a, 2 mm; b, c, f, g, 1 mm; d, e, h–j, 0.5 mm.

gated, shaped like bent hourglasses, WL = 0.5 (LW = 1.9).

Aboral surface of rays smooth, somewhat flattened. On II and IIIBr4(1—2, 3—4), II and $IIIBr_2$ cuneate with exterior lateral margin projecting for articulation of very robust P_{II} and P_{III}; P_{II} and P_{III} so large that the ossicle bearing them almost appears as an asymmetric axil (Fig. 1a). Synarthries on brachitaxes sometimes weakly swollen midaborally. Distal margins of mid-arm brachials finely dentate but not flared or thickened. Distal brachials smooth. Epidermis fairly thick, obscuring several articulations.

First brachial syzygies chiefly $br_{1+2,3+4}$ on arms arising from IIIBr; br_{3+4} alone on exterior arms arising directly from IIBr4 (one with $br_{3+4,4+5}$, another with br_{4+5} instead) (Fig. 1a). On one ray, the exterior arms arising from a pair of adjacent IIIBr2 both lack br_{1+2} (one has br_{3+4}, the other is broken at br_2); interiorly, one of these IIIBr2 bears an arm with $br_{1+2,3+4}$; the other bears a IVBr2(1 + 2) which, in turn, bears an interior arm with $br_{1+2,3+4}$ and an exterior arm with br_{3+4} alone. Next syzygy br_{16+17}. Distal intersyzygial interval chiefly 4 (occasionally 3 or 5).

P_{II} of 35+ segments, comb lost; estimated length ≈14 mm; very robust at base, tapering to slender and flagellate distally; middle segments longer than broad (to LW = 1.5); no spines visible (Fig. 1f). One detached oral comb of 15 teeth possibly belongs to P_{II} or P_{III}. P_1 of 37 segments with 11 teeth, L ≈ 10.0 mm; similar to P_{II} but slightly less robust; apparently shorter with fewer segments. P_2 of 31–33 segments, 12 teeth, L = 8.2 mm; much less robust than P_1 (Fig. 1g). P_c of at least 26 segments with 6 teeth (tip possibly lost), remaining length = 7.6 mm. P_f of at least 22 segments with 7 teeth (tip possibly lost), remaining length = 5.7 mm. Comb teeth tall, triangular or spade-shaped and at least slightly incurved, confluent with exterior lateral margin of pinnular. Initial tooth sometimes slightly twisted (Fig. 1h, i); no initial transverse tooth. [Compare with initial transverse tooth of *Comaster distinctus* (Carpenter), Fig. 1j.] Comb either rising abruptly with tall first tooth, or developing gradually over 1–3 increasingly tall teeth. Distal teeth smaller & shorter but still well developed. Combs coiling planospirally; present to at least P_6.

P_g of 18 segments, no teeth, L = 5.4 mm; most segments (except at base and tip) longer than wide, cylindrical and constricted in middle, LW to 2.0; distal segments with cluster of lateral spines; hooks on last 3 segments. P_7 and P_g first genital pinnules; spherical gonads developed on fourth–sixth segments. Middle pinnules of 17–18 segments, 6.0 mm long; first two segments short, third and fourth squarish; these first four segments stout; following segments narrower so pinnule tapers to slender tip; most segments little longer than broad with bundle of strong spines along lateral margin. Distal pinnules of 17 segments, 7.2 mm long; first two segments short; following segments elongate (except near tip), and of about equal length but becoming more slender distally; LW increasing from about 3.3 proximally to 5.2 distally (not including basal or distalmost segments).

Disk completely naked; oral integument somewhat transparent with tiny sclerites visible in tissue. Mouth central; anal papilla large, about midway between mouth and disk margin; anal interambulacral area only slightly larger than other interambulacral areas.

Color.—White in alcohol.

Distribution.—Kei Islands, Indonesia. Known only from the type specimen.

Remarks.—The identities of the articulations in several brachitaxes are uncertain. The two ossicles of each IBr2 are joined by a tight articulation that may be either a synarthry or cryptosynarthry. No trace of the external perforations exists that would identify these articulations as syzygies and place the specimen in the genus *Comatula.* The articulation has not been dissociated for detailed examination because the specimen is unique. The articulations between the two ossicles of the single IVBr2, and the IIIBr2 that precedes it, are tight, similar to syzygies on the proximal brachials, but with perforations not clearly visible.

The specimen is in somewhat poorer condition than when last photographed (A. H. Clark 1931). However, the current redescription is substantially more detailed and differs in several important respects from those previously published (A. H. Clark 1912, 1918, 1931). I found XXXIV rather than XXVII cirrus sockets with the longest cirrus segment having LW = 2.8 rather than 3 to 4. The previous descriptions refer to a single IIBr2(1—2), nine IIBr4(1—2)(3 + 4), and all IIIBr2(1 + 2). This re-examination clearly shows that syzygies are not present in the IIBr, and that the IIIBr includes 4(1—2, 3—4), 4(1—2, 3 + 4), 2(1—2) and, possibly, 2(1 + 2).

In addition to the diagnostic characteristics of brachitaxes and pinnule combs, several other features also distinguish *A. pulcher* from the several nominal cirrus-bearing species of *Comaster* of similar size: *C. fruticosus* A. H. Clark, *C. brevicirrus* (Bell), *C. schoenovi* A. H. Clark, *C. sibogae,* A. H. Clark, *C. distinctus* (Carpenter) and *C. serratus* (A. H. Clark). In these *Comaster* spp., the longest cirral is usually the fourth, not the third; cirrals bear well developed aboral transverse ridges with a stronger opposing spine; middle brachials are shorter and usually cuneate with everted spinose distal margins; the first syzygy following br_{1+2} (or br_{3+4}, when present) occurs at br_{10+11} to br_{12+13}; the distal intersyzygial interval is usually 3, not 4, and the disks usually bear at least some slender conical nodules.

Acknowledgments

This research was carried out as part of a grant awarded to the author by the Museum national d'Histoire naturelle, Paris for July 1993. I thank Alain Crosnier for making the grant available to me, and for his hospitality, and J. Bleeker of the Instituut voor Taxonomische Zoologie, University of Amsterdam, for making the type specimen of *Comaster pulcher* available to me. I also thank Nadia Cominardi (curator of echinoderms, MNHN) for bringing the availability of funding to my attention, and for providing research space, great assistance and extraordinary generosity during my stay in Paris. This is Contribution no. 8 from the Deep Ocean Society, Inc., Hollywood, Florida.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):662–678. 1995

Gymnotus maculosus, a new species of electric fish (Chordata: Teleostei: Gymnotoidei) from Middle America, with a key to species of *Gymnotus*

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Abstract.—A new species of gymnotoid knifefish, *Gymnotus maculosus,* is described from Pacific drainages of Middle America, from Chiapas, Mexico, to Costa Rica, and an Atlantic drainage in Nicaragua. Morphological, meristic, and pigmentation features are compared with congeners. Variation among the species of *Gymnotus* from many localities in South America remains to be analyzed for a robust hypothesis about numbers of species and their interrelationships. A phylogenetic diagnosis of *Gymnotus,* and a key to the recognized species is provided.

Resumen.—Se describe una nueva especie de anguila electrica, *Gymnotus maculosus.* Esta especie se encuentra en las vertientes Pacíficas de Mesoamérica desde Chiapas, México, hasta Costa Rica, y en una cuenca Atlántica de Nicaragua. Se discuten y comparan características morfológicas, merísticas, y de pigmentación con otros miembros del género. Para poder establecer el número de especies de *Gymnotus* y sus relaciones, es necesario un análisis de la variabilidad entre especies de diversas localidades en Sudamérica. Se provee una diagnosis filogenética del género *Gymnotus* y una clave de identificación de las especies reconocidas.

Gymnotus is the most widely distributed genus of American electric knifefishes (Teleostei: Gymnotoidei). Members of the genus range from the Río San Nicolás of southeastern Chiapas, Mexico, south to the Río de la Plata, Argentina (Eigenmann & Ward 1905, Eigenmann & Fischer 1914, Eigenmann & Allen 1942, Miller 1966, Bussing 1985). Members of this lineage are aggressive, nocturnal predators who prefer small tributaries, lagoons, and backwater swamps, and in Middle America sometimes inhabit highland lakes.

The systematic position and organization of *Gymnotus* are problematic. *Gymnotus* was proposed by Peter Artedi in 1738 to include the type species *G. carapo* Linnaeus. According to Ellis (1913) the original specimens were collected in the Guyanas. Ellis (1913) was the first to propose a formal hypothesis of interrelationships among the major gymnotoid lineages, placing *Gymnotus* and *Electrophorus* as the sister lineage to all other gymnotoids (Ellis 1913, Eigenmann & Fischer 1914). Ellis synonymized all specimens of *Gymnotus* into the type species, *G. carapo.*

There are presently thirteen described species of *Gymnotus,* of which five have been synonymized with the type species (Mago-Leccia 1994). Several additional species are recognized in museum collections, however, so that the actual number of species may be substantially higher. Descriptions of several of these species await the acquisition of sufficient samples from populations across their geographical range (Mago-Leccia 1994). Most specimens of *Gymnotus* in museum collections are identified as *G. carapo,* regardless of their appearance or origin. This is due, in part, to the wide geographical extent of this puta-

Table 1.—Number of precaudal vertebrae in *Gymnotus* species. Counts from a total of 75 specimens are reported.

	30	32	34	36	38	40	42	44	46	48	50	*n*	Mode
anguillaris	0	0	0	0	5	0	0	0	0	0	0	5	38
carapo	0	0	0	0	6	0	0	0	0	0	0	6	38
catanaiapo	0	0	0	0	0	0	0	0	0	0	2	2	50
coatesi	0	0	0	0	0	3	1	0	0	0	0	4	40
cylindricus	2	15	6	0	0	0	0	0	0	0	0	23	32
maculosus	1	11	9	0	0	0	0	0	0	0	0	21	32
pedanopterus	0	0	0	7	0	0	0	0	0	0	0	7	36
stenoleucus	0	0	0	0	0	0	0	0	4	3	0	7	46
Total	3	26	15	7	7	3	1	0	4	3	2	75	

tive species, which is known from Guyana to the Río La Plata basin and many intervening sites. Furthermore, color patterns, and body shapes of specimens referred to *G. carapo* vary widely across the range.

The species diversity of *Gymnotus* is greatest in the Amazon basin, from where six species are recognized. Five of these species also inhabit the Upper Río Orinoco basin (Mago-Leccia 1994). *Gymnotus anguillaris* Hoedeman, originally described from Guyana, has also been collected from the Orinoco, Amazon, and La Plata basins. The other species have more restricted distributions. *Gymnotus coatesi* LaMonte is known only from the western Amazonian lowlands of Brazil and Perú, *G. inaequilabiatus* (Valenciennes) is from the Río de La Plata drainage, and *G. pantherinus* (Steindachner) from Atlantic drainages of southern Brazil.

Gymnotus also ranges into Middle America. Understanding the biogeographic history of *Gymnotus* in northwestern South America and Middle America is confounded by the complex geological history of the region (Bussing 1987, Pittman et al. 1993). Although the species diversity of *Gymnotus* has not been recently studied west of the Andes, there appear to be several unrecognized species inhabiting small coastal streams and rivers along the Pacific coast from Ecuador, north to Chiapas, Mexico. The purpose of this paper is to describe one of these species, discovered one of us (RRM).

Methods.—Methods used herein are modified or elaborated from Lundberg & Mago-Leccia (1986), Fink (1989), and Fink & Machado-Allison (1992). Specimens examined are listed in the Appendix. Museum acronyms are as presented by Leviton et al. (1985). Osteological data were taken from cleared and stained specimens using a modified version of the enzyme technique of Taylor & Van Dyke (1985). Standardized dissection methods of small teleosts were used (Weitzman 1974). We follow Fink & Fink (1981) for bone nomenclature. All drawings were made with the aid of a Zeiss dissecting microscope, equipped with a camera lucida, and edited by means of a PC graphics editor.

Counts of precaudal vertebrae (Table 1) and anal-fin rays (Table 2) were taken from radiographs. The number of precaudal vertebrae includes those of the Weberian apparatus; number of precaudal vertebrae is used here as a proxy for body-cavity length (Albert & Fink, in press). Body proportions reported include head length (HL), from posterior margin of bony operculum to tip of snout; postorbital head length (PO), from posterior margin of bony opercle to posterior margin of eye; preorbital head length (PR), from anterior margin of eye to tip of snout; body depth (BD), vertical distance from origin of anal fin to dorsal body bor-

Table 2.—Number of anal-fin rays in *Gymnotus* species. Counts from a total of 58 specimens are reported.

	155	165	175	185	195	205	215	225	235	245	255	*n*
anguillaris	0	0	0	0	0	1	0	2	1	1	0	5
carapo	0	0	0	0	2	1	2	1	0	0	0	6
catanaiapo	0	0	0	0	0	0	0	2	3	0	1	7
coatesi	0	0	0	0	0	2	1	1	0	0	0	4
cylindricus	0	1	1	5	0	3	3	1	0	0	0	14
maculosus	2	4	2	0	0	0	0	0	0	0	0	8
pedanopterus	0	0	0	0	0	0	1	1	1	1	0	7
stenoleucus	0	0	0	0	2	3	1	1	0	0	0	7
Total	2	5	3	5	4	10	8	9	5	2	1	58

der, with lateral line held horizontal; pectoral-fin length (P1), from dorsal border of fin base where it contacts cleithrum to tip of longest ray; interorbital distance (IO), between dorsomedial margins of eyes; size of branchial opening (BO), from posterodorsal to anteroventral extent of fold along anterior margin; pre-anal distance (PA), from anterior insertion of anal fin and posterior margin of anus. Body size is represented by head length (HL) in millimeters. The use of head length as a rough measure of overall body length is discussed by Albert & Fink (in press). Specimens in which the caudal filament was obviously damaged and unrepaired were excluded from measurements of total length.

Some measurements used in this report differ from those of earlier works on gymnotoids (Mago-Leccia 1978, 1994). Head length, for example, is defined as the distance between tip of snout and posterior extent of the bony opercle. Head length measured from the posterodorsal termination of the branchial opening (Mago-Leccia 1978) is subject to greater preservation-induced artifact and was not used. Measures of pectoral-fin length, postorbital length, and body depth reported here may also differ from results of previous studies. For these measurements, we attempted to use the unambiguous landmarks noted above to define endpoints.

This report is part of a larger research effort by the first author on systematics and evolution of the Gymnotoidei. A total of more than 2400 specimens representing at least 80 gymnotoid species have been examined (Albert 1995). Character polarities were determined from the hypothesis of relationships proposed by Albert (1995; see Discussion).

Monophyly and Nomenclature of *Gymnotus*

Gymnotus Linnaeus 1758

Gymnotus Linnaeus 1758:246 (type species, by original monotypy, *G. carapo* Linnaeus 1758).

Carapus Cuvier 1816 (nec Rafinesque): 237.

Giton Kaup *in* Duméril 1856:201 (type species, by original monotypy, *G. fasciatus* Pallas 1767:35).

Diagnosis.—Species of *Gymnotus* have multiple (13–50) pale oblique bands of reduced melanophore density along lateral surface of body (obscured in some species); anterior narial opening located within gape such that pore opening faces anteroventrally (also present in many rhamphichthyoids); anterior pharyngobranchial (associated with gill arch 3) unossified; all five basibranchials unossified; capacity to regenerate postcoelomic neural spines (Gayet & Meunier 1991); cylindrical or barrel shaped electrocytes, without a stalk, their long axis oriented longitudinally (Bass 1986, fig. 1).

Description.—The polarity of several

characters useful in identifying specimens of the genus *Gymnotus* are ambiguous. Mesethmoid short and broad. Frontals broad. Extrascapular firmly articulated with cranium. Lateral ethmoids absent. Mesopterygoid edentulous, bearing an ascending process. Infraorbital series represented by superficial bony tubes. Urohyal well developed. Four broad branchiostegal rays, two anterior branchiostegals narrower than the others. Basihyal elongate and hollow. Basibranchials not ossified. Three ossified pharyngobranchials. Five epibranchials, fifth one cartilaginous. Gill-rakers small, dentigerous plates, located on both margins of fourth branchial arch and on anterior margin of fifth arch, and covered by connective tissue. Branchial openings large, branchiostegal membrane united across isthmus. Posttemporal not fused with supracleithrum. Mesocoracoid present. Coracoid not bearing ventral process. Four pectoral radials. Lateral line complete. Presence of 30–51 precaudal vertebrae. No displaced hemal spines. Anus not growing anteriorly during ontogeny. Anterior insertion of anal fin not extending anterior to vertical through posterior margin of pectoral fin. Anal fin confluent with tip of tail (rays of the posterior portion of anal fin are tightly aggregated and lie horizontally caudally, making it difficult to count the exact number of rays other than in stained specimens or radiographs).

Species of *Gymnotus* mature at moderate body sizes (approximately 150 to 400 mm TL), possess a cylindrical or subcylindrical body, and are completely covered by cycloid scales on the postcranial part of their bodies. In many species, color pigmentation patterns are formed by alternating bands of dark and pale oblique bands along the body axis. The band-interband contrast increases ventrally, and is generally more pronounced in juveniles (less than 100 mm TL). Although the number, width, and shape of these bands are variable, banding patterns have diagnostic value for several species (Mago-Leccia 1994).

We follow Mago-Leccia (1994) in recognizing the following species of the genus and their synonyms:

Gymnotus carapo Linnaeus
- *G. carapo* Linnaeus, 1758:246 (type locality: America).
- *G. fasciatus* Pallas, 1767:35 (type locality: Brazil).
- *G. albus* Pallas, 1767:35 (type locality: Suriname).
- *G. brachiurus* Bloch, 1787:61, plate 157, fig. 1 (type locality: Brazil).
- *G. putaol* Lacépède, 1800:176 (type locality: Brazil).
- *G. cingulatus* Brind, 1935 (type locality: Brazil).

Gymnotus inaequilabiatus (Valenciennes)
- *Carapus inaequilabiatus* Valenciennes *in* D'Orbigny 1847:11, plate 14 (type locality: Río de La Plata, Argentina).

Gymnotus pantherinus (Steindachner)
- *Giton fasciatus* var. *pantherinus* Steindachner, 1908:129 (type locality: Santos, Brazil).

Gymnotus coatesi LaMonte
- *G. coatesi* LaMonte, 1935:1, fig. 1 (type locality: Rio Amazonas, Brazil).

Gymnotus cylindricus LaMonte
- *G. cylindricus* LaMonte, 1935:2 (type locality: Los Amates, Río Motagua Basin, Guatemala).

Gymnotus anguillaris Hoedeman
- *G. anguillaris* Hoedeman, 1962a:55, fig. 2 (type locality: Coropina Creek, Suriname).
- *G. coropinae* Hoedeman 1962a:55, fig. 1c (type locality: Coropina Creek, Suriname).

Gymnotus cataniapo Mago-Leccia
- *Gymnotus cataniapo* Mago-Leccia 1994: 90, fig. 100, table 9 (type locality: Río Cataniapo, Amazonas, Venezuela).

Gymnotus pedanopterus Mago-Leccia
- *Gymnotus pedanopterus* Mago-Leccia 1994:92, fig. 98, table 10 (type locality: Caño La Esmeralda, Río Orinoco, Amazonas, Venezuela).

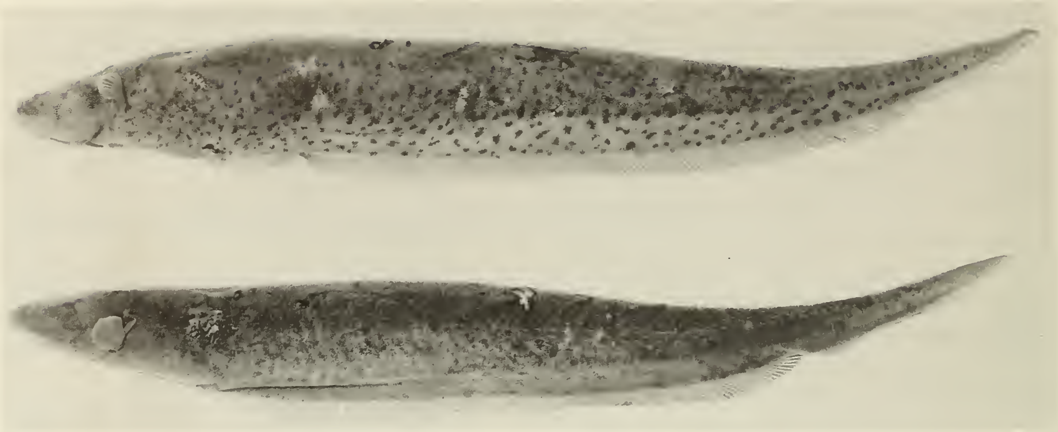

Fig. 1. Lateral view of *Gymnotus maculosus,* paratypes, USNM 134700, 185 and 195 mm TL, Río Buena Vista 8 km W of Pajal, Departamento Santa Rosa, Guatemala.

Gymnotus stenoleucus Mago-Leccia

Gymnotus stenoleucus Mago-Leccia 1994:94, figs. 99–101, table 11 (type locality: Río Cataniapo, Amazonas, Venezuela).

Gymnotus maculosus, new species
Fig. 1–6

Gymnotus carapo in part, Eigenmann & Fisher, 1914:235. Rivers and lakes on both slopes of Guatemala.

Gymnotus carapus Carr & Giovannoli, 1950:11–12. Río Choluteca, Honduras.

Gymnotus cylindricus Bussing, 1985, fig. 36.

Gymnotus sp. Miller, 1966:786 (Pacific slope of Middle America from Guatemala to the Gulf of Fonseca).

Gymnotus sp. Miller, 1986:129 (Pacific slope of Middle America between Tehuantepec and Guatemala).

Gymnotus sp. Espinosa Perez et al., 1993: 29 (Río Usumacinta).

Holotype.—UMMZ 230830, 191 mm TL. Diversion of channel from María Linda, 14°04′N; 90°37′W, c. 20 km. East of Escuintla, Departamento Santa Rosa, Guatemala; collected by D. E. Rosen and R. M. Bailey, 27 March 1971.

Paratypes.—UMMZ 190783, 3 specimens, 176–203 mm TL, type locality. UMMZ 224128, 5 specimens, 158–222 mm, Río Higuerón, Canas, Costa Rica. UMMZ 230354, 20 specimens, Río Buena Vista, trib. of Río Tigre, on road between Escuintla and Chiquimulilla, 8 km. West of Pajal, Departamento Santa Rosa, Guatemala, 128–230 mm, 1946.IV.18. USNM 134700, 49 specimens, Río Buena Vista, 8 km. West of Pajal, Departamento Santa Rosa, Guatemala, 67–195 mm TL, 1946.IV.18. TU 24965, 36 specimens, 60–260 mm TL, Boca del Río Sapoá at Sapoá, Nicaragua.

Diagnosis.—A gymnotid unique in possessing numerous small brown spots, varying in size from two to four times eye diameter, distributed over most of the body surface (Figs. 1, 2). The body lacks distinct oblique bands in both juveniles and adults. Scales above the lateral line large, 6–8 rows to the dorsal midline at about midbody.

Description.—Figure 3 illustrates body shape. Body subcylindrical (its greatest width 0.61–0.84% BD); BD = 10–13% TL; dorsal profile of body almost straight, ventral profile slightly convex; head small, depressed, HL = 9.8–12.7% TL; PO = 58–64.5% HL; anterior nares tubular, partially concealed in labial groove; posterior nares round, and positioned close to eye; mouth

Fig. 2. Lateral view of *Gymnotus maculosus,* paratype, TU 24965, 238 mm TL, Río Sapoá at Sapoá, Nicaragua.

broad, gape large, rictus of mouth not reaching vertical through eyes; lower jaw protruding, teeth small, conical, in a single row in each jaw, with irregular second row; snout blunt, PR = 33.1–37.5% HL; IO = 37.0–41.0% HL; origin of anal fin posterior to tip of pectoral fin, PA = 7.4–11.1% TL; branchial opening large, B0 = 33.0–44.3% HL; nape without pale band; lateral line complete, paralleling main body axis; pectoral fin small, rounded, P1 = 43–48% HL; pectoral-fin rays ii+15–16 (*n* = 8); 30–34 precaudal vertebrae (Table 1, mode = 32, *n* = 21); anus near vertical through branchial opening; anal fin short, 155–182 anal-fin rays (Table 2, mode = 169, *n* = 8).

Color in preservative.—Ground color yellow to pale brown laterally on preserved specimens. Dorsum dark brown due to densely concentrated melanophores. Dark brown dorsally and laterally. Ground color overlaid by numerous brown spots on head and body, ranging in size from about 2 to 4 eye diameters, and varying somewhat in

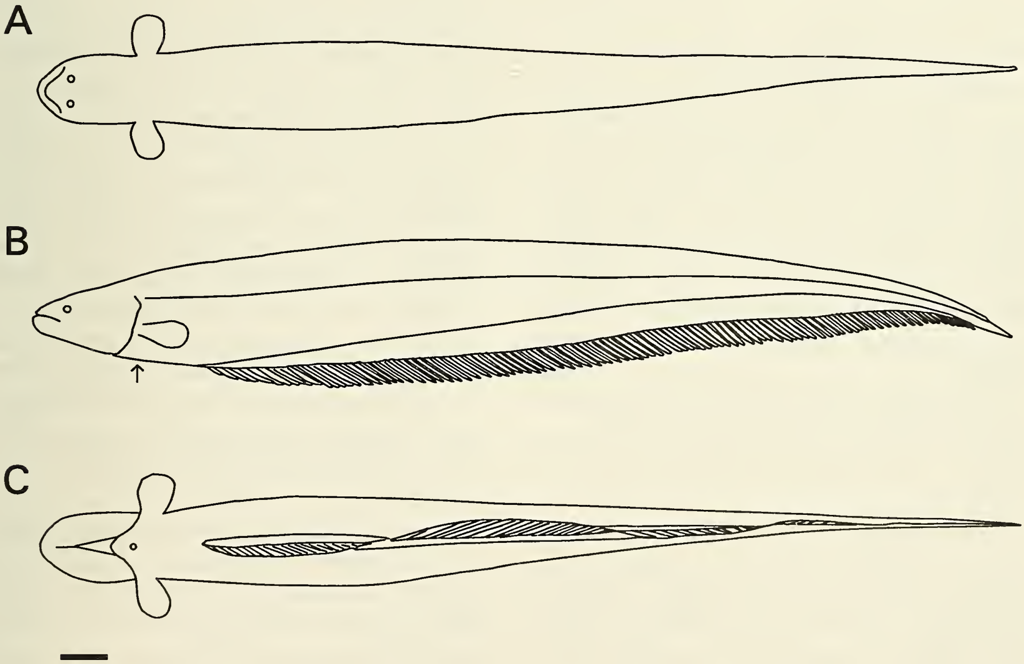

Fig. 3. Diagrammatic representation of *Gymnotus maculosus.* (A) dorsal, (B) lateral, and (C) ventral view. Arrow indicates position of the anus. Scale bar equals 10 mm.

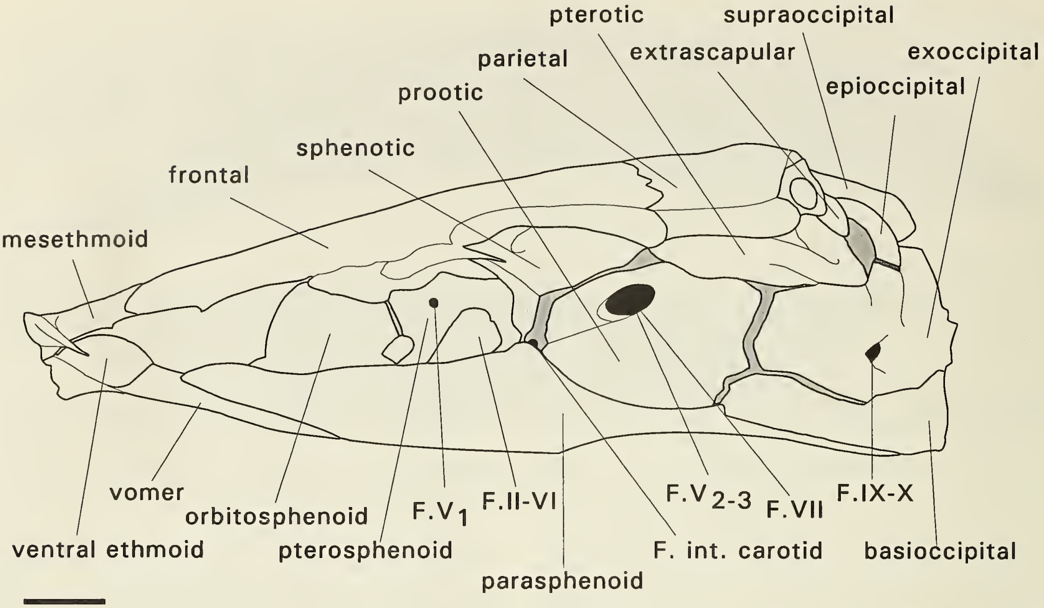

Fig. 4. Lateral view of neurocranium of *Gymnotus maculosus,* UMMZ 190531, 185 mm TL. Cartilage indicated by stippling. Abbreviations: F. V_1, foramen of cranial nerve V_1 (profundus); F. II–VI, foramen of optic tract and cranial nerves III (oculomotor), IV (trochlear), and VI (abducens); F. int. carotid, foramen of internal carotid artery; F. $V_{2\text{-}3}$, foramen of V_2 (superficial ophthalmic and maxillary) and V_3 (internal mandibular) rami of trigeminal nerve; F. VII, foramen of cranial nerve VII (facial); F. IX–X, foramen of cranial nerves IX (glossopharyngeal) and X (vagus). Scale bar equals 1 mm.

size and arrangement. Some specimens with spots arrayed into approximately 13–21 oblique lines, corresponding to oblique lateral bands of other species of *Gymnotus*; other specimens with smaller spots, arrayed into more than 40 oblique lines, or with spots arrayed in a somewhat random pattern. The organization of spot and pigment density is not a function of body size. Anal and pectoral fins without spots. Anal- and pectoral-fin rays and interradial membranes hyaline.

Etymology.—From the Latin *maculosus,* meaning spotted, in reference to the conspicuous color pattern possessed by this species.

Distribution.—Gymnotus maculosus lives in freshwater streams of Middle America (Fig. 7). On the Pacific slope it ranges from the Río San Nicolás (15°20′N, 92°50′W), Chiapas, Mexico, south to tributary streams to the Gulf of Nicoya in northwestern Costa Rica (9°47′N, 84°48′W). On the Atlantic slope it appears to be restricted to streams on the western slope of the Lake Nicaragua basin in Nicaragua, the Río Sapoá of northern Costa Rica, and the San Carlos and Sarapiqui drainages of northeastern Costa Rica. The seemingly disjunct distribution of *G. maculosus* in Fig. 7 is presumed to result from the lack of collections from Pacific slope drainages of El Salvador and Nicaragua.

Remarks.—Gymnotus maculosus shares two characters of ambiguous polarity with *G. cylindricus*; absence of discrete oblique bands along the body, and short body cavity, with 31–35 precaudal vertebrae.

Comparisons with other species.—Gymnotus maculosus can be separated from parapatric members of *G. cylindricus* in the Lake Nicaragua basin by its unique color pattern, by its smaller interorbital distance, and by the larger size of scales above the lateral line. Specimens of *G. cylindricus* possess few if any small brown spots on the

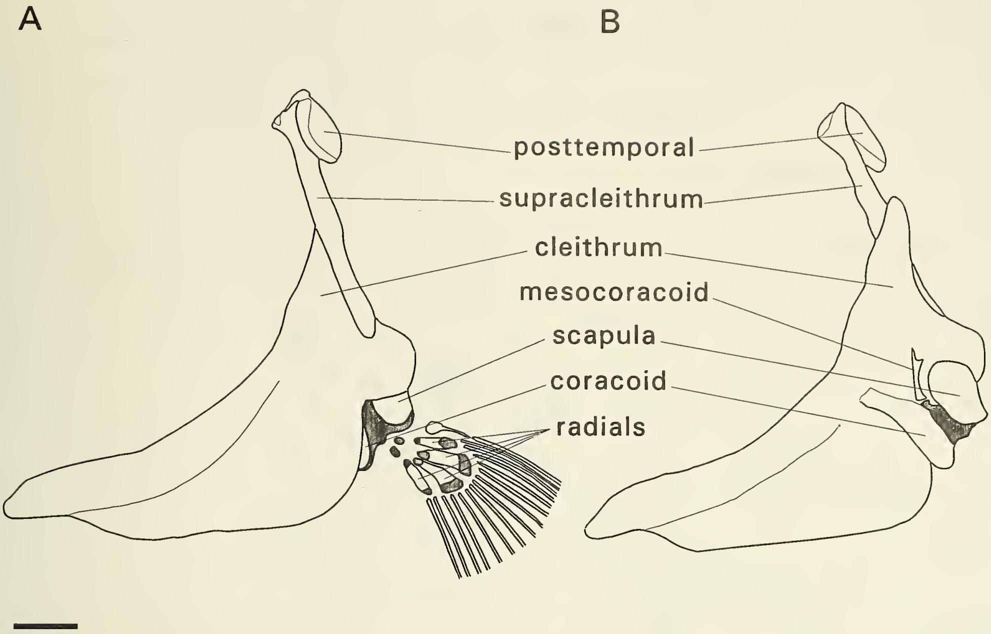

Fig. 5. Pectoral girdle of *Gymnotus maculosus,* UMMZ 190531. (A) lateral view. (B) medial view. Cartilage indicated by stippling. Scale bar equals 1 mm.

body. Although some specimens of *G. cylindricus* possess a mottled appearance, with low contrast, pale spots on the ventral portion of the body, only *G. maculosus* possesses high contrast spots over the entire body. The interorbital distance of *G. maculosus* is 37–41% HL, whereas that of *G. cylindricus* is 41–46% HL. Scales above the lateral line are larger in *G. maculosus,* with 6–8 rows to the dorsal midline at about midbody, whereas those of *G. cylindricus* are smaller, with 10–12 rows above the lateral line at about midbody.

Gymnotus maculosus can be separated from the other species of *Gymnotus* by its color pattern and meristic, features. *Gymnotus maculosus* has fewer precaudal vertebrae (30–34, $n = 21$; vs. 38, $n = 6$) and fewer anal-fin rays (155–182, $n = 8$; vs. 190–222, $n = 6$) than does *G. carapo.* Unlike *G. carapo, G. maculosus* is spotted and does not have conspicuous oblique bands. *Gymnotus maculosus* can be separated from other spotted species of *Gymnotus, G. inaequilabiatus* and *G. pantherinus,* by the same meristic characters used to separate it from *G. carapo.*

Discussion

Variation in characters examined.—Several body measurements vary among and between species of *Gymnotus.* Uses of body depth, head length, interorbital distance, and pectoral-fin length to identify species are noted in the key. Despite this variation, the characters used in the diagnoses do prove useful when making certain comparisons. The deep body of *G. inaequilabiatus* (BD greater than HL), for example, can be used to separate it from all other South American species of *Gymnotus* (except some specimens of *G. cataniapo*) in which the BD is less than HL. Specimens of *G. carapo* and *G. pedanopterus* possess a long head (HL greater than 11.8% TL for specimens 100–250 mm TL) when compared to other species of *Gymnotus.* Although the snout length of most *Gymnotus* species ranges from PR = 32.5–38.0% HL, speci-

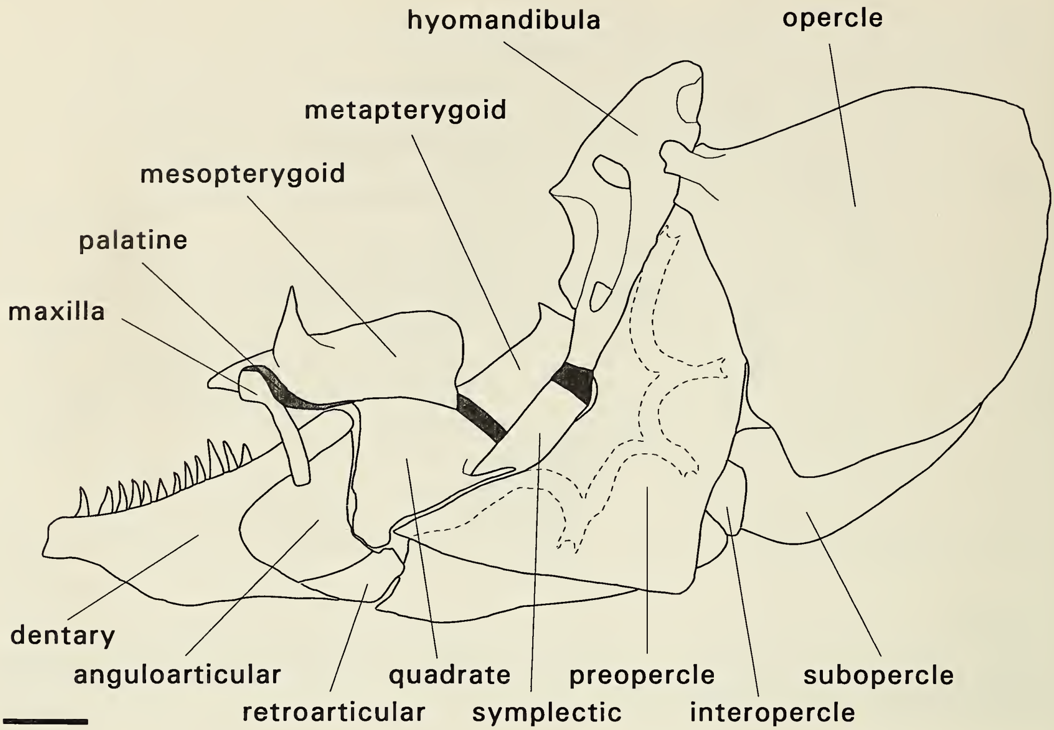

Fig. 6. Lateral view of suspensorium of *Gymnotus maculosus,* UMMZ 190531. Cartilage indicated by stippling. Scale bar equals 1 mm.

mens of *G. anguillaris* tend to have a longer snout (PR = 36.0–41.0% HL), and specimens of *G. coatesi, G. cataniapo, G. pedanopterus,* and *G. stenoleucus* tend to have shorter snouts (PR = 28.5–36.5% HL). The anal fin of *G. carapo* and *G. inaequilabiatus* tends to insert more anteriorly than in other *Gymnotus* species (PA = 55–86% HL vs. 72–112% HL). These measurements exclude two specimens of *G. cylindricus* with abnormally short PA distances (31% and 46% HL). PA data for *G. pedanopterus* and *G. stenoleucus* were not available for this study. The two species of *Gymnotus* from Middle America share a short pectoral fin (P1 = 38.0–47.5% HL) with the Suriname specimens of *G. carapo,* and with the slender species *G. cataniapo, G. pedanopterus,* and *G. stenoleucus.*

Body proportions of *Gymnotus carapo* in South America vary considerably. Specimens examined from Suriname can be distinguished from those in the Amazon basin by having a deeper body (BD = 11.5–12.5% TL vs. 10–11% TL) and a shorter pectoral fin (P1 = 38–45% HL vs. 46–57% HL). The anal-fin origin also tends to be more remote from the anus in the Suriname specimens (PA = 9.5–11.0% HL vs. 6.5–10.0% TL). Specimens collected west of the Andean cordillera in Colombia, from the Río Atrato basin and the Pacific drainage at Pizarro, possess the two diagnostic traits of *G. carapo:* a long head (HL = 11.8–12.5% TL) and a clear anal-fin membrane at the posterior end of the fin. Measurements of these specimens (*N* = 5) reveal that they have the more slender body (BD = 10.0–10.2% TL) and longer pectoral fin (P1 = 45.2–58.3% HL) of *G. carapo* from the Amazon, and the posterior origin of the anal fin (PA = 9.0–11.2% TL) of *G. carapo* from Suriname, and of the other *Gymnotus* species.

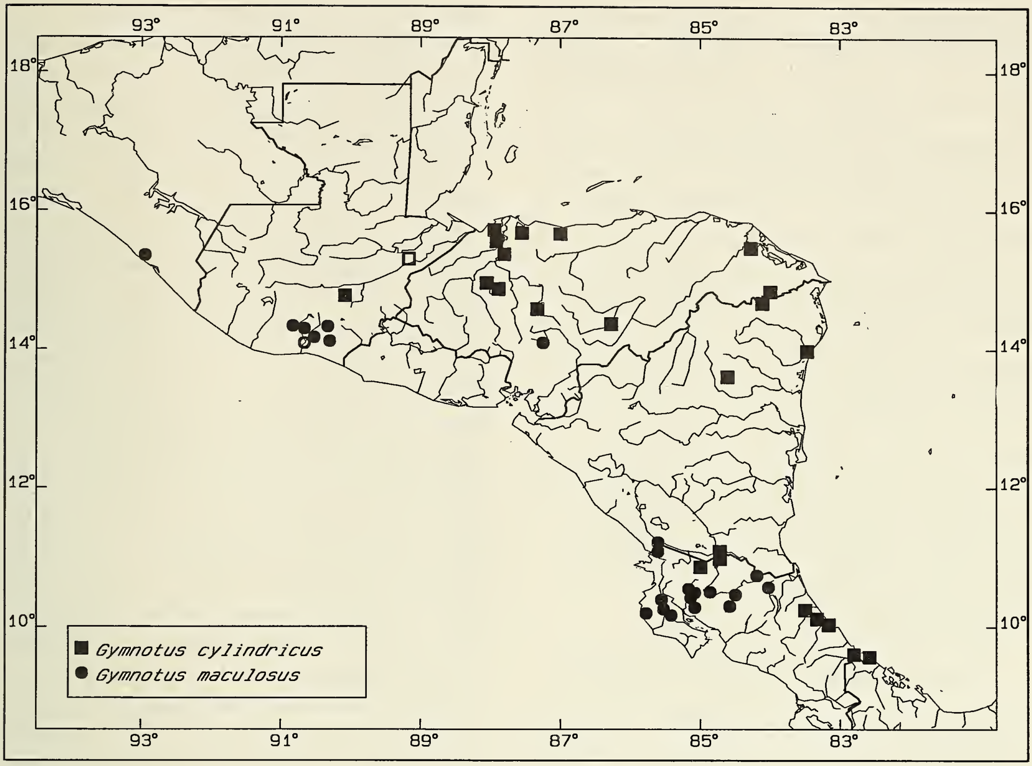

Fig. 7. Geographic distribution of the two Middle American species of *Gymnotus*. Type localities indicated by hollow symbols. The absence of *G. maculosus* from the Pacific slope of El Salvador and Nicaragua is due to sampling bias.

Although color patterns are of use in identifying species of *Gymnotus,* certain aspects are variable (Nijssen & Isbrücker 1968, Mago-Leccia 1994). The trans-Andean specimens of *G. carapo,* for example, differ from other populations *G. carapo* in possessing narrow pale bands. This aspect of coloration is otherwise only observed in elongate, slender species of *Gymnotus* (see below). Another example of variable color pattern is *G. anguillaris* from the Lawa River, Suriname, which resemble *G. carapo* in their dusky brown ground color and in possessing more than 23 alternating pale and dark bands. The pale bands are narrower than the dark bands only on the posterior end of the body. Specimens of *G. anguillaris* from other localities, however, ranging from Guyana to Paraguay, more closely resemble the description of the type specimen in which the pale bands are more narrow along the entire length of the body (Hoedeman 1962a).

Comments on the interrelationships of Gymnotus.—Species diversity and systematics of the Gymnotoidei have received considerable attention in recent years (Mago-Leccia 1978, 1994; Lundberg and Mago-Leccia 1986; Triques 1993; Gayet et al. 1994; Alves-Gomes et al. 1995; Albert 1995). The results of Albert's (1995) study support Ellis's (1913) hypothesis that *Gymnotus* and *Electrophorus* form a monophyletic group, the Gymnotoidea (Gymnotoidei of Mago-Leccia 1978), which is itself the sister lineage to other gymnotoids (Albert 1995, fig. 1; Albert & Fink 1995, fig. 2). The Gymnotoidea is diagnosed by 14 characters. Gape large, extending to vertical through posterior nares; premaxilla large, articulating head of maxilla oriented anteriorly; lateral margin of premaxilla produced into a posterior process; ventral margin of descending maxillary blade with a sharp angle about two-thirds distance to its tip; base of lateral ethmoid narrow; cranial fontanels closed in adults; *m. adductor mandibulae* undivided bundle at origin; lateral portion of valvula cerebelli larger in cross sectional area than medial portion at isthmus; depression on dorsal surface of basihyal; ventral process of coracoid absent; anal-fin pterygiophores long, more than one-third total body depth; caudal fin or filament absent, caudal anal-fin rays extend to tip of tail; body cavity long, more than 30 precaudal vertebrae; posterior chamber of gas bladder elongate, passing between hemal arches of postcoelomic axial skeleton and musculature.

Although a formal hypothesis of relationships among species within *Gymnotus* is beyond the scope of this paper, the data used in this study may be used to divide *Gymnotus* into three species-groups, on the basis of color pattern and general body proportions. Because the characters used to recognize these species-groups are not polarized, the monophyly of these groups and their interrelationships are ambiguous.

One species-group is composed of elongate, slender species, with a BD less than 11% TL. Members of this group also possess a color pattern consisting of alternating dark and pale bands, in which the pale bands are narrower than the dark bands, and the dense brown or grey dark bands extend onto the dorsum. *Gymnotus anguillaris* is the most widely distributed member of this group and exhibits the greatest variation in these characters. Members of the second species-group have deeper bodies, with a BD greater than 11% TL, and the alternating bands of heavy and light pigmentation are of about equal width, grading to a dusky brown on the dorsum. This group includes the type species *G. carapo*. The third species-group is composed of the two exclusively Middle American species of *Gymnotus*. These species lack the oblique nonpigmented bands of South American *Gymnotus* species, and have a shorter body cavity (31–35 precaudal vertebrae), characteristics regarded to be relatively plesiomorphic among gymnotoids (Albert 1995).

Based on both phylogenetic and biogeographic considerations, the Gymnotidae can be presumed to have originated in South America (Lundberg 1993). There is no evidence, however, that the Middle American species of *Gymnotus* are derived from an extant South American congener. If the Middle American species-group were to be identified as the sister taxon to other species of *Gymnotus*, the presence of an elongate body cavity with more than 35 precaudal vertebrae, would be evidence for the monophyly of the *G. carapo* and *G. anguillaris* species-groups. Unfortunately, the polarity of body cavity length in *Gymnotus* is ambiguous. The immediate outgroup taxon, *Electrophorus*, does not possess caudal vertebrae at all; the body cavity and gas bladder extend to the caudal end of the animal, hemal spines do not form, and the hemal arches do not meet along the midline. The next outgroup is not elongate; species of *Sternopygus*, which retain a relatively plesiomorphic gymnotoid morphology, possess fewer precaudal vertebrae than any species of *Gymnotus*. In fact, the phylogenetic distribution of the number of precaudal vertebrae among extant gymnotoid taxa indicates that the plesiomorphic condition for the group is 17–19 (Albert 1995).

The polarity of oblique depigmented bands in *Gymnotus* is also ambiguous. Many rhamphichthyoid species possess alternating color bands, but these bands are vertical regions of pigment investing a nonpigmented background. Narrow bands are not present in *Electrophorus, Sternopygus*, or the plesiomorphic hypopomid *Hypopomus* (Albert 1995). Furthermore, the presumed absence of oblique bands in the Middle American species of *Gymnotus* is not entirely clear; the pattern of spots in some specimens of *G. maculosus* is somewhat similar to the oblique bands of other *Gymnotus,* in position, orientation, and number.

Biogeography of Middle American Gymnotus.—The geographic distribution of *Gymnotus* is discussed by Meek and Hildebrand (1913), Eigenmann & Fischer (1914), Martin (1972), Miller & Carr (1974), Villa (1982), and Bussing (1987). Eigenmann & Allen (1942) claimed a range from Costa Rica to the Río de la Plata. The northernmost record of a South American species of *Gymnotus,* as recognized here, is *G.* cf. *anguillaris* from Almirante on the Atlantic slope of Panamá (Behre 1928, Hildebrand 1938, see Appendix), located about 170 km south of the southern limit of *G. cylindricus* at Tortuguero, Sixaloa, Costa Rica (Gilbert & Kelso 1971). The northern limit of *G. carapo* on the pacific slope is from Pizarro, Choco, Colombia. No references were found for the presence of *G. carapo* from the Río Tuira or elsewhere in Panamá.

The two species of *Gymnotus* limited to Middle America come into closest contact in small streams on opposite sides of Lake Nicaragua, and in several tributaries of the Río San Juan in Northern Costa Rica, an Atlantic drainage. The presence of *G. maculosus* in these localities may have resulted from stream capture due to tectonic uplift of the region in the past several million years (Durham 1944; Miller 1950, 1986). Geologic evidence for the uplift of the Nicaraguan graben is discussed by Riedel (1972).

The parapatric distribution of species of *Gymnotus* is similar to that of some other fishes in the lake Nicaragua basin. The shad *Dorosoma chavesi,* the poeciliid *Poeciliopsis* cf. *turrubarensis,* and the gar *Atractosteus tropicus* found in this basin are otherwise only known from Pacific-slope drainages. A second species of poeciliid recorded from the Lake Nicaragua basin, *P.* cf. *gracilis,* also occurs on the Atlantic slope in southern Mexico and in the Río Motagua of Guatemala. The sawfish *Pristis pectinata,* and the tarpon *Tarpon atlantiicus,* both found in Lake Nicaragua, are confined to the Atlantic basin.

Key to adults of species of *Gymnotus*

(HL greater than 10 mm)

1a. No oblique bands on body; body cavity with 31–35 (mode = 32) precaudal vertebrae 2

1b. Alternating bands of dark and pale pigmentation arranged at an oblique angle along length of body; body cavity with 36–51 precaudal vertebrae 3

2a. Numerous small brown spots on body; eyes set close together, interorbital distance 37–41% HL; scales above lateral line large, 6–8 rows at midbody . . . . *Gymnotus maculosus,* n. sp.

2b. Few if any spots on body; eyes set apart, interorbital distance 41–46% HL; scales above lateral line small, 10–12 rows at midbody . . . . *Gymnotus cylindricus* LaMonte

3a. Body deep, depth at anal-fin origin more than about 9% TL (except *G. pantherinus*); alternating dark and pale oblique bands of equal width at midbody, or pale bands broader; ground color dusky brown on dorsum; anal fin hyaline posteriorly 4

3b. Body slender, depth at anal-fin origin less than about 9% TL; dark oblique bands broader than pale bands at midbody; ground color dark brown or dark grey on dorsum; anal fin pigmented posteriorly 6

4a. Head long, HL greater than about 11% TL for specimens 100–250 mm TL); no spots on body, dark oblique bands uninterrupted; pigment density in middle part of dark bands less dense than near margins; bands present on anterior portion of body . . *Gymnotus carapo* (Linneus)

4b. Head short, HL less than about 11% TL; spots on head and back, dorsal part of dark oblique bands interrupted; dark oblique bands of uniform pigment density; bands not present on anterior half of body in specimens larger than 220 mm TL 5

5a. Body deep, BD greater than 9% TL . *Gymnotus inaequilabiatus* (Valenciennes)
5b. Body shallow, BD less than 9% TL .... *Gymnotus pantherinus* (Steindachner)
6a. Eyes set further apart, IO 39–44% HL; nape dark, pale bands not extending above lateral line on anterior half of the body .. *Gymnotus anguillaris* Hoedeman
6b. Eyes set closer together, IO 25–38% HL (except some *G. cataniapo*); white band at nape, pale bands extending to dorsal midline on anterior half of body 7
7a. 13–23 oblique bands; pectoral fin longer, 38–54% HL 8
7b. 23–50 oblique bands; pectoral fin shorter, 28–37% HL 9
8a. Body cavity shorter, 40–42 precaudal vertebrae; alternate pale bands incomplete .... *Gymnotus coatesi* LaMonte
8b. Body cavity longer, 47–48 precaudal vertebrae; all pale bands complete ..... *Gymnotus stenoleucus* Mago-Leccia
9a. Head shorter, HL 8–10% TL; body cavity shorter, 50–51 precaudal vertebrae; posterior end of anal fin dark .... *Gymnotus cataniapo* Mago-Leccia
9b. Head longer, HL 12–14% TL; body cavity shorter, 36–37 precaudal vertebrae; posterior end of anal fin pale .... *Gymnotus pedanopterus* Mago-Leccia

Acknowledgments

William Bussing, David Catania, Mary Anne Rogers, Bill Saul, and Richard Vari provided many specimens used in this study. Sara Fink helped interpret the morphology of the ethmoid region. Tamaki Yuri helped with construction of the key. Ricardo Campos-da-Paz and John Sullivan provided useful comments on the characters. William Bussing, John Lundberg, and Richard Vari made many useful suggestions on earlier drafts of the manuscript. We thank the Smithsonian Institution photographic laboratory for the photograph reproduced in Fig. 1, and Margaret Van Bolt who retouched the background. Brian Dyer provided the Spanish abstract. We acknowledge the NEODAT project (NSF/AID DEB grant 90-24797) for collection information. We thank Doug Nelson for curatorial assistance, and the Secretaría, Departamento de Pesca, for permission to collect in Mexico. Part of the research reported was conducted in facilities provided by NSF grant BSR 9015158 to Willim Fink.

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Appendix 1

List of 125 lots containing 698 specimens of gymnotids examined. Data are arranged by country, then alphabetically by museum acronym and number. Catalogue numbers are followed in parentheses by number of specimens, and then by locality, size range in millimeters total length (mm), and date of capture.

Gymnotus anguillaris.—Guyana: FAU uncat. (2), Madewini River, 132–165 mm, 1994.IV.20. Paraguay: UMMZ 206080 (21), Arroyo in Parque Nacional Ybycui, 82–260 mm, 1979.VI.20. Suriname: UMMZ 190413 (6), Maka Creek, Lawa River, Morowyne, 1967.IV.21. ZMA 100338 (2), Coropina Creek, 228–236 mm, 1956.V.20.

Gymnotus cf. *anguillaris.*—Panama: CAS 72209 (2), small creek into Río Cricamola, behind Konkintu, Boca del Toro Province, 225–239 mm, 1923.II.25.

Gymnotus carapo.—Bolivia: UMMZ 066433 (2), Lake Rogoagua, Río Beni, 214–338 mm, 1921.IX. UMMZ 066462 (2), Reyes, Río Beni, 205–245 mm, 1921.IX. UMMZ 204299 (1), Costa Marquez, Río Itenez (Guapore), Madeira, 164 mm, 1964.IX.02. UMMZ 204771 (5), Costa Marquez, Río Itenez, 44–51 mm, 1964.X.1. UMMZ 204886 (3), Río Baures, Río Itenez, 145–345 mm, 1964.X.7. Brazil: UMMZ 143282 (2), Lagoa dos Quadros, Rio Grande do Sul, Tramandai, 55–129 mm, 1941.VIII. UMMZ 230732 (2), Aggassiz collections, presumably Brazil, 174–202 mm, Acc. 1876.V.9. UMMZ 230734 (2), Rio Cayari near Benjamin Constant, Amazonas, 190–210 mm, 1993.V.11. USNM 199215 (1), Upper Yuruena, Mato Grosso, 85 mm, 1964.VII.20. USNM 199219 (2), Upper Yuruena, Mato Grosso, 1965.IV.9. Colombia: CAS 072192 (2), Río Sucio, Río Truando, Río Atrato, 150–179 mm, 1913. FMNH 56793 (2), mouth of Río Calima, Río Atrato, 1913. FMNH 56794 (2), Río Sucio, Río Truando, Río Atrato, 174–175 mm, 1913. FMNH 70511 (5), Pizarro, Choco, Pacific drainage, 124–247 mm, 1945.IX. Perú: UMMZ 072636 (2), Yurimaguas, Río Maranon, 148–214 mm, 1920.IX. UMMZ 230733 (1), Quebrada near Buen Sucesso, Rio Javari, Loreto, 250 mm, 1993.V.15. UMMZ 228998 (2), Río Momon, near Iquitos, Río Nanay, Loreto, 38–172 mm, 1993.V.5. UMMZ 228999 (1), Río Tapira, Río Tahuayo, Loreto, 161 mm, 1993.V.7. Suriname: UMMZ 187499 (1), Brokopondo, 195 mm, 1966.IX.15. UMMZ 190414 (6), Brokopondo, 71–225 mm, 1966.IX.15. ZMA 100409 (1), Aloike, Litany River, 71 mm, 1957.XI.27. ZMA 100430 (1), Ile de Cayenne, 305 mm, 1957.X.6. ZMA 100434 (2), Degrad Cacao, 190–255 mm, 1957.XI.10. ZMA 100439 (1), 256 mm, 1957.X.5. Trinidad: UMMZ 169080 (2), Gunupia, Mt. Plaisance, 46–74 mm, 1953.III.12. Venezuela: UMMZ 212345 (1), Esteros de Camaguan, Guarico, Apure, 45 mm, 1981.VIII. UMMZ 214766 (1), Caño Falcón, Portuguesa, 241 mm, 1987.II.19.

Gymnotus cataniapo.—Venezuela: MBUCV-V-14154 (3), caño near Salto Nieve, Río Orinoco, 75–194 mm, 1983.XII.22. MBUCV-V-14300 (1), Caño Merete, Río Casiquiare, 213 mm, 1984.VIII.20. MBUCV-V-14736 (1), San Carlos de Río Negro, Río Orinoco, 253 mm, 1984.X.4. MCUCV-V-14757 (1), Caño Guayabal, near Puerto Ayacuchu, Río Orinoco, 114 mm, 1984.XII.12. MBUCV-V-14781 (15), Caño Las Pevas, Río Casiquiare, 143–316 mm, 1984.VIII.2.

Gymnotus coatesi.—Bolivia: UMMZ 205149 (7), near Guayaramerin, Arroyo Grande, 45–175 mm, 1964.X.23. Paraguay: UMMZ 206155 (2), near San Rafael, Arroyo Tembley, 194–225 mm, 1979.VI.26. Perú: UMMZ 224596 (10), Buen Sucesso, Rio Javari, Loreto, 45–167 mm, 1993.V.15. UMMZ 224599 (2), Quebrada near Buen Sucesso, Rio Javari, Loreto, 1993.V.15. UMMZ 224601 (1), caño near Santa Ana, Río Tahwayo, Loreto, 1993.V.4. UMMZ 224607 (6), near Iquitos, Río Nanay, 30–144 mm, 1993.V.4.

Gymnotus cylindricus.—Costa Rica: UCR 1014-1 (12), Río Escondido, Limon, Río Sixaola, 123–249 mm, 1976.IX..17. UCR 280-2 (3), Río Escondido, Limon, Río Sixaola, 1968.X.3. UMMZ 224129 (10), Río Escondido, Limon, Río Sixaola, 131–205 mm, 1968.X.3. Guatemala: UMMZ 193873 (2), el Progresso, Morazán, Río Yeguare, 192–210 mm, 1973.III.24. UMMZ 193986 (14), Quebrada de Vegega, Los Amates, Río Izabal, 26–183 mm, 1973.IV.5. Honduras: UMMZ 155831 (1), bridge on Tegucigalpa-Danli road, Río Yeguare, 174 mm, 1948.I.30. UMMZ 155832 (2), Quebrada near Los Flores, Río Yeguare, 161–204 mm, 1947.VII.23. UMMZ 188110 (2), Pito Solo, Cortez, Río Jaitique, 93–191 mm, 1948.V.23. UMMZ 188273 (1), Lago Yoyoa, Santa Barbara, Río Yeguare, 135 mm, 1949.VIII.1. UMMZ 188274 (5), Lago Yojoa, Santa Barbara, Río Yeguare, 97–175 mm, 1948.IV.14. UMMZ 188275 (16), Lago Yojoa, Río Yeguare, 166–224 mm, 1949.VIII.10. UMMZ 188296 (2), Quebrada Lagunita, Morazán, Río Yeguare, 120–138 mm, 1947.VII.29. UMMZ 188297 (5) Quebrada behind finca de Rudolfo Rosales, Río Yeguare, 69–129 mm, 1947.XI. UMMZ 199598 (1), Laguna Sikalanka, Río Sucre, 215 mm, 1975.V.11. Nicaragua: CAS 161383 (3), Rio Frio, about 1.5 mi. above San Carlos, in bayou with sluggish current, Lago Nicuaragua drainage, Río San Juan state, 1963.II.12. TU uncat. (1), San Carlos, Lago Nicuaragua drainage, Río San Juan state. UMMZ 199622 (13), SE of Bilwaskarma, Río Kurnog, 1975.V.13. UMMZ 199633 (2), Río Putkrukira near Waspán, Río Coco, 121–194 mm, 1975.V.27.

Gymnotus inaequilabeatus.—Brazil: USNM 1643 (1), Río Paraguay, 791 mm. USNM 1644 (1), Río Paraguay. USNM 1645 (1), Río Paraguay. Paraguay: UMMZ 206939 (1), near Pto. Stroessner, Arroyo Venecia, 154 mm, 1979.VIII.5. UMMZ 206703 (4), Pedro Juan Caballero, Paraná, 113–280 mm, 1979.VI.24. UMMZ 206971 (2), Estancia la Golondrina, Presidente Hayes, Confuso, 255–261 mm, 1979.VIII. UMMZ 207025 (17), marsh 34 km N.W. Pt. Remaro bridge, Río Confuso, 485 mm, 1979.VIII.9. UMMZ 207096 (3), Estancia la Golondrina, Presidente Hayes, Confuso, 132–210 mm, 1979.VIII. UMMZ 207564 (2), Río Pilcomayo near Peurto Falcón, Río Paraguay, 220–242 mm, 1979.VIII.29. UMMZ 207619 (1), Riachúelo Pilco, Presidente Hayes, 144 mm, 1979.VIII.31. UMMZ 207760 (2), Arroyo Peguajho, Ypane, 77 mm, 1979.IX.04. UMMZ 207893 (6), Río Aequidaban near Paso Hasqueta, Río Paraná, 16–390 mm, 1979.IX.6.UMMZ 215183 (1), Estancia la Golondrina, Presidente Hayes, Confuso, 170 mm, 1981.X.02. UMMZ 216576 (1), Estancia la Golondrina, Presidente Hayes, Río Confuso, 322 mm, 1981.X.02. UMMZ 216576 (1), near Trans Chaco-Villa, Presedente Hayes, 322 mm, 1981.X.2.

Gymnotus maculosus.—Costa Rica: TU 24935 (16), La Virgin, Río Sarapiqui, 1960.II.22. TU 25063 (3), Río Tempisque, near Liberia, Guanacaste, 193–218 mm, 1961.I.21. UCR 969-9 (20), Santa Cruz, Río Garzón, Guanacaste, 123–195 mm, 1976.I.25. UCR 980-9 (5), Arenal, Río Dos Bocas, Guanacaste, Río San Carlos drainage, 1968.VI.10. UMMZ 158451 (1), Finca la Trinidad, Guanacaste, 179 mm, 1949.X.21. UMMZ 224128 (5), Río Higuerón, near Canas, Guanacaste, 158–222 mm, 1968.VI.10. Guatemala: UMMZ 188072 (1), Río Bravo, Río Nahualate, 1968.IV.3. UMMZ 190531 (7), El Obraje, Jutiapa, Río Grande de Pasaco, 146–200 mm, 1971.III.9. UMMZ 190783 (3, paratypes), diversion of channel from Rio María Linda, 20 km East of Escuintla, Departamento Santa Rosa, 176–203 mm, 1971.III.27. UMMZ 194122 (6), 2.6 km ESE Eca Cocales, Río La Primavera, 105–135 mm, 1973.IV.20. UMMZ 194150 (2), Río Siguacan, near Escuintla, Santa Rosa, 141–172 mm, 1973.IV.24. UMMZ 197103 (17), near Taxisco, Santa Rosa, 1974.IV.26. UMMZ 197103 (20), Taxisco, Santa Rosa, 78–227 mm, 1974.IV.6. UMMZ 230354 (20, paratypes), Río Buena Vista, trib. of Río Tigre, on road between Escuintla and Chiquimulilla, 8 km West of Pajal, Departamento Santa Rosa, Guatemala, 128–230 mm, 1946.IV.18. UMMZ 230830, (1, holotype), diversion of channel from Rio María Linda, 20 km East of Escuintla, Departamento Santa Rosa, 191 mm, 1971.III.27. USNM 114235 (2), Río Colojate, 1947. USNM 114539 (22), near Malacatan, Río Gramal, 1956.VII.6. USNM 134700 (49, paratypes), near Pajal, Río Buen Vista, 138–226 mm, 1946.IV.18. USNM 225435 (1), Río Chiquimulilla, 1946. USNM uncat. Río Hondo, 1946. USNM uncat. (8), Río Lato, 1946. USNM uncat. (23), Río Grammal, 1947. Mexico: UMMZ 191702 (2), Tapachula, Río San Nicolás, Chiapas, 163–189 mm, 1971.III.13. UMMZ 191712 (3), Tapachula, Río San Nicolás, Chiapas, 184-228, 1971.II.27. Nicaragua: TU 24965 (38, paratypes), Boca de Río Sapoá, Sapoá, Lago Nicaragua drainage, Rivas Province, 1960.IV.23. TU 25032 (1), Boca de Río Sapoá, Sapoá, Lago Nicaragua drainage, Rivas Province, 43 mm, 1961.I.21.

Gymnotus n. sp. N.—Ecuador: FMNH uncat. (46), Aguarico, Río Napo, 1983.XI.21.

Gymnotus pantherinus.—Brazil: USMN 297933 (20), Naneia, São Paulo, 1988.ii.21. USMN 297939 (12), Guaratuba, Río da Praia, 1988.X.3.

Gymnotus pedanopterus.—Venezuela: MBUCV-V-14737 (2), Caño Chola, near San Carlos de Río Negro, Río Casiquiare, 198–228 mm, 1984.XI. MBUCV-V-

14738 (1), Caño Temblador, Río Casiquiare, 215 mm, 1984.XII.5. MBUCV-V-4860 (1), Caño Esmeralda, Río Orinoco, 281 mm, 1966.XI.6. MBUCV-V-7135 (2), El Pozo de Lucas, near San Fernando de Atabapo, Río Orinoco, 109–119 mm, 1973. MBUCV-V-7310 (3), caño near San Fernando de Atabapo, Río Orinoco, 92–185 mm, 1972.IV.14.

Gymnotus stenoleucus.—Venezuela: MBUCV-V-14028 (15), Río Cataniapo, Río Orinoco, 80–171 mm, 1983.III.30. MBUCV-V-14747 (1), Caño Guayabal, near Peurto Ayacuchu, Río Orinoco, 140 mm, 1984.XII.12. MBUCV-V-4644 (2), Río Quiritare, Río Orinoco, 91–95 mm, 1966.X.30. MBUCV-V-6218 (1), Caño Caripo, Río Casiquiare, 140 mm, 1969.I.26. MBUCV-V-9417 (4), Caño Caripo, Río Casiquiare, 91–142 mm, 1969.I.26.

Electrophorus electricus.—Aquarium: UMMZ 183710-S (1), 100 mm+, 1961.VII.1. Bolivia: UMMZ 204426-S (2), Costa Marques, Rio Itenez, Rio Madeira, 940 mm, 1964.IX.12. Guyana: USNM 228883 (3), Essequibo River. UMMZ uncat. (1), 1000+ mm, 1992.XII.12. Suriname: USNM 225669 (1), Amotopa landing, Nickerie District, Rio Corantijn, 511 mm, 1980.VII.19.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):679–686. 1995

A new species of the genus *Bryconamericus* Eigenmann, 1907 from southern Brazil (Ostariophysi: Characidae)

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Abstract.—A new characid species, *Bryconamericus lambari,* is described from Southern Brazil. This fish is known only from the arroio Feitoria, a small and rocky mountain tributary of the rio Caí, laguna dos Patos drainage, from município de Dois Irmãos, Rio Grande do Sul, Brazil. The identities of other *Bryconamericus* species described from southern South America are briefly discussed. *Bryconamericus boops* is considered a junior synonym of *B. iheringii* and a lectotype is designated for *Tetragonopterus iheringii.*

Resumo.—*Bryconamericus lambari,* espécie nova, é descrita para o sul do Brasil. A espécie é conhecida somente do arroio Feitoria, um pequeno arroio tributário do rio Caí, sistema da laguna dos Patos, município de Dois Irmãos. A identidade de outras espécies do gênero *Bryconamericus* descritas para o Sul da América do Sul é discutida. *Bryconamericus boops* é considerado sinônimo de *B. iheringii.* É designado o lectótipo de *Tetragonopterus iheringii.*

The characid genus *Bryconamericus* Eigenmann (*in* Eigenmann, McAtee & Ward, 1907) comprises 30–40 species distributed through freshwater basins of South and Central America (Géry 1977). The current definition of the genus follows Eigenmann (1927), who included in *Bryconamericus* all characid fishes that possesses a single row of teeth on the dentary, two rows of teeth on the premaxilla with four teeth in the inner series, a low number of teeth along the anterior margin of the maxilla, a lack of scales on the caudal fin, a large third infraorbital contacting the preopercle along its posterior and ventral margins, setiform gillrakers, a complete laterosensory canal system on the body, and the absence of a glandular pouch on the caudal fin in males, as recently summarized by Vari & Siebert (1990:517). The naturalness of Eigenmann's genera have been long discussed by several authors and for *Bryconamericus* most recently by Fink (1976), Vari & Siebert (1990) and Malabarba & Malabarba (1994).

We here describe a new species, *Bryconamericus lambari,* from the laguna dos Patos drainage, Rio Grande do Sul, Brazil. We assign the new species to *Bryconamericus* because it has the combination of characters used by Eigenmann to define the genus. A phylogenetic study of the relationships of *Bryconamericus* species and a reconsideration of its monophyly are beyond the scope of this paper.

Type specimens of other southern South American species at present assigned to *Bryconamericus* were examined during this study. Comments about the identity of these species are provided.

Methods

Specimens examined belong to ANSP—Academy of Natural Sciences, Philadelphia;

BMNH—Natural History Museum, London; CAS—California Academy of Sciences, San Francisco; MAPA—Museu Anchieta, Porto Alegre; MCP—Museu de Ciências, now Museu de Ciências e Tecnologia, Pontificia Universidade Católica do Rio Grande do Sul, Porto Alegre; UFRGS—Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre; and USNM—National Museum of Natural History, Smithsonian Institution, Washington.

Counts and measurements follow Fink & Weitzman (1974), except for number of scale rows between lateral line and pelvic fin origin, counted from the scale row immediately ventral to lateral line to the scale row closest to the first pelvic-fin ray. Counts of vertebrae and procurrent rays of caudal fin were taken from radiographed and cleared and stained specimens. C&S indicates specimens cleared and stained for cartilage and bone according to the method of Taylor & Van Dyke (1985).

Bryconamericus lambari, new species
Fig. 1, Table 1

Bryconamericus sp.—Malabarba, 1989:131 (undescribed species from laguna dos Patos drainage).

Holotype.—MCP 15448 (55.9 mm SL, male), small creek flowing into arroio Feitoria, under bridge of avenida Ipiranga, município de Dois Irmãos, Rio Grande do Sul, Brazil, 51°07′S, 29°36′W, 4 December 1991, Eunice A. Isaia and Andreas Kindel.

Paratypes.—MCP 15449 (14 specimens, 41.4–56.3 mm SL), MCP 15450 (2 specimens C&S, 44.9–52.5 mm SL), USNM 324628 (3 specimens, 42.2–52.9 mm SL), collected with holotype. UFRGS 4539, (1 specimen, 38.5 mm SL), UFRGS 4513 (3 specimens, 50.5–63.5 mm SL), same locality as the holotype, 4 September 1991, Eunice A. Isaia and Andreas Kindel. UFRGS 1784 (2 specimens C&S and 5 specimens colored with alizarin only, 27.3–46.3 mm SL), arroio Feitoria, município de Dois Irmãos, Rio Grande do Sul, Brazil, Luiz R. Malabarba.

Diagnosis.—*Bryconamericus lambari*, new species, is distinguished from all other species assigned to *Bryconamericus* by a combination of the following characters: the total number of anal-fin rays (19–22); number of perforated scales along the lateral line (38–40); its elongated body with greatest depth 24.6–29.8% of standard length; lack of dark pigmentation on the distal tips of the caudal fin; 3 or 4 maxillary teeth; and 5 or 6 scale rows between the lateral line and dorsal-fin origin. *Bryconamericus lambari* is further distinguished from *B. iheringii* (Boulenger 1887), the second species of the genus found in the laguna dos Patos drainage (Malabarba 1989), by the shallower body depth and shorter pelvic fins (Tables. 1 & 2). *Bryconamericus lambari* is further distinguished from *B. stramineus* Eigenmann, 1908 described from the rio Uruguai drainage in its absence of a conspicuous and wide midlateral stripe (present in *B. stramineus*).

Description.—Body elongate, fusiform, laterally compressed. Greatest body depth anterior to or at dorsal-fin origin. Dorsal body profile convex from tip of supraoccipital to dorsal-fin origin; nearly straight from base of last dorsal-fin ray to caudal peduncle. Ventral body profile convex from tip of lower jaw to anal-fin origin; nearly straight or slightly concave along anal-fin base. Dorsal and ventral profiles of caudal peduncle slightly concave.

Snout deeply rounded from margin of upper lip to vertical line through anterior nostrils. Mouth slightly inferior. Maxilla short, reaching vertical line through anterior border of eye. Ventral profile of head gently convex.

Dentary with 4 large teeth, each with 5 cusps, median cusp distinctly larger; followed by smaller teeth (3 or 4 teeth counted in cleared and stained specimens) either with 3–5 cusps or conical. Premaxilla with two tooth rows. Outer row with 3 or 4 (usually 3) teeth, each tooth with 3–5 cusps.

Table 1.—Morphometric data of *Bryconamericus lambari,* new species. Standard length in mm, measurements numbered 2–11 as percents of standard length and 12–14 as percents of head length. Data of the smallest paratype (UFRGS 1784—27.3 mm SL) and of UFRGS 4539 paratype not included.

Character	Holotype	*n*	Range	$\bar{X}$
1 Standard length	55.9	28	30.9–63.5	45.6
2 Predorsal distance	52.6	28	49.1–55.0	51.4
3 Prepelvic distance	45.4	28	43.8–48.4	45.5
4 Anal-fin base	22.9	28	21.0–26.0	23.1
5 Caudal peduncle length	17.2	27	16.1–18.3	17.1
6 Caudal peduncle depth	10.9	28	10.2–11.4	10.8
7 Body depth at dorsal-fin	27.6	28	24.6–29.8	26.9
8 Dorsal–fin length	20.8	24	20.0–24.2	21.8
9 Pelvic–fin length	12.7	28	12.1–15.1	13.4
10 Pectoral fin length	17.7	28	16.6–21.1	18.6
11 Head length	22.7	28	21.2–26.3	23.2
12 Upper jaw length	36.2	28	29.4–37.4	33.9
13 Orbital diameter	37.8	28	36.0–44.2	38.7
14 Interorbital width	33.9	28	27.1–35.5	31.2

Table 2.—Morphometric (1–14) and meristic (15–25) data of the type specimens of *Tetragonopterus iheringii* (A—lectotype—BMNH 1886.3.15.30, and 4 paralectotypes—BMNH 1886.3.15.31-34), *Tetragonopterus pliodus* (B) *Astyanax eigenmanni* (C) and *Bryconamericus boops* (D). Standard length in mm; measurements numbered 2–11 as percents of standard length and 12–14 as percents of head length.

Character	Lecto-type	A range	$\bar{X}$	B	C	D
1 Standard length	64.7	48.8–66.8	58.1	55.9	61.1	59.2
2 Predorsal distance	54.6	55.5–56.8	55.9	49.0	49.8	50.1
3 Prepelvic distance	47.0	46.8–48.0	47.4	46.9	44.3	45.7
4 Anal-fin base	24.4	20.1–23.4	22.1	22.7	23.2	28.5
5 Caudal peduncle length	14.5	14.6–16.0	15.3	14.5	16.7	16.3
6 Caudal peduncle depth	12.9	11.3–12.6	11.7	11.6	13.2	9.8
7 Body depth at dorsal-fin	39.1	32.7–38.1	35.6	34.0	31.2	27.8
8 Dorsal-fin length	25.0	22.7–25.8	24.2	23.6	22.1	23.3
9 Pelvic-fin length	16.5	15.4–18.0	17.2	16.5	16.5	16.6
10 Pectoral-fin length	22.1	19.8–21.7	20.8	20.8	21.1	22.6
11 Head length	24.1	23.1–25.4	23.8	23.1	23.6	23.7
12 Upper jaw length	32.4	33.8–34.7	34.2	35.7	31.3	29.3
13 Orbital diameter	35.6	34.0–38.3	36.3	38.0	30.6	38.7
14 Interorbital width	33.1	31.3–34.5	32.7	33.3	33.3	33.8
15 Unbranched anal fin rays	3	3	3.0	3	3	3
16 Branched anal–fin rays	17	15–17	16.0	17	15	19
17 Dorsal–fin rays	10	10	10.0	10	9	11
18 Pelvic–fin rays	8	8	8.0	8/9	8	8
19 Pectoral–fin rays	12	12	12.0	13	12	13
20 Caudal–fin rays	19	19	19.0	19	19	NC
21 Perforated lateral line scales	37	37–38	37.3	38	38	38
22 Scale rows between lateral line and dorsal fin	6	5–6	5.3	5	5	5
23 Scale rows between lateral line and anal fin	3	3	3.0	3	3	4
24 Predorsal scales	12	11–13	12.0	12	12	12
25 Scale rows around caudal peduncle	14	14	14.0	14	14	14

Fig. 1. Holotype of *Bryconamericus lambari*, new species (MCP 15448, male, 55.9 mm SL).

Four teeth in the inner row, all with 5 cusps, except medial tooth with 4 cusps. Maxilla with 3 or 4 teeth with 3–5 cusps; teeth gradually becoming smaller posteriorly. All maxillary teeth with median cusp distinctly larger.

Dorsal-fin rays ii, 8; tip not reaching adipose fin when fin depressed. Posterior border of dorsal fin straight, perpendicular to body margin when fin erect. Adipose fin present. Caudal fin forked, lobes equal in size, rounded; 8–11 procurrent rays dorsally and ventrally.

Anal-fin rays iii–iv, 14–19 (usually 15–18). Distal margin of anal fin concave with the 6 anterior branched fin-rays longest and gradually decreasing in size posteriorly. Anal-fin origin along vertical line through base of last dorsal-fin ray. Anal fin of males bearing bony hooks from last unbranched ray to 11th branched ray in some individuals, usually reaching the 5th branched ray. Anal-fin rays with 1 pair of hooks per segment, hooks present in posterolateral surface of ray and only caudal branch of each anal-fin branched ray that bears hooks. Hooks retrorse, curved towards ray base. Hooks typically present on up to 10 segments of anterior anal-fin rays; number progressively reduced posteriorly, with hooks on only one segment on last anal-fin ray that bears hooks.

Pectoral-fin rays i, 11–12 (i, 14 in one specimen). Pectoral fin rounded; tip of fin not reaching pelvic-fin origin. Pelvic-fin rays i, 6–7 (i, 6 in only one specimen). Pelvic-fin margin rounded distally, not reaching anal-fin origin. Pelvic-fin rays of males with ventromedial retrorse bony hooks. Hooks present on all branched rays but absent on unbranched ray. Usually 1 pair of slender, long hooks per segment along medial branch and most of their lengths. Hooks also present on other branches of third to fifth rays.

Scales cycloid. Caudal fin without scales. Single row of 4–7 scales on base of anterior 4–7 branched anal-fin rays. Lateral line complete with 38–40 perforated scales. Scale rows between dorsal-fin origin and lateral line 5–6; scale rows between lateral line and pelvic-fin origin 4–5. Predorsal scales 11–14, usually in regular series. Scale rows around caudal peduncle 14. Precaudal vertebrae 16–18; caudal vertebrae 20–22.

Color in alcohol.—Ground color yellowish. Dark midlateral horizontal stripe indis-

Figs. 2–4. 2, Lectotype of *Tetragonopterus iheringii* Boulenger, 1887 (BMNH 1886.3.15.30, male, 64.7 mm SL); 3, Holotype of *Astyanax eigenmanni* Evermann & Kendall, 1906 (USNM 55570, male, 61.1 mm SL); 4, Holotype of *Bryconamericus boops* Eigenmann, 1927 (MCZ 20700, male, 59.2 mm SL).

tinct anteriorly but becoming well defined posterior to vertical line through dorsal-fin origin. Caudal peduncle without a well defined spot. Scattered chromatophores on posterior border of scales. Pigmentation most intense on dorsal portions of head and above midlateral stripe on body. Humeral spot roundish and well defined, centered on fourth to sixth scales of scale row just dorsal to lateral line.

Sexual dimorphism.—Males of *B. lambari* are easily recognized by presence of bony hooks on anal and pelvic fins.

Etymology.—The species name, lambari, refers to the common name of small characids in southern Brazil.

Distribution.—Despite extensive collections that have been made in several tributaries of laguna dos Patos drainage, *B. lambari* have been found only in the type basin: the arroio Feitoria and tributaries, rio Caí drainage, laguna dos Patos drainage, Rio Grande do Sul, Brazil. Additional collections were also made in other tributaries of rio Caí to determine whether the species also ocurred elsewhere in the basin, but no additional specimens were collected. These other localities are inhabited by *B. iheringii,* which occurrs in the same drainage, but was never found syntopic with *B. lambari.* We cannot explain this peculiar distribution.

Ecology.—All specimens of *B. lambari* were collected in a small sandy and rock bottomed river in the Serra Geral formation of Rio Grande do Sul, Brazil. Although the river consists mainly of rapids, the specimens were caught in areas of low current flow.

Discussion

We examined and compared the type specimens of four species of *Bryconamericus* described from South Brazil, Uruguay and Argentina. *Tetragonopterus iheringii* Boulenger (1887:172–173), with *Tetragonopterus pliodus* Cope (1894:90–91) as a junior synonym, were both described based on specimens originating in laguna dos Patos tributaries, Rio Grande do Sul, Brazil. *Astyanax eigenmanni* Evermann & Kendall (1906:83) was described from the lower rio Paraná, Argentina, and *Bryconamericus boops* Eigenmann (1927:371) was described from a small coastal drainage at Maldonado, Uruguay.

All these species, now assigned to *Bryconamericus,* are deep bodied fishes, and clearly differ from *B. lambari* in body shape and greatest body depth (Figs. 1–4, Tables 1 & 2). However, we found no differences in examined features that clearly permit the recognition of multiple deep bodied *Bryconamericus* species in the region (Table 2). The differences found among the type specimens fall within the range of what we identify as *B. iheringii,* when comparing different samples of that species from several laguna dos Patos tributaries.

Eigenmann (1927:377) previously placed *Tetragonopterus pliodus* as a junior synonym of *B. iheringii,* both species having been described from the same drainage. We follow Eigenmann in maintaining *Tetragonopterus pliodus* as a junior synonym of *B. iheringii.* Eigenmann (1927:380) also pointed out the close similarity of *B. eigenmanni* and *B. iheringii,* but retained both as valid species. The holotype of *B. eigenmanni* presents no clear differences in counts and measurements to *B. iheringii* (Table 2), but we also keep both as valid species. We suggest that a useful comparison needs an in depth statistical study of good population samples from the areas of distribution of both nominal species and the only material we examined from lower rio Paraná was the holotype of *B. eigenmanni.*

The type specimen of *B. boops* (Fig. 4) is an abnormal specimen as was already noted by Géry (1977:390), who nonetheless retained it as a valid species. The measurements presented in Table 2 for *B. boops* are not comparable to the other species. We have found no specimens at the type locality of this species with such a profile presented by the holotype, but rather found only specimens refereable to *B. iheringii.* We propose *B. boops* as a junior synonym of *B. iheringii,* hypothesizing that the holotype of *B. boops* is a deformed specimen of *B. iheringii.*

Comparative material:

Bryconamericus iheringii: BMNH 1886.3.15.30 (*Tetragonopterus Iheringii*

Boulenger, 1887—Lectotype by present designation—64.7 mm SL, male), São Lourenço, Rio Grande do Sul state, Brazil, H. von Ihering. BMNH 1886.3.15.31-34 (*Tetragonopterus Iheringii* Boulenger, 1887—paralectotypes, 11 ex., 48.8–66.8 mm SL, five males and six females), collected with the lectotype. ANSP 21578 (*Tetragonopterus pliodus* Cope, 1894—holotype, 55.9 mm SL, female?), Rio Grande do Sul, Brazil, H. H. Smith (type locality restricted to laguna dos Patos drainage by Malabarba, 1989:120–121, 131). MCZ 20700 (*Bryconamericus boops* Eigenmann, 1927—holotype, 59.2 mm SL), Maldonado, Uruguai, T. G. Cary. Rio Grande do Sul, Brazil: MCP 10074 (57 ex.) Barragem Ernestina, rio Jacui, 16 November 1983, C. A. S. Lucena & L. R. Malabarba. MCP 8430 (33 ex.), açude Garcia, km 56 of road BR 116, Barra do Ribeiro, 18 June 1985, C. A. S. Lucena & R. E. Reis. MCP 11446 (133 ex.), rio Camaquã e poças laterais, Camaquã, 5 May 1987, C. A. S. Lucena, L. R. Malabarba & E. Pereira. MCP 11492 (19 ex.), arroio Chasqueiro, BR 116, between Pelotas and Jaguarão, Arroio Grande, 9 January 1987, C. A. S. Lucena, A. Bergmann & P. Azevedo. UFRGS 2874 (4 ex.), UFRGS 710 (2 ex.), Estação Ecológica do Taim, Rio Grande, 7–8 May 1981, R. E. Reis & J. R. Stehmann. MCP 11264 (176 ex.), arroio Jaguarão, Passo do Centurião, Herval, 8–9 Jan 1987, R. E. Reis, P. Azevedo & I. Costa. Maldonado, Uruguai: MAPA 2056 (16 ex.), arroio Salso, Ruta 9, km 122, 12 Jan 1982, P. A. Buckup & R. E. Reis.

Bryconamericus eigenmanni: USNM 55570 (Holotype of *Astyanax eigenmanni* Everman & Kendal, 1906—61.1 mm SL, male), rio Primero, Cordoba, Argentina, 1903–1904, J. W. Jüteomb.

Bryconamericus stramineus: CAS 40833 (holotype, 39.5 mm SL, female?), Piracicaba, São Paulo, Brazil, R. von Ihering.

Acknowledgments

We are indebted to G. Howes, J. Chambers (BMNH), F. Meyer (MAPA) and K. Hartel (MCZ) for the loan of specimens; R. Vari and M. Weitzman (USNM) for permission to examine type specimens under their care and on loan (*B. stramineus* and *Tetragonopterus pliodus,* respectively). The photograph of the holotype of *B. boops* was taken by S. Weitzman. This work was supported by grants from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq—proc. 414067/90-0) and by a scholarship (CNPq—proc. 806.041-88.9) to Andreas Kindel. This paper was improved with comments from C. Lucena, R. Reis, Z. M. Lucena, R. Vari, S. Weitzman and an anonynous reviewer.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):687–694. 1995

Gobiodon acicularis, a new species of gobioid fish (Teleostei: Gobiidae) from Belau, Micronesia

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Abstract.—A new species of gobiid, *Gobiodon acicularis,* bearing an unusual, highly elongate first dorsal spine, is described. Other distinguishing characters, in combination, include lack of post-symphysial canine teeth in the lower jaw, high number of papillae on the dorsum, overall uniform pigmentation of head, body and fins, lack of an interopercle-isthmus groove and a narrow gill opening. The material forming the basis of the description was collected in Belau (Palau) in the 1950's. Available habitat data indicate that the species occurs in reef margin or lagoonal habitats.

The Indo-Pacific genus *Gobiodon* Bleeker, 1856, is a group of gobies that live as adults as obligate associates of corals of the genus *Acropora* (Patton 1994). The species, which reach up to about 40 mm SL, are characterized by a scaleless body covered by a thick mucus layer, a reduced head papillae pattern, and generally small jaw teeth with the exception of one or two pairs of well-developed canine teeth posterior to the dentary symphysis. *Gobiodon* appears to share with another hermaphroditic goby genus, *Paragobiodon,* an unusual and probably derived gonad structure (Cole 1990). *Pseudogobiodon* Bleeker, 1874, is similar to *Gobiodon* but the post-symphysial canine teeth are lacking in the only known species, *P. macrochir* Bleeker, 1875 (*Gobius citrinus* Rüppell, 1838, was erroneously ascribed to *Pseudogobiodon,* as the type species, by Bleeker 1874:309). Whether or not species lacking these canine teeth should be considered generically distinct from *Gobiodon* is a phylogenetic problem we hope to solve in the near future.

Many of the described species are brightly colored, often with distinctive body bars, spots and/or fin striping (see, for example, Akihito 1984:265–266, plate 246, F–P). *Gobiodon* has attracted considerable attention from systematists, resulting in more than 30 nominal species that can be attributed to it. Of these described species we currently recognize 14 as valid: *G. albofasciatus* Sawada & Arai, 1972; *G. axillaris* De Viz, 1884; *G. ceramensis* (Bleeker, 1852); *G. citrinus* (Rüppell, 1838); *G. fulvus* Herre, 1927; *G. heterospilos* Bleeker, 1856; *G. histrio* (Valenciennes, 1837); *G. micropus* Günther, 1861; *G. oculolineatus* Wu, 1979; *G. okinawae* Sawada et al., 1972; *G. quinquestrigatus* (Valenciennes, 1837); *G. reticulatus* Playfair, 1867; *G. rivulatus* (Rüppell, 1830) (not of Suzuki et al. 1995); and *G. unicolor* (Castelnau, 1873).

During our survey of collections of *Gobiodon* from throughout the Indo-Pacific region we found the present undescribed species in the collection of the California Academy of Sciences. Since this species so clearly differs from all other congeners, we have decided to describe it now, making its name available for other, planned papers on the genus.

Materials and Methods

Determination of meristic character values follows Hubbs & Lagler (1947), with exceptions given below. Osteological characters determined from three paratypes (ROM 1603CS, 27.2 mm SL ♂ and 31.3 mm SL ♀; CAS 81515, 34.0 mm SL ♀) cleared and stained following the method outlined by Potthoff (1984). Vertebral and caudal-fin ray counts were taken from radiographs. The last branched ray of the dorsal and anal fins is divided to its base and is counted as a single element. Caudal-fin ray counts are given as the number of segmented and unsegmented rays, as opposed to procurrent and principal rays (see Hoese & Gill 1993:419), and the number of unbranched and branched rays. First dorsal-fin pterygiophore formula follows Birdsong et al. (1988:175). Terminology for lateralis pores follows Lachner & Karnella (1980): AI, anterior interorbital; AO, anterior otic; IT, intertemporal; NA, nasal; PI, posterior interorbital; POP, preopercular; SO, superior otic. Meristic data are reported as the range with the value for the holotype underlined, followed, in parentheses, by the mean and number of specimens counted. Institutional abbreviations follow Leviton et al. (1985).

Morphometric measurements were made to the nearest 0.1 mm using digital calipers interfaced by a Smartcable (Gage Connections, Inc.) with the software DATAQ, version 1.02 (D. L. Schultz). Data were analyzed for univariate statistics using SAS (SAS Institute Inc.) for personal computers, version 6. Standard length (SL) was measured from the median point of the premaxillary groove (anteriormost point of snout) to midlateral base of caudal fin. Head length (HL) was measured from the snout tip to posteriormost position on opercular membrane. The following measurements are reported as percentages of either HL (measurements of the head) or SL (all others): snout to origin of first dorsal fin; origin of first dorsal fin to origin of second dorsal fin; origin of second dorsal fin to origin of anal fin; anterior base of pelvic spine (pelvic-fin origin) to origin of anal fin; snout to pelvic-fin origin; origin of first dorsal fin to pelvic-fin origin; origin of first dorsal fin to origin of anal fin; anterior base of pelvic spine to origin of second dorsal fin; pelvic-fin length, pelvic-fin origin to tip of longest ray; anal-fin length, anterior base of third branched ray to its tip; first dorsal-fin first spine length, anterior base of first spine of first dorsal fin to its tip; first dorsal-fin sixth spine length, anterior base of sixth spine of first dorsal fin to its tip; second dorsal-fin length, anterior base of first branched ray of second dorsal fin to its tip; pectoral-fin length, base of longest ray of pectoral fin to its tip; caudal peduncle length, anterior base of central caudal rays to posterior base of last ray (insertion) of anal fin; caudal-peduncle depth, insertion of last ray of second dorsal fin to insertion of last ray of anal fin; orbit diameter, the maximum diameter in horizontal plane; snout length, minimum distance from anterior margin of orbit to tip of snout; interorbit (bony), minimum distance between orbits.

Gobiodon acicularis, new species

Figs. 1, 2, Table 1

Holotype.—CAS 81525 (31.4 mm SL), western Pacific Ocean, Belau (Palau), off Babelthuap Island, coral-enclosed area north of Arakataoch Stream, collected by H. A. Fehlmann et al., 22 Sep 1957.

Paratypes.—CAS 81515 (5, 30.1–34.3 mm SL), western Pacific Ocean, Belau (Palau), north shore of Korer Island, reef bordering eel-grass flat east of Ebadel's Pier (T-dock), collected by R. R. Harry et al., 4 Aug 1955; CAS 81522 (6, 31.0–39.1 mm SL), western Pacific Ocean, Belau (Palau), Auluptagel Island in Ngarahelngael Pass, ca. 45 meters north of Ngarahelngael, collected by H. A. Fehlmann et al., 9 Oct 1957; CAS 82377 (5, 21.5–30.4 mm SL), ROM 1603CS (2, 27.2–31.3 mm SL, CS), collected with holotype; ROM 69038 (2, 33.1–36.6 mm SL), collected with CAS 81522.

Diagnosis.—A species of *Gobiodon* that is distinguished by a derived, highly elon-

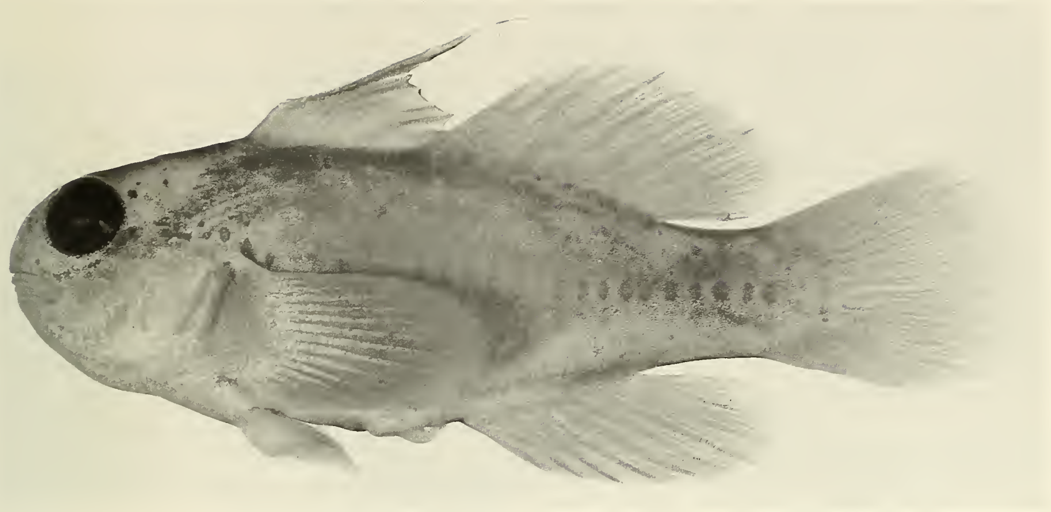

Fig. 1. *Gobiodon acicularis,* lateral view, left side (holotype, CAS 81525, 31.4 mm SL).

gate (18.7–50.7 % SL) spine I of the first dorsal fin and, in combination, by lack of post-symphysial canine teeth in the lower jaw, spines of first dorsal fin decreasing in length progressively from anterior to posterior, subequal upper jaw teeth (i.e., outer teeth not prominently enlarged), an absence of stripes or other markings, 16 or 17 pectoral-fin rays, more than four papillae in the anterior predorsal group and lack of an interopercle-isthmus groove.

Description.—Dorsal-fin rays VI + I, 10–11 ($\bar{X} = 10.2$, $n = 16$), first spine filamentous and highly elongate (Fig. 1), its relative length variable but not varying by sex or body size, in some specimens length of the spine reaching one half of standard length (Table 1); spines of first dorsal fin decreasing sequentially in length posteriorly; a shallow notch present between dorsal fins; first dorsal-fin pterygiophore formula 3-22110; second dorsal-fin posterior rays elongate, in some specimens reaching posteriorly as far as bases of dorsal segmented caudal-fin rays; anal-fin rays I, 9 in all specimens, posterior rays elongate, reaching bases of segmented caudal-fin rays as with second dorsal fin; pectoral-fin rays 16–17 ($\bar{X} = 16.1$, $n = 20$), fin extending posteriorly as far as second or third branched anal-fin ray in some specimens; pelvic-fin rays I,5 in all specimens; pelvic-fin fraenum and basal membrane complete, fin relatively large, usually reaching as far as anus and occasionally base of genital papilla; segmented caudal-fin rays 9 + 8, dorsal unsegmented rays 5–6 ($\bar{X} = 5.6$, $n = 11$), ventral unsegmented rays 5–6 ($\bar{X} = 5.7$, $n = 11$); dorsal branched caudal-fin rays 8–9 ($\bar{X} = 8.3$, $n = 11$); ventral branched caudal-fin rays 7–8 ($\bar{X} = 7.2$, $n = 11$); scales absent; first gill slit open; gill opening restricted, ending ventrally opposite bases of pectoral-fin ray 11–14–16 ($\bar{X} = 13.5$, $n = 19$); gill rakers, short, basally ossified 1 + 2, 1 + 4, 2 + 5 ($n = 3$); mouth small, terminal, gape extending posteriorly to below anterior one-half of eye; upper jaw teeth subequal, small, conical to slightly recurved, arranged in 2 to 3 irregular rows; lower jaw teeth similar to those of upper jaw, post-symphysial canine teeth absent; anterior nasal opening at tip of long fleshy tube, posterior nasal opening with raised rim or short tube; anterior oculoscapular canal pores 6 (NA, AI, PI, SO, AO, IT) (Fig. 2); preopercular canal pores 3; head papillae in a reduced transverse pattern (Fig. 2), with suborbital row

Table 1.—Morphometric characters of *Gobiodon acicularis,* based on the holotype, CAS 81525, and 19 paratypes, CAS 81515, CAS 81522, CAS 82377, ROM 69038 and ROM 1603CS, all from Belau. Standard length in mm; interorbital width, horizontal eye diameter, snout length and upper jaw length as percentages of head length; all other morphometric characters as percentages of standard length.

	Holotype	Range	$\bar{X}$
Standard length	31.4	21.5–39.1	31.0
Snout to first dorsal–fin origin	34.4	33.1–39.2	35.7
First dorsal–fin origin to second dorsal–fin origin	23.9	21.0–26.7	23.4
Second dorsal–fin origin to anal–fin origin	34.4	33.5–40.7	36.6
Pelvic–fin origin to anal–fin origin	27.7	25.9-35.5	30.0
Snout to pelvic–fin origin	33.4	33.0–40.1	35.4
First dorsal–fin origin to pelvic–fin origin	35.7	35.6–42.1	38.3
First dorsal–fin origin to anal–fin origin	43.6	43.6–51.7	46.7
Pelvic–fin origin to second dorsal–fin origin	42.0	40.1–49.1	44.4
Pelvic–fin length	16.9	16.9–23.3	18.7
Anal–fin length	19.7	18.4–28.4	22.2
First dorsal–fin first spine length	36.6	18.6–50.7	38.3
First dorsal–fin sixth spine length	13.6	8.0–16.3	12.5
Second dorsal–fin length	19.4	15.2–24.5	18.8
Pectoral–fin length	31.8	29.4–38.6	34.4
Caudal–peduncle length	24.8	22.0–25.3	23.9
Caudal–peduncle depth	18.8	17.6–20.8	19.3
Head length	26.8	26.0–30.3	28.3
Interorbital width	22.6	15.1–23.6	19.2
Horizontal eye diameter	10.2	7.9–11.4	9.6
Snout length	27.4	23.3–30.3	27.0
Upper jaw length	30.9	27.1–34.5	30.2

6–$\underline{7}$–8 ($\bar{X}$ = 7.6, *n* = 14), dorsal preopercular row 6–$\underline{7}$–9 ($\bar{X}$ = 7.1, *n* = 14) and ventral preopercular row 4–$\underline{7}$–8 ($\bar{X}$ = 6.9, *n* = 14); two clusters of papillae on predorsal surface (Fig. 2), anterior cluster 1 + 1–$\underline{2}$–3, posterior cluster $\underline{1}$–2 + 1 with anterior papilla in cluster located anteriorly or anterolaterally to posterior papilla; tongue rounded; no groove present between interopercle and isthmus; branchiostegal rays 5; vertebrae 10 + 15 + ural centrum = 26; epurals 1; morphometric values given in Table 1.

Color in alcohol (all material preserved in 55 % isopropyl alcohol).—Head and body covered nearly uniformly with small, pale brown chromatophores, except on posterior margin of gill membrane where they are slightly larger and darker; all fins with many scattered, small chromatophores similar to those of body; pectoral fin and distal margin of first dorsal fin distinctly darker than other fins and body; no stripes or other markings present.

Etymology.—The name is based on the Latin adjective *acicularis,* meaning like a needle, in reference to the elongate spine I of the first dorsal fin.

Remarks.—*Gobiodon acicularis* is distinguished from all other described congeners by its highly elongate first spine of the first dorsal fin. In other respects the new species resembles *G. ceramensis* (Bleeker, 1852) and the adults, according to a manuscript key (D. F. Hoese, pers. comm.), of *G. albofasciatus* Sawada & Arai, 1972 with which it shares relatively uniform body pigmentation without markings, lack of a groove between the interopercle and isthmus, and the outer row of the upper jaw teeth not prominently enlarged. Both of these species share with *G. acicularis* the possibly derived first dorsal fin shape with the lengths of the spines decreasing progressively from anterior to posterior. Unlike *G. acicularis, G. albofasciatus* has a relatively broad gill opening, occupying nearly the entire base of the pectoral fin. The gill opening of *G. acicularis* is quite narrow, terminating ventrally at the level of the base of the 14th to 16th pectoral-fin ray. *Gobiodon citrinus* is also similar to the above species in the shape of the first dorsal fin, but has prominent transverse stripes on the head and body posterior to the pectoral-fin base and a dusky spot at the dorsal margin of the gill opening. This species is further distinguished by its relatively small pelvic fin and narrower gill opening.

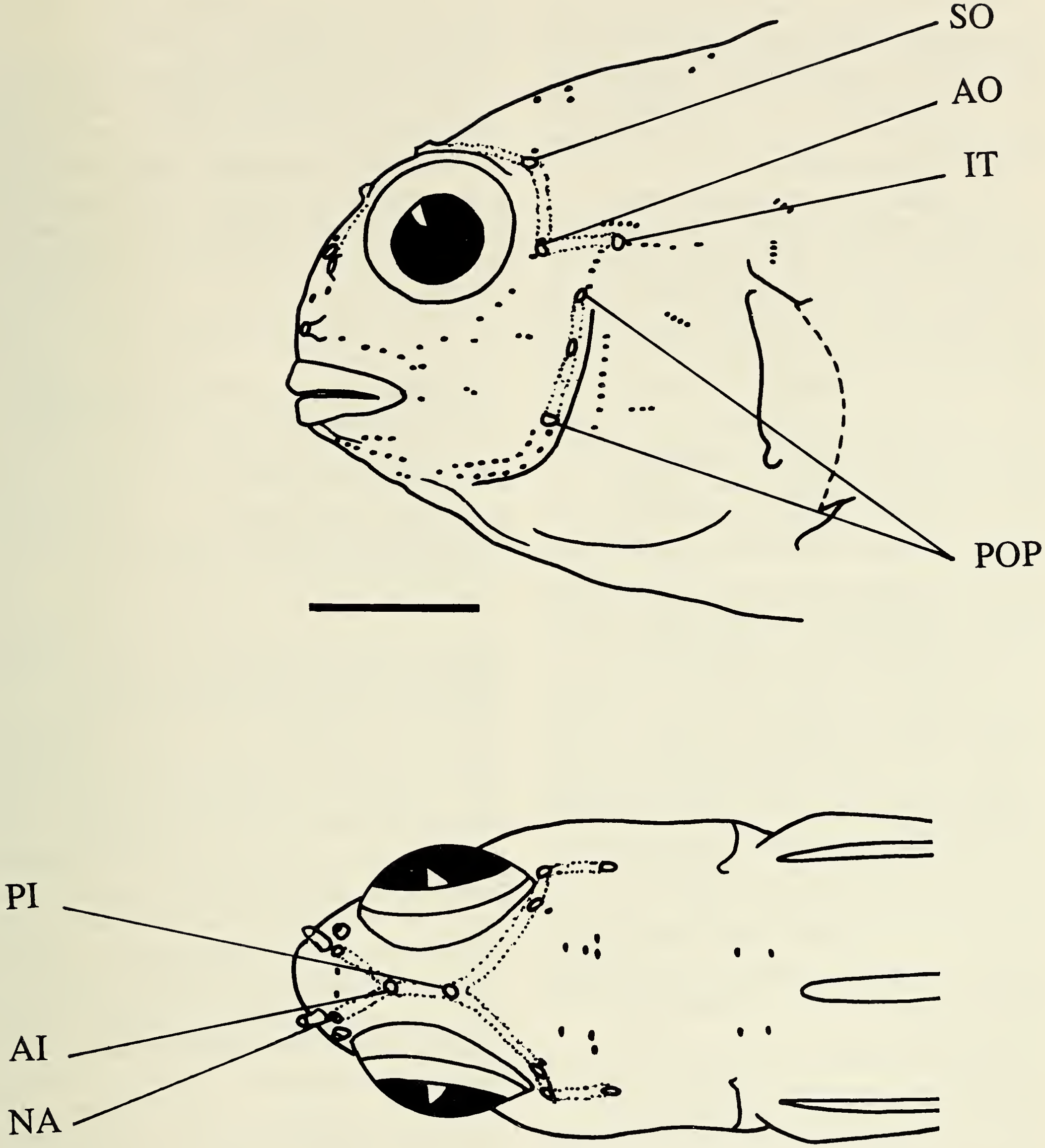

Fig. 2. Head of *Gobiodon acicularis* (paratype, CAS 82377, 26.3 mm SL) showing arrangement of papillae and lateralis pores in left lateral (above) and dorsal (below) views. Abbreviations for lateralis pores, following Lachner and Karnella (1980): AI, anterior interorbital; AO, anterior otic; IT, intertemporal; NA, nasal; PI, posterior interorbital; POP, preopercular; SO, superior otic. Scale bar = 3 mm.

The morphology of *Pseudogobiodon macrochir* Bleeker, 1875 also bears some, possibly important, similarities to *G. acicularis.* Bleeker's erection of *Pseudogobiodon* for *P. macrochir* distinct from *Gobiodon,* was based on its slightly enlarged outer teeth of the upper jaw and, more importantly, the absence of post-symphysial canine teeth in the lower jaw. Neither of these characters are likely to be of use in diagnosing *Pseudogobiodon* based on observed variation within and between *Gobiodon* species and the very small sample size upon which Bleeker's description was based (we only know of the holotype). *Pseudogobiodon* is almost never used in regional faunal works on Indo-Pacific fishes (see Koumans 1953:13, for example).

Our examination of the holotype of *P. macrochir* (RMNH 4463, 26.7 mm SL) reveals that the upper jaw teeth are subequal, as they are in *G. ceramensis* and *G. citrinus,* for example, a condition which is probably derived within *Gobiodon.* We confirm that the post-symphysial dentary canine teeth are absent in the holotype of *P. macrochir,* as described by Bleeker (1875). Post-symphysial canine teeth are absent in *G. acicularis,* variously present or absent in adults of another, probably undescribed, *Gobiodon* species and present, but reduced in size, in adults of *G. okinawae* (Sawada et al. 1972:59, fig. 2). Reduction of these canine teeth is probably derived and may support the monophyly of a clade. Pending results of our phylogenetic analysis, if such a clade, or *P. macrochir* alone, were found to be the sister group of a clade comprising all other *Gobiodon* species then the former could be referred to *Pseudogobiodon.* If, however, *P. macrochir* is found to be nonbasal in the *Gobiodon* clade then *Pseudogobiodon* should be synonymized with *Gobiodon* to preserve the monophyly of the latter genus.

Harrison (1989:348) indicated that some features of the skull of a species of *Gobiodon* (not identified to species) he examined were unique among gobioids and therefore likely derived. These characters are: (1) an enlarged supraoccipital crest with additional, paired crests anteriorly formed by dorsal extensions of the frontals along their medial surfaces, and (2) a deepened sphenotic and pterotic. These features are common to all species of *Gobiodon* we have examined, including *G. acicularis,* and to *Pseudogobiodon macrochir.* Given these shared, derived characters, *Gobiodon* can be provisionally diagnosed, whereas *Pseudogobiodon* cannot, and the former is therefore the appropriate genus for the new species.

Specific characters shared by *P. macrochir* and *G. acicularis* include a uniformly pigmented body with some fins, especially the first dorsal, noticeably darker than the body, lengths of the spines of the first dorsal fin decreasing progressively from anterior to posterior, and modally 16 pectoral-fin rays. Bleeker (1875:117) does not mention a horizontal stripe at the base of the second dorsal fin in *P. macrochir,* nor is one shown in the recently published illustration (Bleeker 1983: pl. 431, fig. 4). However, we have found there to be a lightly pigmented stripe along the base of each dorsal fin in the holotype of *P. macrochir,* indicating an important difference in pigmentation from *G. acicularis.*

Gobiodon acicularis is known only from the collections reported here from Belau. That the species is recognized now for the first time in spite of there being many collections of *Gobiodon* from reefs throughout the Indo-Pacific, including Belau (Randall, pers. comm.), is possibly explained by a restricted geographic distribution and/or what we know of its ecology so far. Collections from Belau were all made in back-reef areas where there may have been less collecting effort than at other locations where *Gobiodon* species occur. We have no information on host corals that might have been present, but given the general water conditions it is likely that *G. acicularis* occupies an unusual, probably derived, habitat with respect to congeners (see, for example, Patton 1994), which, as adults, are commensal primarily on *Acropora* species. New collections with detailed habitat data would be invaluable, if not essential, in our attempt to trace the evolution of host-commensal relationships in the genus.

Acknowledgments

We are grateful to W. Eschmeyer, D. Catania and J. Fong, CAS, who made the material available for this study, and to E. O.

Murdy and J. T. Williams for their helpful comments on the manuscript. Thanks are also due M. Rouse and C. Gilmore, ROM, for their technical assistance with radiography and B. Boyle for photography. Financial support for this study was provided through Natural Sciences and Engineering Research council of Canada operating grant A 7619 to RW.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):695–716. 1995

South American rocky habitat *Leptodactylus* (Amphibia: Anura: Leptodactylidae) with description of two new species

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Abstract.—There are four groups of populations of *Leptodactylus* associated with rocky habitats in northern South America. The available data are most consistent with recognizing three species for these four units: *L. rugosus* and two new species, *L. lithonaetes* and *L. myersi.* A single specimen from Paraguay, although distinctive, is considered to be conspecific with *L. syphax,* previously known from disjunct localities in eastern Brazil. Data are inadequate at present to determine whether the South American species of *Leptodactylus* associated with rocky habitats are a monophyletic group.

Charles W. Myers brought my attention to a distinctive new species of the frog genus *Leptodactylus* that he had collected from granitic outcrops in the State of Roraima, Brazil. As study of the material progressed, comparisons were made between the new species from northern Brazil with *Leptodactylus rugosus,* a species from granitic and sandstone habitats of the Guiana shield region. It became apparent that there was considerably more variation among populations of the Guiana shield frogs than recognized previously (Heyer 1979). From the other end of South America, a single specimen of *Leptodactylus* was collected several years ago from rocky outcrops in Paraguay; this specimen's affinities are problematic. The purpose of this paper is to re-evaluate the species status of the *Leptodactylus* associated with granitic and sandstone habitats in South America.

Methods and Materials

As aspects of variation in *Leptodactylus syphax* have recently been addressed (Cardoso & Heyer 1995), members of that species are not treated in detail here. As many specimens as possible were borrowed of all other granitic and sandstone habitat *Leptodactylus.* Data were taken on patterns of the dorsum, upper lip, posterior thigh, and upper shank using the standards described in Heyer (1979). In addition, belly and ventral thigh surface patterns were recorded. Information was noted on dorsal folds, texture of the dorsum, upper shank, outer tarsus, and foot, as well as male secondary sexual characteristics. The snout–vent length (SVL) was recorded for all specimens. For all adults and specimens near adult size, the following measurements were also recorded (following Heyer et al. 1990): head length (HL), head width (HW), eye–mid-nostril distance (E–N), tympanum diameter (TD), thigh, shank, and foot. Statistics were analyzed with SYSTAT for Windows, version 5 (1992). Museum abbreviations are those recommended by Leviton et al. (1985) with the addition of IND-AN = INDERENA, Ministerio de Agricultura, Bogotá, Colombia.

Variation in Northern South American Rocky Habitat *Leptodactylus*

As data were being collected on specimens from northern South America, it be-

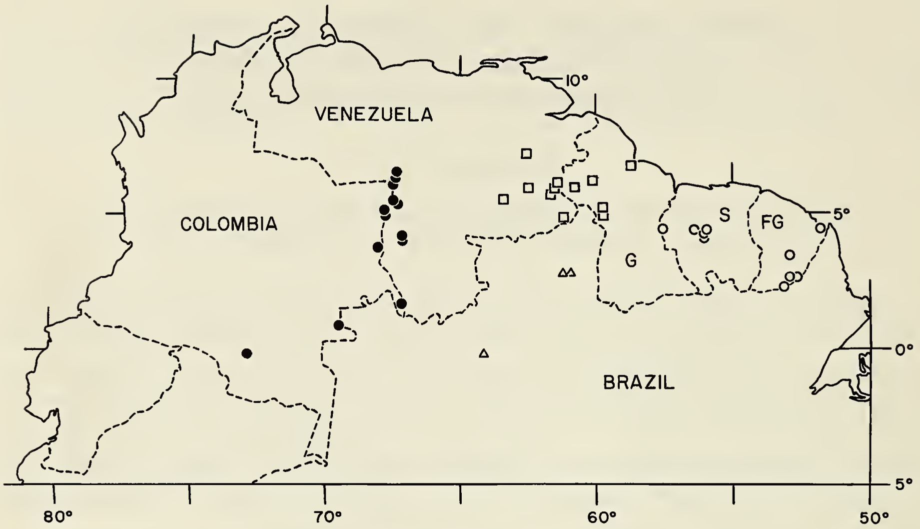

Fig. 1. Localities for Group 1–4 specimens from northern South America. Group I = dots (*L. lithonaetes*), Group II = squares (*L. rugosus*), Group III = triangles (*L. myersi*), Group IV = circles (*L. myersi*).

came apparent that there were four groups involved based on character states and geographic distributions. Each group is discussed in some detail and then decisions are drawn with respect to species limits. There are few tadpole samples; those that are available do not all contain Gosner (1960) stage 25–32 specimens. Tadpole characteristics described in this section are based on Gosner stage 33–42 specimens. Because recordings of advertisement calls exist for only Group 2 individuals, those data are not discussed.

Group 1.—Specimens in this group are from Colombia and Venezuela near the Colombian border (Fig. 1). Seventeen adult females, 31 adult males, 176 total specimens.

Dorsal patterns characteristically have a series of 3–4 (rarely 2) pairs of spots ranging from small to large in size and ranging from discrete to patterns of fusion with other spots both across, as well as, lengthwise along the dorsum (Heyer 1979, fig. 1, patterns H through K). About 10% of the individuals have a uniform dorsum.

Upper lip patterns show a continuum among the following states. Thirteen percent of the specimens have little pattern on the upper lip (Heyer 1979, fig. 2, patterns C, E); 32% have some expression of alternating light and dark vertical bars (Heyer 1979, fig. 2, pattern J); 29% have some form of alternating light and dark oblique bars (Heyer 1979, fig. 2, pattern N); and 26% have some sort of irregularly defined light area in the loreal region to under the eye (Heyer 1979, fig. 2, pattern M).

The posterior thigh surface pattern also shows a complete continuum among the following conditions. The posterior thigh surfaces are indistinctly mottled in 39% of the individuals (Heyer 1979, fig. 3, pattern P); distinctly mottled with small light irregular marks in 17% of the individuals (Heyer 1979, fig. 3, patterns B, C, D); distinctly mottled with large light irregular spots and marks in 38% of the individuals (Heyer 1979, fig. 3, pattern A); 5% of the individuals have distinctly mottled thigh surfaces with some expression of light vertical marks or bars on the upper portions of the thigh surfaces (Heyer 1979, fig. 3, pattern I); one individual has a large light area on the lower thigh surface containing a few distinct dark spots; one individual has a large light area on the upper thigh surface.

One juvenile has a distinct lengthwise light band in the middle of the ventral thigh surface, 8% of the juveniles have a noticeable light band, whereas no adults have any indication of such a band; 76% of juveniles and 44% of adults have very light ventral thigh surfaces with few or no melanophores (Fig. 2); 9% of juveniles and 33% of adults have almost uniformly dark ventral thigh surfaces; 3% of juveniles and 12% of adults have lightly to moderately mottled ventral thigh surface patterns; 3% of juveniles and 10% of adults have the upper-lateral sector boldly mottled and the rest of the ventral thigh surface uniformly light.

Sixteen percent of the juveniles and 45% of the adults have relatively uniform gray/brown bellies, although in some, the posterior belly is lighter than the anterior; 50% of the juveniles and 2% of the adults have uniformly light bellies with very few melanophores (Fig. 2); 9% of the juveniles and 22% of the adults have dark bellies with moderate to low contrast light spots and/or vermiculations; 1% of the juveniles and 16% of the adults have a mottled pattern of smaller irregular lighter areas on a darker ground; and 24% of the juveniles and 14% of the adults have a bold mottled pattern of large light spots/flecks on a darker ground color.

Dr. Charles W. Myers (pers. comm.) provided life color information based on specimens AMNH 100656–100667 from the southwest sector of Cerro Yapacana, Amazonas, Venezuela: "Small white markings on lip. Rear of thigh usually suffused with orange (dotted pale tan on black in one specimen). Ventral surfaces grayish white. Juvenile (small specimen, 14875) [= AMNH 100666, 20.7 mm SVL] has pure white venter and bright orange under thighs, and a strong suffusion of orange on rear of thigh. Iris overall pale bronze, or pale bronze above and pale gray below—with overall dense black venation." Dr. John D. Lynch (pers. comm.) provided life color information based on specimens from Cueva Arévalo, Vichada, Colombia, especially ICNMNH 13972–13974: "Dorsum brown with slightly darker brown and black spots on upper flanks. Patches on head and center of back rust. Pale brown (almost cream) interorbital bar and some marks on back. Face cream with black canthal stripe. Tympanum reddish-brown. Limb bands black. Yellow warts on flanks (glands). Venter and throat cream with brown spots and reticulation. Undersides of thighs pink. Posterior surfaces of thighs marbled black with faint rose spots. Iris bright copper above, gray below, flecked with black and bearing black horizontal streak. Other individuals may have posterior thighs black with small yellow spots above, becoming more rose below. Dorsum varies from tan to nearly black. In males the lateral ⅓ of the gula is black (center white). Face generally pale (some dark individuals do not have the pale labial patch). Venter scarcely to heavily spotted with brown. Some dorsal patches have olive cast. Variation based on series of 15 individuals. . . . "

The degree of juvenile and adult pattern differences from individuals from the same localities, although noticeable in preserved specimens, is not striking. The most noticeable features are that the bellies and ventral thigh surfaces are lighter than in the adults, but these differences are more of degree than fundamentally different.

The commonest conditions for dorsolateral fold development are either no indication of dorsolateral folds or one short pair of ridges or elongate warts in the shoulder region. Some specimens have series of warts or ridges in the dorsolateral fold field, some extending the entire length of the dorsum from behind the eye, others extending only to the sacrum.

Most individuals have a shagreen together with black and/or white tubercles on the dorsum. When tubercles are present, they are more abundant on the posterior dorsum. Most juveniles (80%) either have a moderate to pronounced shagreen and/or small bumpy glands without any black and/or

Fig. 2. Characteristic ventral patterns of juveniles. Upper left, Group I, ICNMNH 13980; upper right, Group II, USNM 291249; lower left, Group III, AMNH 128023; lower right, Group IV, RMNH 23921.

white tubercles; 31% of adults lack tubercles.

The upper shank surface may have a shagreen or not. Most specimens (93%) have few to many black and/or white tubercles; few specimens (7%) have very few or no tubercles.

The texture of the outer tarsus may be shagreened or not. Most specimens (81%) have few to many black and/or white tubercles; some specimens (19%) have very few or no tubercles.

Texture of the foot is usually smooth, lacking shagreen or tubercles (86%); some individuals (12%) have no more than a few black and/or white tubercles; very few individuals (2%) have a weakly developed shagreen.

Adult males have one black thumb spine on each hand and a pair of chest spines. There is also a band of black tubercles across the chest in larger males. Males have a patch of black chin tubercles on the anterior portion of the throat. The vocal sacs are laterally expanded and darkly pigmented.

Adult females range between 54.8 and 78.4 mm SVL, adult males 45.3 and 71.4 mm SVL. A principal components analysis was run on the measurement data for adult specimens. No obvious outliers are evident on the resultant plot of individuals using the first two factors.

Two series of tadpoles are available, one well-preserved series of specimens from Cerro Patavá, Colombia, and two alcohol preserved dehydrated specimens from Canaripo, Venezuela. It is difficult to determine to what degree the differences observed between larvae from these two localities are due to preservation artifact. Tadpoles from both localities demonstrate the semiterrestrial ecomorph as described by Altig & Johnson (1989). The body length is 28–31% of the total length in the Cerro Patavá tadpoles, 31–32% in the Canaripo tadpoles. The anterior oral gap is 80–88% of the oral disk width in the Cerro Patavá specimens, 64–77% in the Canaripo specimens. The upper beak is highly arched; its depth is 27–37% of the upper beak width in the Cerro Patavá sample, 36% in the Canaripo sample. The body is flattened, with body depth 67–74% of body width in the Cerro Patavá larvae, 46–56% in the Canaripo larvae. Larvae have series of glandular ridges on the body above the abdominal cavity.

Habitat notes are available from AMNH 100656–100667 collected at Cerro Yapacana, Amazonas, Venezuela, 18–19 February 1978 (C. W. Myers, pers. comm.): "Mountain stream by night, sitting on the rock stream bed at or near edge of water. . . . They are timid and quick to take cover in crevices and under large boulders if one's light is not kept on them while approaching; they seem to avoid diving into the water."

Group 2.—This group includes specimens from Guyana and southeastern Venezuela (Fig. 1). Seventeen adult females, 35 adult males, 126 total specimens.

Most specimens have a dorsal pattern of a series of 3–4 (rarely 2) pairs of large to small spots ranging from discretely defined to patterns of fusion with other spots both across the dorsum as well as lengthwise along the dorsum (Heyer 1979, fig. 1, patterns H through K). Twenty-seven percent of the individuals have uniform or almost uniform dorsal patterns.

Upper lip patterns represent a continuum among the following states. Eleven percent of the specimens have little pattern on the upper lip (Heyer 1979, fig. 2, patterns C, E); 8% have some expression of alternating light and dark vertical bars (Heyer 1979, fig. 2, pattern J); 43% have some form of alternating light and dark oblique bars (Heyer 1979, fig. 2, pattern N); 26% have some sort of irregularly defined light area in the loreal region to under the eye (Heyer 1979, fig. 2, pattern M); 7% have an irregularly defined light area in the loreal region, separated from light oblique bars behind the eye by irregular dark bars (Heyer 1979, fig. 2, pattern K); and 3% have extensive dark mottling on the upper lip, heaviest near the mouth.

Posterior thigh surface patterns are quite variable, with a continuum including the following states. The posterior thigh surfaces are indistinctly mottled in 8% of the individuals (Heyer 1979, fig. 3, pattern P); distinctly mottled with small light irregular marks in 4% of the individuals (Heyer 1979, fig. 3, patterns C, D); distinctly mottled with large light irregular spots and marks in 40% of the individuals (Heyer 1979, fig. 3, pattern A); the upper thigh surfaces have some sort of light vertical marks or bars in 15% of the individuals (Heyer 1979, fig. 3, patterns E, F); the lower thigh surface has one or more extensive light area, sometimes with a few small dark spots in 22% of the specimens; and the upper thigh surface has a large light area in 10% of the individuals.

The ventral thigh surfaces are very light with few or no melanophores in 72% of the juveniles and 31% of the adults (Fig. 2); the ventral thigh surfaces are almost uniformly dark in 13% of the adults (no juveniles); the ventral thigh surfaces are lightly to moderately mottled in 5% of the juveniles and 37% of the adults; the ventral thigh surfaces have the upper-lateral sector boldly mottled with the rest of the thigh surface uniformly light in 23% of the juveniles and 18% of the adults.

Two percent of the juveniles and 21% of the adults have relatively uniform gray/brown bellies; 44% of the juveniles and 13% of the adults have almost uniformly light bellies with very few melanophores (Fig. 2); 3% of the juveniles and 8% of the adults have dark bellies with moderate to low contrast light spots and/or vermiculations; 17% of the juveniles and 45% of the adults have a mottled pattern of smaller irregular lighter areas on a darker ground; and 33% of the juveniles and 13% of the adults have a boldly mottled pattern of large light spots/flecks on a darker ground.

Donnelly & Myers (1991:22) provided color descriptions for specimens from Cerro Guaiquinima, Bolívar, Venezuela: "In life, some juveniles had white-edged dorsal blotches whereas others were uniformly blackish. The throat was heavily marked with gray mottling on white and there was less gray on the venter. The body glands of the groin and the ventral and posterior thigh surfaces had variable suffusion of orange that was bright in some individuals. The iris was bronze above, white on the medial ventral section, and brown between, with dense black venation overall." Dr. Robert P. Reynolds (pers. comm.) provided copies of his color notes for specimens from Kaieteur Falls, Guyana. A series of adults and small juveniles (USNM 291245–291250) had the following: "Brown dorsally with warty rugose skin. . . . Venter cream with darker mottling. Rose-orange groin and undersurfaces of thighs. Bronze-gold iris." A female (USNM 291251) was: "Dorsally greenish with dark speckling throughout. Rims of eyelids yellowish with yellow band between eyelids. Three–4 light spots on lower eyelid. Yellowish with mottled brown between upper lip and eyelid. Tympanum rust brown. Iris bronze. Venter brownish with white throughout. Rear of thigh gold and brown mottled." A series of adults of both sexes (USNM 291252–291256) were: "Dorsally greenish brown with yellow mottling. Three distinct yellow lines from eye to lip. Yellow line between eyes on top of head and a line from rear of each eye back to rear of head. Rust wash over neck and shoulder area. Mottled light and dark venter. Undersides of legs rose tint with dark spots." A single male (USNM 342151) had: "Dorsum reddish brown, limbs with reticulate dark markings, light line between orbits, bronze eye, dark canthal stripe; chin, throat, chest and belly with dark grey spotting, underside of thighs and calfs salmon red."

The degree of juvenile and adult pattern differences from individuals from the same localities are striking with respect to ventral patterns, especially when small juveniles are compared with adults. The throats and bellies of juveniles are bright white in recently preserved specimens (Kaieteur National Park, Guyana), whereas the throats and bellies of adults are densely mottled dark gray; the ventral thigh surfaces of the juveniles lack melanophores and stand in contrast to the dark pigmented ventral thigh surfaces of adults. No differences in dorsal pattern between juveniles and adults are evident.

The commonest conditions for dorsolateral fold development are either no indication of dorsolateral folds or one short pair of ridges or elongate warts in the shoulder region. Three individuals were recorded as having two pair of short ridges and three individuals were recorded as having a series of short ridges in the dorsolateral fold field.

Most individuals have a shagreen and black and/or white tubercles on the dorsum. When tubercles are present, they are more abundant on the posterior dorsum. Twenty-two percent (20 individuals) of the juveniles have a pronounced dorsal texture of a strongly developed shagreen with glandular warts; only 5% (2 individuals) of the adults have the same texture.

The upper shank surface may have a shagreen or not. Almost all specimens (122 of 124 recorded) have few to many black and/or white tubercles; only 2 individuals have very few or no tubercles.

The texture of the outer tarsus may be shagreened or not. Almost all specimens (98%) have few to many black and/or white tubercles; only 2 individuals (2%) have very few or no tubercles.

The texture of the foot is smooth, lacking shagreen or tubercles in 50% of the individuals; 49% of the specimens have no more than a few black and/or white tubercles; very few individuals (2%) have a weakly developed shagreen.

Adult males have one or two black thumb spines on each hand and a pair of chest spines. There is no distinctive band of black tubercles across the chest in larger males. Males lack a patch of black chin tubercles on the anterior portion of the throat. The vocal sacs are laterally expanded and darkly pigmented.

Adult females range between 53.6 and 73.5 mm SVL, adult males 50.9 and 71.6 mm SVL. A principal components analysis was run on the measurement data for adult specimens. There is a general cluster of points on the plot of individuals using the first two factors, but three individuals lie somewhat outside the general cluster. KU 166499 is an individual from a locality in which all other specimens lie in the general cluster of points. RMNH 23906 and USNM 258130 are the only adult individuals from each of two different localities. Re-examination of these specimens does not indicate that any change should be made in their assignment to the geographically based four clusters.

Data were taken from a single tadpole from Cerro Auyantepui, Venezuela, a single tadpole from La Escalera, Venezuela (both alcoholic) and seven larvae from Kartabo, Guyana (formalin). These tadpoles demonstrate the semiterrestrial ecomorph as defined by Altig & Johnson (1989). The body length is 28–29% of the total length. The anterior oral gap is 75–81% of the oral disk width. The upper beak is highly arched; the upper beak depth is 33–40% of the upper beak width. The body is flattened; the depth is 64–70% the body width. Larvae have series of glandular ridges on the body above the abdominal cavity.

Habitat information specific for members of Group 2 has been published by Donnelly & Myers (1991:22) for specimens from Cerro Guaiquinima, Bolívar, Venezuela: "Adults were taken at night in the rocky stream bed at Camp 2 and in the north stream at Camp 1. At Camp 2, several adults were collected by night in water in the middle of small waterfalls. Juveniles were active both day and night. During the day, juveniles were commonly seen in exposed situations, sitting on rocks around small pools and jumping into the pools when disturbed." Robert P. Reynolds (pers. comm.) collected a series of specimens (including USNM 291245–291256) at night at Kaieteur National Park, Guyana, 29–30 March 1989, on a trail from the airstrip to the guest house above Kaieteur Falls. Some individuals were calling and others were not. On the afternoon of 7 April 1994, Reynolds collected USNM 342151–342160 on bedrock puddles, near the airstrip at Kaieteur Falls.

Group 3.–Specimens from this group are from northern Brazil (Fig. 1). Three adult females, 13 adult males, 47 total specimens.

The dorsal patterns characteristically have two large dark spots on the dorsum (Heyer 1979, fig. 1, pattern K). The spots may have fuzzy borders, or be well defined with a black outline border, or be well defined by a contrasting light border. The spots may be fused with each other and the interocular spot. Nine percent of the individuals have a dark dorsum with a few small, discrete, irregular, lighter spots. One individual has paired series of dark dorsal spots (Heyer 1979, fig. 1, pattern H). No individual has a completely uniform dorsum.

Upper lip patterns demonstrate a continuum among the following states. Nine percent of the specimens have little pattern on the upper lip (Heyer 1979, fig. 2, patterns C, E); 49% have some expression of dark vertical bars (Heyer 1979, fig. 2, patterns A, J); 16% have some form of alternating light and dark oblique bars (Heyer 1979, fig. 2, pattern N); 20% have some sort of irregularly to regularly defined light area in the loreal region to under the eye (Heyer 1979, fig. 2, patterns L, M); and 7% have a mottled upper lip with small dark spotting.

The posterior thigh surface patterns grade among the following states. A single individual has an indistinctly mottled posterior thigh surface (Heyer 1979, fig. 3, pattern A); one specimen has an almost uniformly dark thigh surface; 70% have large light spots on the upper portion of the posterior thigh surfaces with or without smaller light spots on the lower portion of the posterior thigh surfaces; 15% have narrow vertical light stripes on the upper portion of the posterior thigh surface; and 11% have few to several distinct small light spots on the posterior thigh surface (Heyer 1979, fig. 3, patterns N, O).

Most juveniles (79%) have at least a noticeable lengthwise light band in the middle of the ventral thigh surfaces (very distinct in 38% (Fig. 2)), whereas only one adult has a faint indication of this band; one juvenile and most adults (69%) have almost uniformly dark gray or brown ventral thigh surfaces; 17% of the juveniles and 25% of the adults have lightly to moderately mottled ventral thigh surfaces.

No juveniles, but 29% of the adults, have relatively uniform gray or brown bellies; 63% of the juveniles, but no adults, have dark bellies with very contrasting distinct light spots (Fig. 2); 33% of the juveniles and 71% of the adults have dark bellies with moderate to low contrast distinct light spots or vermiculations.

Ronald I. Crombie (pers. comm.) took the following notes on a 79.4 mm SVL juvenile female (USNM 302192): "Light markings on back rich tan, especially on head, darker markings deep wood brown. Warts on side with reddish brown markings. Venter gray with lighter gray spots, lighter marks distinctly greenish in groin and under legs. Red-brown pustules under arms and near axilla (parasites?). Rear of thighs black with a few greenish blotches and some red-brown ones near anus. Soles of hands and feet dark gray, feet almost black. Iris gold with brassy vermiculations above, dark below." Crombie noted that on two other large juveniles (USNM 302194, 72.3 mm SVL; USNM 302195, 69.8 mm): "Considerable red spotting on anterior and posterior thighs." Charles W. Myers (pers. comm.) took color notes for adults and juveniles: "Adults [AMNH 128021–128022 = CWM 18514, 18516]: Throats blackish gray; rest of ventral surfaces gray, with or without small white spots. Thighs above with black bands separated by brown interspaces that may have a faint reddish suffusion (not bright as in juveniles). Rear of thigh black with a line of silvery white dots. Iris pale bronze with reddish brown horizontal stripe. Juveniles [AMNH 128023–128031 = CWM 18526–18534]: Throat and other ventral surfaces gray with irregular white spotting. Thighs with black bands and bright orange-red interspaces antero- and posterodorsally (red color not continuous across dorsal midline of thigh). Iris pale bronzy gray on upper half—above an ill-defined reddish brown horizontal stripe—and with a faint reddish suffusion on lower part of iris."

The degree of juvenile and adult pattern differences from the same locality is striking in preserved specimens. The most noticeable differences occur on the thighs. The upper portion of the posterior thigh surfaces in juveniles have well defined large light spots (bright red in life), whereas such spots are not distinct or completely absent in adults. In most juveniles, there is a distinct light longitudinal band on the midventral thigh surfaces; no such distinct light band occurs in adults. The belly spotting differences between juveniles and adults are not as striking as the thigh surface pattern differences—in juveniles, the dark bellies have more distinct light spots than adults.

No dorsolateral folds are evident in 16% of the individuals examined. In most specimens (77%) dorsolateral folds are distinct, but broken (not continuous) and range from short (extending only to the shoulder region) to long (entire length of back from behind eye to leg). Only two individuals have almost continuous dorsolateral folds extending to the sacrum, and only one specimen has a continuous dorsolateral fold extending to the leg.

Most specimens have a shagreen and white tubercles on the dorsum. When tubercles are present, they are more abundant on the posterior dorsum. Only in juveniles (60%) is a strong warty shagreen developed.

The upper shank usually has a shagreen (93%). Most specimens (87%) have few to many black and/or white tubercles; some (13%) have very few or no tubercles.

The texture of the outer tarsus is usually shagreened (85%). Most specimens (93%) have few to many black and/or white tubercles; a few (7%) have very few or no tubercles.

The texture of the sole of the foot is usually smooth (87%); 11% have a weak shagreen; only one individual has scattered white tubercles.

Adult males have one black spine on each thumb. There is no indication of chest spines, chest tubercles, or chin tubercles. Vocal sacs are neither laterally expanded nor differentially patterned.

Adult females range from 103.8 to 112.9 mm SVL, adult males 74.2 to 116.8 mm SVL. The relatively small sample size does not justify analyzing the measurement data with principal components to identify potential outlier individuals.

No tadpoles are available for this group.

Habitat notes are available from two sets of collectors from the same rock outcrop from Mucajaí, Roraima, Brazil. Charles W. Myers (pers. comm.) indicated for specimens AMNH 128021–128031, collected on 11 July 1987: "On granite inselberg surrounded by humid scrubby forest with many palms. Some juveniles by day under granite flakes microsympatric with *Tropidurus hispidus* and *Leptodactylus fuscus.* Other juveniles by night, sitting on bare rock or in small pools of water (with sparse aquatic vegetation) on the bare rock. The four adults all in the small pools by night." On 30 May–1 June 1988, Ronald I. Crombie (pers. comm.) collected USNM 302066–302068, 302190–302203, MZUSP 660889 at night from on or under rock. Ronald I. Crombie (pers. comm.) documented that USNM 302267 from Colônia Apiaú, Roraima, Brazil, collected on the afternoon of 14 June 1988, was taken from under roofing tiles at an abandoned hunting camp in the forest, not near any rocky outcrop.

Group 4.—Specimens in this group are from French Guiana and Surinam (Fig. 1). One adult female, 1 adult male (both from French Guiana), 54 total specimens.

Most specimens have two large, dark, relatively well-defined blotches on the dorsum posterior to the dark interorbital blotch (Heyer 1979, fig. 1, pattern K); these blotches may be outlined by a white ring or a dark border. A few specimens have some paired large or small dark spots on the dorsum (Heyer 1979, fig. 1, patterns H, J). A few have fused blotches (Heyer 1979, fig. 1, patterns D, I). Uniform patterns (Heyer

1979, fig. 1, pattern C) occur in 9% of the sample.

Upper lips demonstrate variability among the following states. Seven percent of the specimens have little pattern on the upper lip (Heyer 1979, fig. 2, patterns C, E); 54% have some expression of alternating light and dark vertical bars (Heyer 1979, fig. 2, patterns A, J); 13% have some form of alternating light and dark oblique bars (Heyer 1979, fig. 2, pattern N); and 26% have some sort of irregularly defined light area in the loreal region which may extend to under the eye (Heyer 1979, fig. 2, patterns K, M).

The posterior thigh surface patterns are quite variable. They are distinctly mottled with small irregular light marks in 13% of the individuals (Heyer 1979, fig. 3, patterns C, D); distinctly mottled with large light irregular spots and marks in 13% (Heyer 1979, fig. 3, patterns A, F, K); mottled with some expression of light vertical marks or bars on the upper portions of the thigh surfaces in 11% (Heyer 1979, fig. 3, pattern I); mottled with large distinct light spots or blotches on the upper portions of the thigh surfaces (light marks may be confluent with each other) in 51% of the individuals; one individual has distinct light spots on the posterior thigh surfaces (Heyer 1979, fig. 3, pattern N); three specimens have some large dark blotches on the lower portion of the thigh surfaces; two specimens have relatively uniform thigh surfaces.

Juveniles do not have a distinct light band lengthwise in the middle of the ventral thigh surfaces, although 21% of the juveniles have a noticeable light band (Fig. 2), neither adult has any indication of a light band; 21% of the juveniles have very light ventral thigh surfaces with few or no melanophores, neither adult has this pattern; no juveniles have almost uniformly dark ventral thigh surfaces, one adult has this pattern; 4% of the juveniles have lightly to moderately mottled ventral thigh surfaces, one adult has heavily mottled ventral thigh surfaces; 50% of the juveniles have the upper-lateral sector of the ventral thigh surfaces boldly mottled with the rest of the ventral thigh surface uniformly light, neither adult has this pattern.

No juveniles, but both adults, have a relatively uniform gray/brown belly; 23% of the juveniles have a uniform and light belly with very few melanophores; 27% of the juveniles have a dark belly with distinct light spots/vermiculations of moderate to low contrast; 25% of the juveniles have a mottled belly of smaller irregular light areas on a darker ground; 25% of the juveniles have a bold mottled belly pattern of large light spots/flecks on a darker ground (Fig. 2).

Dr. Charles W. Myers (pers. comm.) took color notes on a series of juvenile specimens from Voltzberg, Surinam (AMNH 87705–87736): "Dorsal surfaces brown with a remarkably constant pattern of darker brown markings that are outlined in light yellowish brown. Top of thigh with orange-red flash mark (which is concealed in frog's normal position) that is broken by black bars; the flash mark is present in all but is quite faint on several specimens of different size. Rear of thigh black with pale blue or greenish blue dots. Venters white with variable amounts of gray mottling, turning light gray underneath limbs. Iris pale bronzy orange, in some individuals turning pale gray below pupil; dense black venation and a tendency for a brownish horizontal streak."

There is no locality for which a series of adults and juveniles are available. In comparing adults and juveniles from different localities, the degree of adult and juvenile pattern differences in preserved specimens is noticeable but not striking. Most noticeable are the upper posterior thigh light spots/blotches (red in life) on juveniles, that are not present in either adult. The bellies and ventral thigh surfaces are much lighter than in the adults, with the smallest juveniles having the lightest bellies, with a size gradient of darkening evident.

Almost all individuals (94%) have some

sort of dorsolateral fold development (the 4 individuals scored as having no indication of dorsolateral folds perhaps due to preservation artifact?); 34% of the specimens have a pair of entire dorsolateral folds extending from behind the eye to at least as far as the sacrum; 60% of the individuals have a pair of interrupted folds to a series of ridges or elongate warts to at least the sacral region.

All individuals have at least a weakly-developed dorsal shagreen. Two juveniles have a pronounced shagreen with small bumpy glands. Thirty-one percent of the juveniles have at least a few tubercles on the dorsum, that are more abundant posteriorly. Both adults have a weakly developed dorsal shagreen; one lacks noticeable tubercles, the other has very few white dorsal tubercles.

Most specimens have a shagreen on the dorsal shank surface (lacking in only two). Most specimens (89%) have few to many white tubercles; few specimens (11%) have very few or no white tubercles.

The texture of the outer tarsus may be shagreened or not. Many specimens (70%) have few to many white tubercles; some specimens (30%) have very few to no white tubercles.

Only two specimens have a weak shagreen on the sole of the foot; only one specimen has a few white tubercles; all others have a smooth sole that is lacking shagreen or tubercles.

The single adult male has one white spine on each thumb and one white bump on each prepollex. There is no indication of chest spines, chest tubercles, or a patch of tubercles on the chin. Vocal sacs are neither laterally expanded nor differentially pigmented.

The adult female is 111.2 mm SVL, the adult male 117.6 mm SVL.

No tadpoles are available for this group.

Habitat data are available from Saramacca, Surinam (Charles W. Myers, pers. comm.) for AMNH 87705–87736 collected 23 February 1972 from a granite outcrop: "Three specimens of a considerably larger *Leptodactylus* [not collected] were seen on the granite at night, but when approached they backed under rock crevices in which lizards were sleeping. [Following notes for juveniles.] Several by day, under rock flakes around edges of bare granite surfaces; a few in pools in circular depressions after afternoon rain, an hour or so before dark. Most however at night, when they proved to be exceedingly abundant out on bare rock far away from any cover or crevice. The majority were sitting in the little damp gullies that resulted from overflowing of water from the circular holes and other depressions on the granite."

Intergroup differentiation and evaluation of species limits.—The group characterizations described in the preceding section are used to evaluate differentiation among the groups. In addition, some data are available for two or three of the groups that pertain to group differentiation. These additional data are presented below.

The preceding group characterizations demonstrate that the greatest differentiation occurs between the combined Groups 1 and 2 on the one hand and Groups 3 and 4 on the other. The most distinctive differentiating characteristics are size of adults, secondary male features, and contrast of juvenile and adult color patterns (Table 1).

Discriminant function analyses using measurement data support this clustering, although there are not enough data to include Group 4 in the analyses. Data run separately for males and females show the same results. Results of the male data show somewhat less differentiation among groups, so they are described as examples for both sets of analyses. Data for the Group 4 individual were not used in estimating the multivariate models. The posterior classifications based on group discriminant function means for Groups 1, 2, and 3 result in rather good group assignments overall, but most robust for Group 3, with only one male being posteriorly assigned to the wrong group (Group 1, Table

Table 1.—Distribution of certain characteristics among four groups of rocky habitat *Leptodactylus* from northern South America. Group 1 is from Colombia and nearby Venezuela, 2 from southeast Venezuela and Guyana, 3 from northern Brazil, 4 from Surinam and French Guiana.

	Group 1	Group 2	Group 3	Group 4
Female size in mm	55–78	54–74	104–113	111
Male size in mm	45–71	51–72	74–117	118
Number of spines/thumb in males	1	1–2	1	1
Chest spines in males	+	+	–	–
Band of chest tubercles in males	+	–	–	–
Chin tubercles in males	+	–	–	–
Vocal sacs laterally expanded and darkly pigmented	+	+	–	–
Juvenile and adult color patterns strikingly different	–	+	+	–

2). The graphical results when the first canonical factor is plotted against the second (Fig. 3) indicates that Group 3 individuals are separated from Group 1 and 2 individuals along the first axis, typically size related, which is consistent with the adult size distributions of the three groups. The single Group 3 individual that was posteriorly classified as belonging to Group 1 rather than 3 (USNM 302202) is the left-most symbol for Group 3 individuals in Fig. 3 and is the smallest male in the Group 3 sample.

Some micro-complement fixation tests, comparing albumins of some of these frogs included one sample from Group 2 and one sample from Group 3. Although materials were insufficient to raise antisera to either the Group 2 or Group 3 specimens, both samples were tested against antisera to albumins of other members of the *L. pentadactylus* species group. Results (Table 3) indicate that the Group 2 and Group 3 samples are not identical and, in fact, suggest that they are quite different.

Table 2.—Discriminant function analyses for male data for Groups 1 (Colombia and nearby Venezuela), 2 (southeast Venezuela and Guyana), and 3 (northern Brazil).

	Number of observations classified into groups		
	Group 1	Group 2	Group 3
Group 1	26	5	0
Group 2	4	31	0
Group 3	1	0	12

Thus, the data are unequivocal that at the very least, Groups 1 and 2 combined represent a distinct species from Groups 3 and 4 combined. The more difficult questions to resolve are whether Group 1 represents a species distinct from Group 2 and whether Group 3 represents a species distinct from Group 4. Each of these two situations is discussed in turn.

The greatest differences between Group 1 and Group 2 individuals are with male secondary sexual characteristics (Table 1). Whereas males in Group 1 have chin tubercles and, in the larger adults, a band of chest tubercles, no males in Group 2 have such tubercles. Whereas some males in Group 2 have two spines per thumb, all males in Group 1 have but one spine per thumb. There are differences in terms of degree of expression of states in the upper lip patterns, posterior thigh surface patterns, ventral thigh surface patterns, belly patterns, outer tarsal texture, and foot texture. Whereas there is complete overlap of adult sizes between the two groups, there is some morphological differentiation demonstrated by measurement data (Fig. 3). There is clearly some separation of Group 1 from Group 2 along the second canonical factor, indicating some differentiation of shape. The dependent variables that have the highest values on the second canonical factor

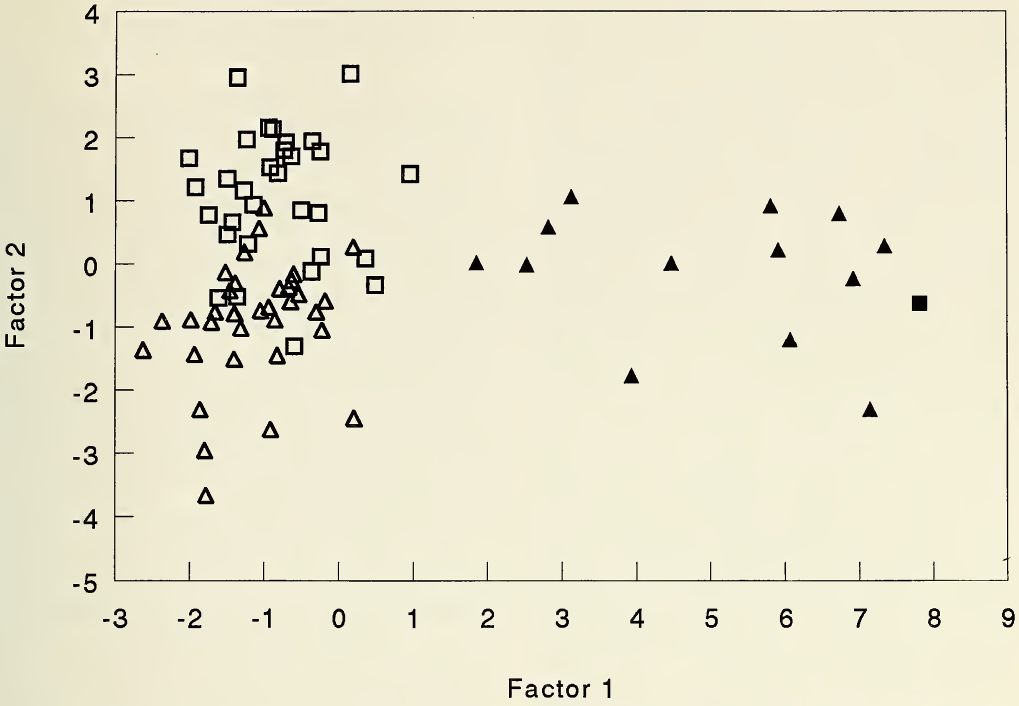

Fig. 3. Graph of first and second canonical factors for Group I–IV males. Group I = open squares, Group II = open triangles, Group III = filled triangles, Group IV = filled square.

for females are shank length (0.275), head length (0.253), thigh length (0.251), eye–nostril distance (0.250), and head width (0.236) and for males are thigh length (−0.512), shank length (−0.493), eye–nostril distance (−0.446), and foot length (−0.413), suggesting an overall shape difference. Given the discrete differences of male secondary sexual characteristics, combined with the evidence of demonstrable differentiation in pattern and morphology between Groups 1 and 2, the evidence is most consistent with recognizing members of these two groups as distinct species.

Evaluating the differentiation between Groups 3 and 4 is confounded by the fact that there is but a single adult male and a single adult female available for Group 4. In comparing the available data, there is less apparent differentiation between Groups 3 and 4 than between Groups 1 and 2 (also see Table 1). Group 3 juveniles differ from Group 4 juveniles in terms of ventral coloration pattern. Group 3 juveniles often have a very distinct longitudinal light band on dark ventral thigh surfaces; no Group 4 juveniles have this expression. Group 3 juveniles often have very light patterns over the entire ventral thigh surface; no Group 4 juveniles have this expression. Most Group 3 juveniles have very contrasting belly patterns of distinct light spots on

Table 3.—Immunological distances between albumins of two samples of northern South American granitic outcrop associated *Leptodactylus*.

	Immunological distance			
Samples	Anti-serum-*L. pentadactlus*	Anti-serum-*L. fallax*	Anti-serum-*L. flavopictus*	Anti-serum-*L. labyrinthicus*
Group 2 (Bolívar, Venezuela)	67	24	43	57
Group 3 (Roraima, Brazil)	22	30	57	43

a dark belly; no Group 4 juveniles have this pattern. As a consequence of these differences in juveniles, the contrast between juvenile and adult ventral patterns is more pronounced in Group 3 than in Group 4. The single adult male in Group 4 is 117.6 mm SVL, minimally larger than the largest Group 3 male, 116.8 mm SVL. The Group 4 male has a single white spine on each thumb and the merest indication of a second spine. White thumb spines in *Leptodactylus* occur due to two different reasons. They are characteristic of very young males, which have just become sexually mature, and some *Leptodactylus* seasonally shed the black keratin sheath of the spine. If the white spine condition of the Group 4 male is because it is a young male, then there is probably a size difference between Group 3 and 4 adults. When actually comparing the available adults from Group 3 and 4 side-by-side, I find no differences among them other than the male thumb condition noted. The data indicate that there has been some differentiation between Groups 3 and 4, but the data are not at all conclusive in deciding whether Groups 3 and 4 represent one or two species. Given the lack of advertisement calls and adequate samples of adults of Group 4, I prefer to take the nomenclaturally conservative (and very possibly the biologically incorrect) position of recognizing a single species for Group 3 and Group 4 combined.

Nomenclature.—Only a single name has been proposed for any of the frogs involved in this portion of the study: *Leptodactylus rugosus* Noble, 1923. As Donnelly & Myers (1991:23) pointed out, the holotype (AMNH 1169, 38 mm SVL) from near Kaieteur Falls, Guyana, described as an adult by Noble (1923:297), is in fact a juvenile. *Leptodactylus rugosus* applies to the frogs of Group 2 in this paper. Without available names for the other two species recognized as distinct, they are described as the following new species.

Leptodactylus lithonaetes, new species
Figs. 4A, 5

Holotype.—AMNH 100656, an adult male from Venezuela; Amazonas, SW sector Cerro Yapacana, 600 m, 3°57′N, 67°00′W. Collected by Charles W. Myers and John Daly on 18–19 February 1978.

Paratopotypes.—AMNH 100657–100666, 100668, same data as holotype except collected from 18–22 February 1978.

Diagnosis.—The species of *Leptodactylus* that share conditions of free toes (no lateral fringe) and indistinct dorsolateral folds (at least in some individuals) with *L. lithonaetes* are *bufonius, labialis, labyrinthicus, laticeps, latinasus, myersi, rugosus, syphax,* and *troglodytes.* The upper shank and posterior tarsus of *bufonius, labialis, latinasus,* and *troglodytes* are covered with large prominent white tubercles and males lack thumb spines; the upper shank and posterior tarsus of *lithonaetes* has black-tipped tubercles (in some preserved specimens the black tips may be lost, leaving white tubercles which are noticeably smaller than those of *bufonius,* etc.), and the males have a spine on each thumb. *Leptodactylus laticeps* has a tile-like dorsal pattern (Heyer 1979, fig. 1, pattern F) and is larger (minimum adult SVL 91 mm) than *lithonaetes* (maximum adult SVL 78 mm), which does not have a distinct tile-like pattern. *Leptodactylus labyrinthicus* is larger (minimum adult SVL 117 mm) than *lithonaetes*; no *L. labyrinthicus* have light loreal blotches, whereas several *lithonaetes* do. *Leptodactylus myersi* is larger (females 104–113 mm SVL, males 74–118 mm SVL) than *lithonaetes* and *myersi* males lack the chest spines found on *lithonaetes. Leptodactylus lithonaetes* is most likely to be confused with *L. rugosus* and *syphax*; the most distinctive characteristics among these three species are male secondary sexual characteristics. *Leptodactylus lithonaetes* has a single black spine on each thumb and a patch of brown/black tubercles on the chin/throat; all *L. syphax* and some *rugosus* have two spines per thumb and no *syphax* or *rugosus* males have a patch of chin tubercles.

Description of holotype.—Snout rounded from above and in profile; canthus rostralis indistinct; loreal weakly obtuse-concave; tympanum distinct, greatest diameter about ¾ eye diameter; vomerine teeth in strongly arched series, between and posterior to choanae, separated medially by about ⅙ length of single vomerine tooth series; vocal slits present; vocal sacs expanded laterally and darkened; finger lengths in increasing order II just < IV < I just < III; extensive finger ridging best developed on medial surfaces of fingers II and III; metacarpal tubercles large, about same size, inner triangular shaped, outer ovate and bifid; arms strongly hypertrophied; thumb with one large black medial spine, one pair of large bicuspid black chest spines, narrow band of brown-black tubercles across chest, field of brown-black tubercles on thumb on either side of spine, well developed field of brown-black tubercles on chin medially extending posteriorly to about mid-throat; dorsum relatively smooth, a few scattered black tubercles posteriorly; one short pair of interrupted dark-outlined ridges behind eye and above and posterior to tympanum, well developed supratympanic fold from eye to humerus; commissural gland well developed, flanks with three large irregular glands on each side, lower posterior thigh with elongate longitudinal gland; ventral texture smooth; belly disk fold well developed; toe tips bulbous, broader than toes immediately behind tips; toes free, lacking fringe or web; subarticular tubercles well developed, ovoid; outer rounded metatarsal tubercle relatively well developed, about ¼ size ovoid inner metatarsal tubercle; tarsal fold moderately developed, sinuous, extending about ⅘ length of tarsus; no metatarsal fold; outer tarsus with several brown-black tubercles; sole of foot smooth.

SVL 71.4 mm, head length 27.2 mm, head width 27.4 mm, eye–nostril distance 6.4 mm, interorbital distance 5.1 mm, greatest tympanum diameter (including annulus) 6.3 mm, thigh length 31.5 mm, shank length 31.5 mm, foot length 36.1 mm.

Dorsum with a light interocular bar; rest of back with ill-defined pattern of series of fused blotches on each side of midline and series of darker brown flecks more numerous posteriorly; upper limbs with faint suggestion of transverse bands, most distinct on dorsal surfaces of tarsus and foot; irregular dark canthal stripe, with an irregular light tan loreal blotch ventrally; upper lip with irregular dark border. Throat almost uniformly dark brown medially, laterally expanded vocal sacs dark brown, edges of jaws with black borders; chest, belly, and ventral limb surfaces with extensive, fine brown mottling. Posterior surface of thigh with large irregular-shaped dark and light blotches.

Etymology.—From the Greek *lithos,* stone, rock and *naetes,* inhabitant, in reference to its habitat.

Variation.—Variation is described earlier in the paper under Group 1 individuals.

Larval characteristics (based on sample from Cerro Patavá, Colombia, UTA 23499, 23507–23510, $n = 10$).—Dorsal head and body relatively uniform brown, dorsal pattern ending somewhat abruptly on side of head-body; oral disk lacking melanophores; belly with or without white flecks; ventral region anterior to guts with melanophores visible under skin; tail dorsal fin and most of muscular region mottled, with or without darker flecks and/or weakly-developed light ocelli; ventral musculature and tail fin lacking melanophores entirely or with melanophores on distal half, most heavy at tip region; nostril nearer eye than tip of snout; internarial distance greater than interorbital distance; eye diameter 14–16% head-body length; oral disk width 25–26% head–body length for Gosner stages 28–29, 22–26% head–body length for Gosner stages 35–40; anterior oral papilla gap 80–88% oral disk width; 32–34 denticles on one side of split tooth row anterior to beak (row A-2) for Gosner stages 28–29, 42–51 denticles for

Fig. 4. New species of *Leptodactylus.* A. Male paratopotype (AMNH 100668) of *Leptodactylus lithonaetes.* Photograph courtesy of C. W. Myers, American Museum of Natural History. B. Male paratopotype (AMNH 128021) of *Leptodactylus myersi.* Photograph courtesy of C. W. Myers, American Musuem of Natural History.

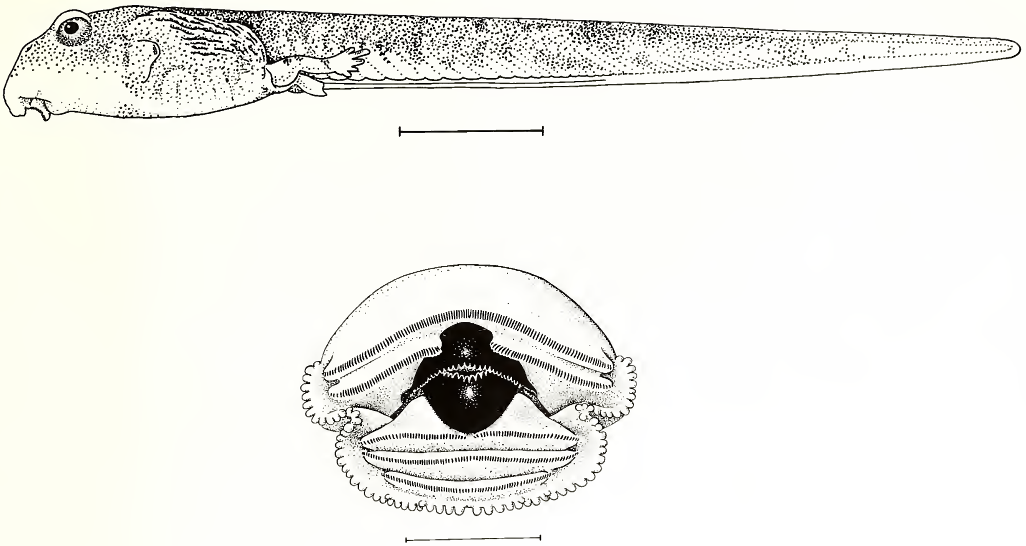

Fig. 5. Lateral view and mouthparts of larval *Leptodactylus lithonaetes*. Scale bars 5 and 1 mm respectively. Diagrammatic illustrations based on specimen from UTA-A 23509, Gosner stage 38.

Gosner stages 35–40; upper beak width 11–12% head–body length; upper beak depth 30–33% upper beak width for Gosner stages 28–29, 27–37% for Gosner stages 35–40; single row of marginal papillae; tooth row formulae 2(2)/3 or 2(2)/3(1); field of glandular ridges on body above abdominal cavity; spiracle sinistral; vent median; fins 29–33% tail depth at maximum tail depth for Gosner stages 28–29, 23–36% for Gosner stages 35–40; body depth 38–42% head–body length for Gosner stages 28–29, 42–48% for Gosner stages 35–40; body width 55–56% head–body length for Gosner stages 28–29, 58–64% for Gosner stages 35–40; body depth 70–75% body width for Gosner stages 28–29, 67–74% for Gosner stages 35–40; head–body length 32–35% total length for Gosner stages 28–29, 28–31% for Gosner stages 35–40; total length, stage 38, 36.1 mm (Fig. 5).

Advertisement Call.—Not recorded.

Karyotype.—Unknown.

Referred specimens (specifically not designated as types).—COLOMBIA. AMAZONAS: Río Igará-Paraná, 50 km arriba "La Chorrera," IND-AN 2822. GUAINÍA: Puerto Inírida, Río Atabapo, IND-AN 2808, 2811; Río Negro, opposite Casiquare Canal and Guainía, AMNH 23160–23162. VAUPES: Cerro Patavá, IND-AN 3399, UTA-A 3724–3725, 3772–3785, 3857–3877, 23499–23500 (larvae), 23503–23510 (larvae). VICHADA: Parque Nacional Natural El Tuparro, ICNMNH 14045–14047, IND-AN 2303–2304, 3736; Puerto Carreño, Cueva de Arévalo, ICNMNH 13970–13996.

VENEZUELA. AMAZONAS: Canaripo, RMNH 23913–23916, 23931–23950, 23970–23973 (plus 5 unnumbered juveniles and metamorphs and 3 larvae); Cerro Yapacana, AMNH 100667 (skinned specimen); Mision Coromoto-Atures, USNM 137186–137192; Puerto Ayacucho, AMNH 23209–23219, FMNH 175460–175465, 176197–176201, 176203–176222, KU 207531–207533, USNM 80634, 80665–80673, 291081–291082; Sanariapo, MCZ 27827, USNM 80635–80639. APURE: Hato Caribén, 46 km NE Puerto Páez, Río Cinaruco, USNM 216795–216797. BOLÍVAR: 3 km E Río Orinoco just below Río Horeda, 100 m, AMNH 62169; mouth of Río Parguaza, AMNH 62168.

Leptodactylus myersi, new species
Fig. 4B

Holotype.—MZUSP 66089, an adult male from Brazil; Roraima; Mucajaí, 2°25′N, 60°55′W. Collected by Celso Morato de Carvalho and Ronald I. Crombie on 31 May 1988.

Paratopotypes.—AMNH 128021–128031, MZUSP 70976–70986 collected by Celso Morato de Carvalho, Charles W. Myers, Thelma Schmidt, and P. E. Vanzolini on 11 July 1987, USNM 302190–302203, collected by Celso Morato de Carvalho and Ronald I. Crombie on 30 May–1 June 1988, USNM 302204–302205, collected by Carvalho and Crombie on 20 June 1988.

Diagnosis.—The species of *Leptodactylus* that share conditions of free toes (no lateral fringe) and indistinct dorsolateral folds (at least in some individuals) with *L. myersi* are *bufonius, labialis, labyrinthicus, laticeps, latinasus, lithonaetes, rugosus, syphax,* and *troglodytes.* The upper shank and posterior tarsus of *bufonius, labialis, latinasus,* and *troglodytes* are covered with large prominent white tubercles and males lack thumb spines; the upper shank and posterior tarsus of *myersi* has black-tipped tubercles (in some preserved specimens the black tips may be lost, leaving white tubercles which are noticeably smaller than those of *bufonius,* etc.) and the males have a spine on each thumb. *Leptodactylus laticeps* has a very distinct tile-like dorsal pattern (Heyer 1979, fig. 1, pattern F); *L. myersi* does not have a tile-like dorsal pattern. *Leptodactylus labyrinthicus* is larger (minimum adult SVL 117 mm) than *myersi*; all large (>170 mm SVL) male *labyrinthicus* have chest spines, no *myersi* males have chest spines. *Leptodactylus syphax* is smaller (maximum adult SVL 78 mm) than *myersi* (maximum adult SVL 118 mm) and male *syphax* have two spines per thumb in contrast to the single thumb spine found in *myersi. Leptodactylus lithonaetes* and *rugosus* are smaller (maximum adult SVL 78 mm) than *myersi.* The males of *L. lithonaetes* and *rugosus* have laterally expanded vocal sacs; the male vocal sacs of *L. myersi* are not expanded externally.

Description of holotype.—Snout nearly rounded from above and rounded in profile; canthus rostralis indistinct; loreal obtuse-concave; tympanum distinct, greatest diameter about ⅔ eye diameter; vomerine teeth in arched series, between and posterior to choanae, separated medially by about ¼ length of single vomerine tooth series; vocal slits present; vocal sac single, internal; finger lengths in increasing order II just < IV < I just < III; finger ridges well developed medially on fingers II and III; inner and outer metacarpal tubercles large, about same size, outer bifid; arms moderately hypertrophied; thumb with one large black medial spine; no chest spines; band of black tubercles aross chest, on ventral surfaces of upper arms, on flanks near axilla and along lateral edges of jaws ventrally; dorsum relatively smooth, a few small black or white tubercles scattered posteriorly; extensively interrupted pair of dark-outlined dorsolateral folds from eye to beyond sacrum, distinct continuous supratymypanic fold from eye to humerus; flanks glandular; belly smooth; belly disk fold discernible but weak; toe tips bulbous, broader than toe widths just behind tips; toes ridged laterally, especially on toes I, II, and III, not developed into fringe; subarticular tubercles well developed, ovoid; outer metatarsal tubercle round, flattened, about ½ size of ovoid inner tubercle; tarsal fold well developed, extending about ⅔ length of tarsus; no metatarsal fold; outer tarsus with a few small white or black tubercles; sole of foot smooth.

SVL 109.4 mm, head length 47.2 mm, head width 44.1 mm, eye–nostril distance 9.9 mm, interorbital distance 8.4 mm, greatest tympanum diameter (including annulus) 7.8 mm, thigh length 47.2 mm, shank length 44.1 mm, foot length 46.8 mm.

Dorsum dark gray brown with irregular darker brown interorbital blotch and two darker dorsal chevrons, one in shoulder region, one in sacral region; dark well-defined canthal stripe; upper lip rather uniform gray-brown; upper limbs transversely banded. Venter dark and gray, chin and throat uniform, chest and belly with indistinct light, small vermiculations. Upper portion of posterior thigh surface with extension of dorsal band pattern, lower portion with black elongate oval region containing a few contrasting small light regular and irregular spots.

Etymology.—Named for Dr. Charles W. Myers for his contributions to Neotropical herpetology in general and bringing this new species to my attention in particular.

Variation.—Variation is described earlier in this paper under Group 3 and Group 4 individuals.

Advertisement Call.—Unknown.

Karyotype.—Unknown.

Referred Specimens (specifically not designated as types).—BRAZIL.[1] AMAZONAS: Rio Aracá (Serrinha), MZUSP 59016, 59018, 59026-59028. RORAIMA: Colonia Apiaú, MZUSP 65949, USNM 302267; Mucajaí, USNM 302206 (gutted and partially deboned).

FRENCH GUIANA. No further locality, MNHN 1982-81; Massif des Emerilions, MNHN 1982-82; Montagne St. Marcel, MNHN 1982-73–1982-80; Montagne des Trois Pitons, MNHN 1982-153; Peolaeu (Haut Oyapock), MNHN 1982-83; Trois Saut, MNHN 1982-84.

SURINAM. BROKOPONDO/NICKERIE: Tafel Berg, 1025 m, MCZ 97259–97261, 97299, 97303, 97306, 97308, RMNH 23912, 23919–23930, 23951–23961. NICKERIE: Amotopo, RMNH 23964–23968; Blanche Marie-Vall, RMNH 23910–23911. SARAMACCA: Raleighvallen-Voltzberg Nature Preserve, MCZ 92363; Voltzberg, RMNH 23974–23976.

Disposition of Specimen from Paraguay

On 22 July 1973, the mammalogist Philip Myers collected a single specimen of *Leptodactylus,* MVZ 111027, that resembles *L. syphax* from a rocky region with caves 1 km S of Tobatí, La Cordillera, Paraguay (25°15′S, 57°04′W). The same cave system has been re-collected by mammalogists, who have also collected whatever frogs they encountered (P. Myers, pers. comm.). Even though these newer collections contain *Leptodactylus,* none of them are the same species as MVZ 111027.

Description of the adult female from near Tobatí follows: tympanum large, greatest diameter about ⅞ eye diameter; vomerine teeth in arched series posterior to the choanae, contacting medially; palatine teeth present; inner metacarpal tubercle ovoid, the outer (about same size as inner) somewhat rounded, tubercles separated by less than width of inner tubercle; dorsum glandular and smooth; supratympanic fold distinct, no other folds present; no distinct glands other than the general glandular structure of skin on top of shanks and on back; venter smooth; ventral disk not well defined; tips of toes barely swollen; toes lacking fringe or web; no metatarsal fold; tarsal fold weakly developed extending about ⅗ length of tarsus; dorsal shank and outer tarsus surfaces glandular with scattered white tubercles; sole of foot smooth; side of head uniform brown; dorsum brown with faint quadrangular ocellations; upper arm surfaces almost uniform brown; upper leg surfaces weakly cross banded with darker brown; venter cream, lacking melanophores; posterior surfaces of thighs distinctly mottled, almost spotted; SVL 79.7 mm, head length 31.7 mm, head width 29.1 mm, eye–nostril distance 7.4 mm, tympanum diameter 6.5 mm, thigh length 28.7 mm, shank length 30.0 mm, foot length 30.6 mm.

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[1] After the manuscript was submitted for publication, another locality for *L. myersi* was discovered in the collections at MZUSP. MZUSP 28405, 54110–54114 are from Brazil, Pará, Igarape Jaramacaru, Campos do Ariramba, 1°09′S, 55°54′W. The frogs were collected from sandstone formations (P. E. Vanzolini, pers. comm.), a common feature within the Campos do Ariramba region (Egler 1960).

Fig. 6. Known distribution of *Leptodactylus syphax* in Brazil and Paraguay. Political boundaries outlined for Brazil and Paraguay. Map truncated at 40°S.

The Tobatí specimen is very similar to *L. syphax* from Brazil. They are the same size and share the same features of pattern and texture. The shared pattern of a low-contrast mosaic pattern of quadrangular ocellations is uncommon in the genus. The striking visual difference between the Tobatí specimen and Brazilian *L. syphax* is the short leg of the Tobatí specimen. The thigh/SVL, shank/SVL, and foot/SVL ratios for the Tobatí specimen are 36%, 38%, and 38% respectively. The mean female ratios for *L. syphax* are 42%, 42%, and 44% respectively. The only other feature that differs between the Tobatí specimen and Brazilian *L. syphax* is that the subarticular tubercle on the thumb of the Tobatí specimen is less pronounced than in Brazilian *L. syphax*.

Without additional material, it is impossible to know whether the short leg of MVZ 111027 is characteristic of the population or is an individual aberration. The species identification of the Tobatí deme is made more difficult by the lack of both advertisement call data and information on male secondary sexual characteristics. Given the available data, I think the best taxonomic conclusion is to consider that the Tobatí specimen is conspecific with *L. syphax*. This conclusion should only be taken as a working hypothesis until further data become available. The geographic extension into Paraguay of *L. syphax*, although considerable, might be expected given the disjunct nature of the rest of the known populations of *L. syphax* (Fig. 6).

Discussion

The main conclusion of this study is that there is considerably more variation among populations of *Leptodactylus* associated with rocky habitats than previously summarized (Heyer 1979). Fully understanding and interpreting that variation is not possible at this time. Two suites of questions are raised: those associated with distributions and those associated with relationships.

The degree of habitat restriction to rocky habitats, either streambeds or outcrops, is not known for certain, but such habitat fidelity is high, if not complete. The semiterrestrial larval ecomorph of *L. lithonates* and *rugosus* is certainly an adaptation associated with rocky substrates and probably flowing water. The larvae of *L. myersi* and *syphax* are unknown, but adults and juveniles of both have been collected most frequently (entirely so for *L. syphax*) from rocky outcrops. The scanty data suggest a greater association of *L. lithonaetes* and *rugosus* with rocky streams (either in a granite or sandstone setting) and *L. myersi* and *syphax* with granitic or sandstone outcrops. The patchy distributions of the taxa also indicate a high fidelity to rocky habitats, which themselves are patchily distributed. This habitat fidelity allows prediction of where the species should occur in areas where they have not been collected up to the present. For example, the easternmost locality in Colombia for *L. lithonaetes* (Amazonas, Río Igará-Paraná), coincides reasonably well with an isolated occurrence of Precambrian-aged rocks with granite being among the most common rock types (Kroonenberg 1985, fig. 1, p. 58). There are additional isolated patches of Precambrian rocks of the same formation in Colombia (Kroonenberg 1985:58) from which *L. lithonaetes* are currently unknown. *Leptodactylus lithonaetes* would be expected to occur (at least historically, if not currently) on these Precambrian rock formations if running water exists in the formations.

There are several questions remaining regarding relationships. Although *L. lithonaetes* is considered distinct from *rugosus* in this paper, it is possible that the differences between the two taxa represent (pronounced) geographic differentiation in a single species. On the other hand, the differences herein interpreted to represent geographic variation between the Surinam and French Guiana populations of *L. myersi* and the Roraima, Brazil, populations of *myersi,* may be too conservative an interpretation and two species should be recognized instead. The species allocation of the frogs from Brazil, Amazonas, Rio Aracá need verification. At present, only rather small-sized juveniles are available from the Rio Aracá site. The characteristics they have are consistent with being conspecific with *L. myersi* (my best guess), or *L. lithonaetes,* or representing yet another new species. The Paraguayan population needs resampling to verify whether it is conspecific with *L. syphax.* It is very likely that advertisement call data could resolve the outstanding species level problems. At another level, the available data can not answer the question whether the rocky habitat associated species of *Leptodactylus* are a monophyletic cluster, having a common ancestor that became adapted to the habitat, or not. Larval information for *L. myersi* and *syphax* may resolve this question, but it is more likely some appropriate molecular based analysis is needed to answer it.

Given the many questions about relationships, any detailed discussion of zoogeography of these species is premature.

Acknowledgments

Charles W. Myers, AMNH, alerted me to the new species from Roraima, freely shared all the extensive data he had collected on frogs studied in this paper, and reviewed the manuscript. Linda R. Maxson, The University of Tennessee, kindly provided the micro-complement fixation data reported herein. For providing color and habitat notes, I thank Ronald I. Crombie (USNM), John D. Lynch (University of Nebraska), Charles W. Myers, and Robert P. Reynolds (National Biological Service). Kate Spencer drew the tadpole illustrations (Figure 5). George R. Zug (USNM) reviewed the manuscript.

For their patience in allowing me to study materials on loan over a several year period, I thank the following institutions and their curatorial staffs: AMNH—Charles W. Myers; BMNH—Barry T. Clarke; CM—Ellen J. Censky and the late Clarence J. McCoy; FMNH—Harold Voris and Alan Resetar; ICNMNH—María Christina Ardila-R. and Pedro M. Ruiz-C.; IND-AN—José Vicente Rueda-A.; KU—William E. Duellman and John E. Simmons; MCZ—José P. Rosado and Ernest E. Williams;

MNHN—Alain Dubois; MZUSP—P. E. Vanzolini; RMNH—Marinus S. Hoogmoed; UMMZ—Ronald A. Nussbaum and Gregory Schneider; UTA—Jonathan A. Campbell and William F. Pyburn.

Research for this paper was supported by the Instituto Nacional de Pesquisas da Amazônia as part of the "Herpetofauna of Roraima" Project under the direction of Celso Morato de Carvalho; the Museu de Zoologia da Universidade de São Paulo and retired Director P. E. Vanzolini; and the Smithsonian Institution's Neotropical Lowlands Research Program, funded by the International Sciences Program and the Director's Office (USNM).

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):717–728. 1995

The taxonomic status of the shrew of St. Lawrence Island, Bering Sea (Mammalia: Soricidae)

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Abstract.—Shrews of the subgenus *Otisorex* inhabit two islands in the Bering Sea, within the limits of the former Beringian Refugium. Whether those taxa represent independent species, or subspecies of the nearctic *Sorex cinereus* Kerr, has remained uncertain. The karyotype (2N = 66, FN autosomes = 70) of one of these, described as *Sorex jacksoni* Hall et Gilmore from St. Lawrence Island, has been defined and compared with that of *S. c. cinereus* on the Alaskan mainland, from which it could not be distinguished. No differences could be discerned between the two taxa in structure of the glans penis or in relationships of the medial tines of the incisors. The shrew on St. Lawrence Island is regarded as being a subspecies of *S. cinereus,* for which the designation *S. c. jacksoni* Hall et Gilmore is applicable. A review of published karyograms and other information supports the concept that no species of the subgenus *Otisorex* is holarctic.

Sorex cinereus Kerr has the most extensive geographic range of any species of shrew in the Nearctic, occurring in North America from approximately lat. 35°N to the northern shores of Alaska and Canada (Hall 1981, map 14). Records of Rancholabrean age indicate that its distribution had been more extensive in the southern regions of the continent (Kurtén & Anderson 1980: 105). The fossil record of that species dates from deposits of late Mindel-Kansan time, and possibly earlier.

Diverse interpretations concerning the taxonomy and the geographic ranges of some shrews of the *Sorex cinereus*-group (subgenus *Otisorex*) have been given in the recent literature, especially relating to the northern forms. Hall (1981) distinguished 12 nearctic subspecies of *S. cinereus,* including *S. c. jacksoni* Hall et Gilmore, on St. Lawrence Island (Bering Sea), and *S. c. ugyunak* Anderson et Rand, which inhabits mainly the treeless regions of the continent from northwestern Alaska eastward to the western shores of Hudson Bay and Foxe-Basin. Another of the group, *S. pribilofensis* Merriam, occurs on St. Paul Island, Pribilof Islands (Bering Sea) (Hoffmann & Peterson 1967). In Eurasia, Stroganov (1956) described *S. c. portenkoi* from the vicinity of Anadyr' (Chukotka) (approx. 64°40′N, 177°20′E), providing the first indication that *S. cinereus* might have an holarctic distribution. Two additional subspecies have been recognized in northeastern Eurasia: *S. c. camtschaticus* Iudin, 1972 (type locality: Kambal' Bay, Ust'-Bol'sheretsk region, Kamchatka) (approx. 52°45′N, 156°30′E), and *S. c. leucogaster* Kuroda, 1933 (syn. *S. beringianus* Iudin, 1967) (type locality: Paramushir Island, Kurile Islands).

On the basis of morphometric analysis, van Zyll de Jong (1982) tentatively considered that *S. cinereus, S. jacksoni,* and *S. pribilofensis* are independent species. According to his concept, *S. jacksoni* would be holarctic in distribution, with *S. j. jacksoni* on St. Lawrence Island, *S. j. ugyunak* in northern North America, and *S. j. portenkoi* and *S. j. leucogaster* in Eurasia. The taxon previously designated *S. c. camtschaticus* was considered also to represent a distinct species. The results of van Zyll de Jong's (1991) further analyses of cranial characters were taken to be compatible with those taxonomic conclusions, except that *leucogaster* also was regarded as being an independent species. Van Zyll de Jong pointed out that his conclusions were tentative, and that study of other taxonomic criteria, particularly cytogenetic and biochemical, was needed. He earlier (1982) noted that "clarification of phallic morphology is needed." Hutterer (1993) acknowledged van Zyll de Jong's concept that *ugyunak* may be specifically distinct from *cinereus.* Junge & Hoffmann (1981) considered *S. jacksoni* and *S. pribilofensis* (designated by them as *S. hydrodromus* Dobson) to be distinct from *S. cinereus.* Okhotina (1984) retained the Eurasian taxa as subspecies of *S. cinereus.* A different concept was presented by Ivanitskaia & Kozlovskii (1985), who proposed on the basis of chromosomal criteria that *S. cinereus* does not occur west of Bering Strait. They regarded *S. c. ugyunak* (without karyological data) as being a distinct species with an holarctic distribution, represented in Eurasia by *S. u. portenkoi.* Zaitsev (1988) pointed out that in such case the trivial name *ugyunak* would have to be replaced by *portenkoi* on grounds of priority. In their review of the systematics of mammals of the USSR, Pavlinov & Rossolimo (1987) concluded that *S. cinereus* does not occur in Eurasia, and that no species of the subgenus *Otisorex* is holarctic. They distinguished three palaearctic taxa in that subgenus: *S. leucogaster, S. ?portenkoi,* and *S. camtschaticus.*

To contribute towards a resolution of some of the taxonomic uncertainties involving shrews of the *cinereus*-group, we describe here the karyotype of *S. c. cinereus* on the basis of shrews collected on the Alaskan mainland, and compare that of *S. c. jacksoni* (Fig. 1) on St. Lawrence Island. The structure of the glans penis and other taxonomic characters are also compared. Our attempt to collect *ugyunak* in the vicinity of Barrow, Alaska, during August 1994 was unsuccessful, and its karyotype has not been defined. Indications of its intergradation with *S. c. cinereus* along the northern front of the Brooks Range, arctic Alaska, are briefly discussed.

Material and Methods

For convenience, and with respect to our conclusion concerning the status of one of the taxa studied, we apply the nomenclature of Hall (1981) for subspecies of *Sorex cinereus.* The specimens examined consisted of 239 shrews of the *S. cinereus*-group, collected by us and coworkers in Alaska during the period 1949–1975 and by us during 1980–1994. Specimens of the taxa considered here included *S. c. cinereus,* 90; *S. c. jacksoni,* 77; *S. c. hollisteri* Jackson, 58; and *S. c. ugyunak,* 14, along with measurements of nine additional specimens for which skulls were not retained. Standard data were recorded for all specimens collected, as well as information about reproductive status; skulls or skeletons were routinely prepared. Since many of the shrews were collected primarily for helminthological investigations, skins were prepared only as time permitted; nonetheless, small series were available for all of the taxa considered. For examination of the glandes, entire penes were usually fixed in extended condition in 10% formalin solution. One each from *S. c. cinereus* and *S. c. jacksoni* was stained in acetic carmine, dehydrated in ethanol, and cleared in terpineol for examination. Two additional male specimens of *S. c. jacksoni* (August 1957 and May 1993) were used only for the study of the genital organs. Measurements of larger cranial dimensions were made by means of a dial-caliper, graduated in tenths of millimeters and provided with a fine adjustment.

Fig. 1. *Sorex cinereus jacksoni.* Photographed on 15 June 1992, approximately 1 km west of Savoonga, St. Lawrence Island.

In measuring tooth-rows and other features of small size, a stereoscopic microscope with a calibrated scale, graduated in tenths of millimeters, was used. Degrees of latitude and longitude given below are approximate.

Chromosomes were examined from 7 specimens of *S. c. cinereus* collected in Alaska as follows: 1 female (August 1972), Chena Hot Springs Road (64°53′N, 147°W); 1 female (August 1993), 6 km NE of Palmer (61°39′N, 149°13′W); 1 female, 1 male (August 1991), 16 km N of Gakona Junction Village (62°24′N, 145°22′W); 1 male (August 1993), 35 km S of Paxson (62°52′N, 145°29′W); 2 females (August 1993), 17 km S of Copper Center (61°51′N, 145°15′W). From *S. c. jacksoni,* preparations were made from 5 adults and 2 embryos collected near Savoonga, St. Lawrence Island (63°42′N, 170°29′W): 3 males (June 1980, June 1984, June 1987); 1 female (June 1987), and 1 female (June 1988), with one female and one male embryo.

Cells from marrow and lymphatic tissue were treated with colchicine and hypotonic solution, centrifuged, fixed, and placed on slides in the field, where also testicular tubules were fixed and stained in acetic orcein, employing standard karyological procedures. Most preparations were stained in the laboratory at the University of Washington; in some cases, only orcein-staining was feasible. Banding of chromosomes was produced by application, for G-banding, of the method of Seabright (1972), and for C-bands, that of Sumner (1972). Chromosomes were counted and evaluated in intact cells in metaphase; at least 10 cells were photographed from each animal, from which, in non-banded complements (standard Giemsa stain), measurements were made as recommended by Levan et al. (1964). In karyograms constructed for comparisons, arm-ratios and size were the bases for assembling pairs of non-banded chromosomes. Those with G-bands were distinguished according to banding pattern and size; C-banded chromosomes were identified by size and by location of centromeric heterochromatin. The fundamental number

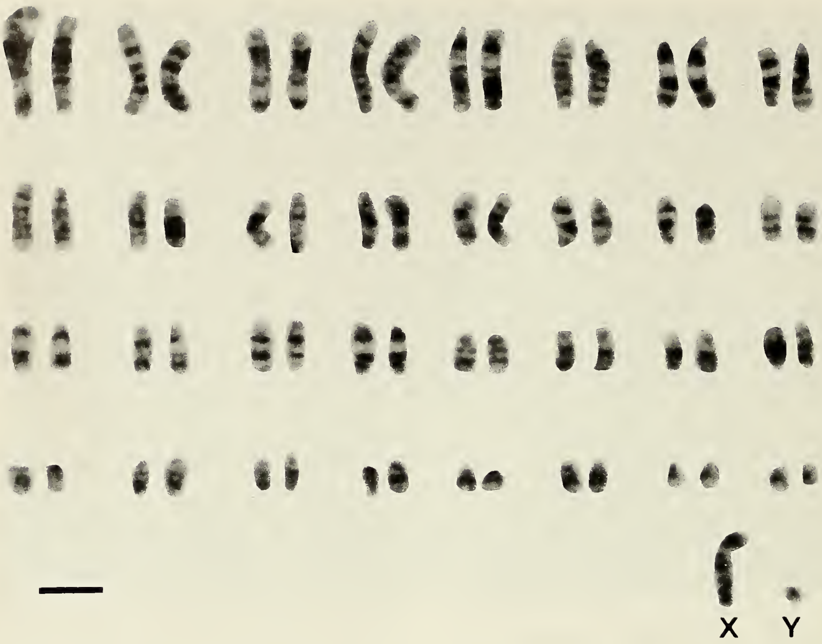

Fig. 2. Karyogram of *Sorex c. cinereus,* male. Giemsa-banding. Scale-bar represents 5 micrometers.

(FN) of major chromosomal arms was determined according to the method of Matthey (1945).

Voucher-specimens of the two subspecies of *Sorex cinereus* have been deposited as follows: Burke Memorial Washington State Museum, University of Washington, Seattle, No. 39403 (*Sorex cinereus jacksoni*); and Museum of Southwestern Biology, University of New Mexico, Albuquerque, Nos. 69701, 69702, 69703 (*Sorex cinereus jacksoni*), and Nos. 69704 and 69705 (*Sorex cinereus cinereus*).

Results

Karyograms.—Sorex cinereus cinereus: The diploid complement (66) consisted of the following: autosomes–centromere in subterminal to near-terminal region (pairs 1–31) (range of arm-ratio 3.8 to 12.0); centromere in median region (pair 32) (arm-ratio 1.2 to 1.4); sex chromosomes–X-chromosome with centromere in submedian region (range of arm-ratio 2.0 to 2.7), in metaphase usually approximately equal in total length to that of largest autosomes; Y-chromosome with centromere in subterminal region (arm-ratio not determined). The Y-chromosome (in metaphase) was the smallest of the complement (Fig. 2). The FN was calculated to be 70. The distribution of constitutive heterochromatin in the diploid complement (C-banded) is shown in Fig. 3.

Meylan (1968) preliminarily reported a diploid number of 66 and FN of 70 for two female specimens of *S. c. cinereus* collected in the Province of Ontario, Canada; that publication appeared later than his description and illustration of the chromosomal complement (Meylan 1967). Recently, Volobouev & van Zyll de Jong (1994) provided karyograms of a male shrew of that species from Pennsylvania. We conclude that the aforementioned specimens, all collected near the eastern limits of the range of *S. c. cinereus,* were karyotypically identical with those obtained in Alaska. The karyotype of *S. c. cinereus* is probably uniform throughout its geographic range.

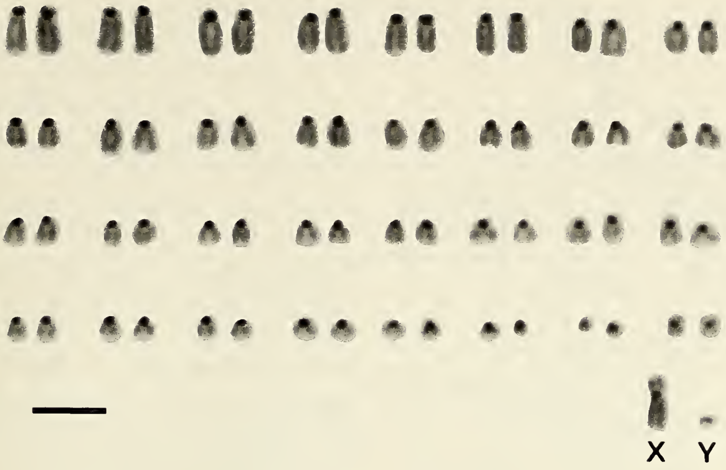

Fig. 3. Karyogram of *S. c. cinereus,* male. C-banding. Scale-bar represents 5 micrometers.

Sorex cinereus jacksoni: The diploid complement (66) consisted of the following: autosomes–centromere in subterminal to near-terminal region in 31 pairs (1–31) (range of arm-ratio 3.6 to 13.6); centromere in median region (pair 32) (arm-ratio of 1.1 to 1.6); sex chromosomes–X-chromosome with centromere in submedian region (range of arm-ratio 1.7 to 2.6); Y-chromosome (metaphase) was the smallest in the complement (Fig. 4). As in *S. c. cinereus,* the FN of *S. c. jacksoni* was 70. The preparations from all but two were processed with acetic orcein; G-banded chromosomes were not of uniform quality, but homologues could be identified and compared by selecting the best individuals from each preparation. We were unable to discern karyological differences between *S. c. cinereus* and *S. c. jacksoni.*

The glans penis.—The glans penis of *S. c. cinereus,* first illustrated by Iudin (1969), differs in form from that of any other species of *Sorex* for which information is available. We compared the glandes of six specimens of *S. c. jacksoni* with four from *S. c.*

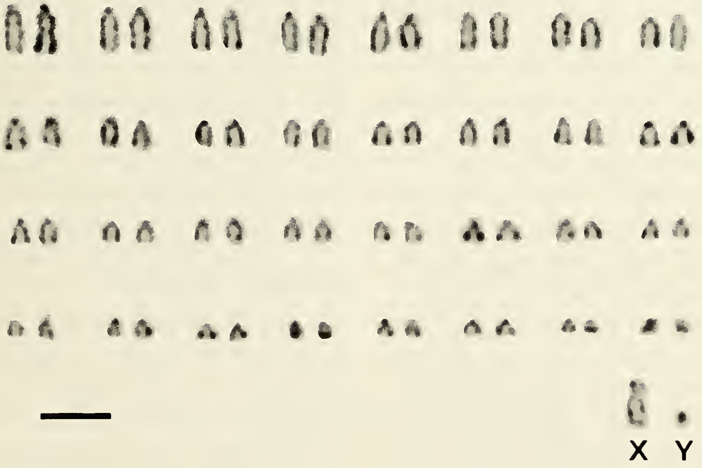

Fig. 4. Karyogram of *S. c. jacksoni,* male. Orcein. Scale-bar represents 5 micrometers.

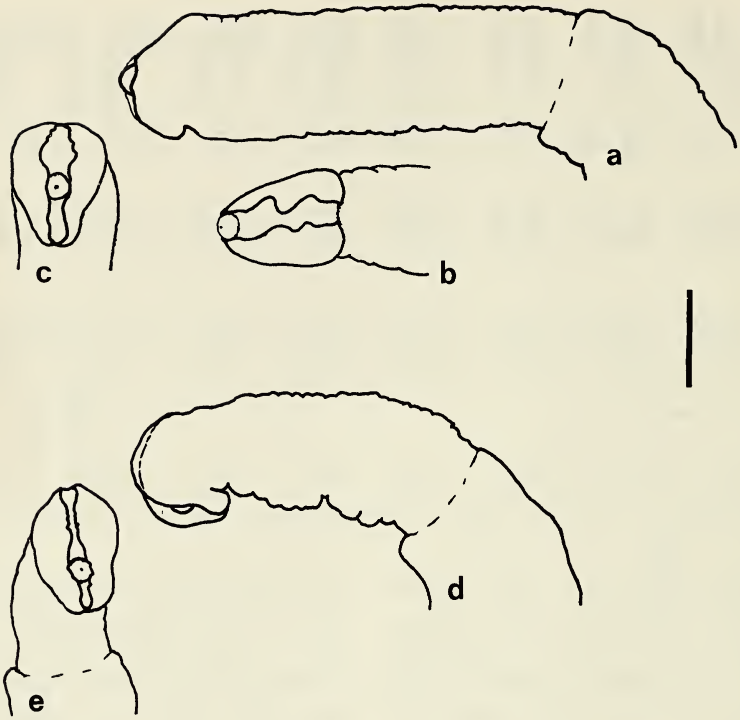

Fig. 5. Glans penis of *S. c. cinereus* (a–c) and *S. c. jacksoni* (d–e). a, lateral view of penis; b, dorsal view of glans; c, *en face* view of glans; d, semi-lateral view of penis; e, *en face* view of glans. Scale-bar represents 1 millimeter.

cinereus. The penes of both were of approximately uniform diameter distally, and were about 1 to 1.5 mm in diameter just posterior to the glans. When not fully extended, the surface of the penis immediately posterior to the glans exhibited folds, some of which extended around the entire circumference of the organ. In our specimens, such folding of the superficial tissue was not so strongly defined as was portrayed by Iudin (1969). In lateral view, the anterior surface of the glans appeared truncate to curved, with its distal portion projecting ventrad or ventroposteriad, depending on degree of contraction (Fig. 5a). In en face view, the glans was more or less cordate in shape, and was bisected by a medial groove extending anteriad and ventrad from the dorsal surface to the end of the ventral protrusion (Fig. 5c). The orifice of the urethra was situated in that groove near the middle of the anterior surface of the glans, opening at the apex of a small papilla, which in some cases protruded slightly above the surrounding surface of the glans (Fig. 5a, b). In one specimen, the end of the urethra protruded from the papilla, appearing as a processus urethrae; probably, however, it was a structural artifact, produced in the process of removing the organ for fixation. It was evident that the glans is subject to muscular control, which may cause slight modification in its shape. The glandes of *S. c. jacksoni* (Fig. 5d, e) were indistinguishable from those of *S. c. cinereus.* A fully relaxed penis of *S. c. jacksoni* was 19 mm long from its point of attachment to its distal end. The animal (TL 91 mm) was in breeding condition, with testes measuring 5 × 3.5 mm. Also compared was the glans penis of one specimen of *S. c. hollisteri* collected at Hooper Bay (Kuskokwim-Yukon delta) (61°27′N, 166°W) in May 1966 and preserved intact in formalin solution. The glans was indistinguishable from that of *S. c. cinereus* and *S. c. jacksoni.*

Other morphological characters.—Cranial characters of shrews of the *cinereus*-group have been compared by van Zyll de Jong (1976, 1982, 1991). We found in *S. c. jacksoni* that the accessory medial tines of the incisors, also important taxonomically (Junge & Hoffmann 1981; Dannelid 1989, 1994) did not differ in position from those of *S. c. cinereus, S. c. hollisteri,* and *S. c. streatori,* from the Alaskan mainland, but were perhaps slightly greater in length. Like some other small mammals inhabiting islands in the Bering Sea, *S. c. jacksoni* is somewhat larger than shrews representing the various subspecies of *S. cinereus* on the Alaskan mainland. External measurements (Table 1) were based on a series of 38 males and 23 females, judged to be adults on the basis of the reproductive status of those collected during July and August, and on the large size of those obtained during September through November. Another series of 23 specimens collected in June, considered to be over-wintered adults, averaged somewhat smaller (Table 1). Compared with specimens of *S. c. cinereus* collected in east-central Alaska during August, mean total lengths of *S. c. jacksoni* were greater and tail-length was less. Weights were not obtained for the series of *S. c. cinereus.* Youngman (1975) found weights of nine specimens from the southern Yukon Territory to range from 3.1 to 5.1 g ($\bar{X}$ = 4.3 g). Mean total length for a series of 18 specimens of *S. c. hollisteri* (one collected in June, the remainder in August) from Napaskiak (62°41′N, 161°54′W) on the lower Kuskokwim River was similar to that of males of *S. c. jacksoni*; *S. c. jacksoni* had a shorter tail, and the mean body-weight was greater (Table 1). For the series of *S. c. jacksoni* collected in summer, weights of 13 non-pregnant females ranged from 4.8 to 7.3 g ($\bar{X}$ = 5.0 g). In 11 pregnant animals,

Table 1.—Body measurements (mm) and weights (g) of some subspecies of *Sorex cinereus.*

Subspecies	Total length				Length tail				Hind foot				Weight			
	n	Range	$\bar{X}$	*SD*	*n*	Range	$\bar{X}$	*SD*	*n*	Range	$\bar{X}$	*SD*	*n*	Range	$\bar{X}$	*SD*
jacksoni	31 ♂♂	92–103	97.8	(2.67)	38 ♂♂	32–38	35.2	(1.39)	38 ♂♂	12–13	12.4	(0.44)	35 ♂♂	4.1–7.0	5.5	(0.81)
(July–Nov)	17 ♀♀	89–105	99.4	(4.10)	23 ♀♀	32–37	34.5	(1.61)	23 ♀♀	11.5–13	12.3	(0.43)	19 ♀♀	4.3–8.8	6.3	(1.20)
jacksoni	13 ♂♂	91–100	94.9	(3.47)	13 ♂♂	30–38	34.8	(2.34)	13 ♂♂	12–13	12.5	(0.48)		—		
(June)	11 ♀♀	91–104	95.7	(5.60)	11 ♀♀	31–36	34.3	(2.09)	11 ♀♀	12–13.5	12.5	(0.52)		—		
cinereus																
(10 ♀♀ 2 ♂♂)	12	89–101	93.2	(3.78)	12	36–43	38.5	(2.21)	12	10–13	12.2	(1.06)		—		
hollisteri																
(8 ♀♀ 7 ♂♂ 3?)	18	91–101	97.7	(2.72)	18	32–41	37.2	(2.19)	18	11–13	11.7	(0.55)	14	3.8–6.5	4.5	(0.75)

the numbers of embryos ranged from 5 to 14, with a mean of about 10 (9.7).

Discussion

With respect to the relationships and distributional status of shrews of the subgenus *Otisorex,* two differing hypotheses have been proposed: *Sorex jacksoni* may be an independent species, with three subspecies, *S. j. jacksoni* (St. Lawrence Island), *S. j. portenkoi* (NE Siberia), and *S. j. ugyunak* (tundra of NW North America); *S. pribilofensis* (St. Paul Island), *S. leucogaster* (Paramushir Island), and *S. camtschaticus* (NE Siberia) would each be specifically distinct; or *jacksoni* and *leucogaster* may be closely related if not conspecific, and *ugyunak* would be an independent species, represented in North America by *S. u. ugyunak* and in Eurasia by *S. u. portenkoi.* Since *portenkoi* (a prior name, see introductory remarks) would then replace *ugyunak,* the subgenus *Otisorex* would be represented in Eurasia by the species *leucogaster, camtschaticus,* and *portenkoi,* of which the last would be holarctic. Karyological investigations, although incomplete, have been helpful in resolving some of the questions about conspecificities.

As described and illustrated by Ivanitskaia & Kozlovskii (1985), the karyotype of *portenkoi* (2N = 60, FN = 60) distinguishes that taxon from *S. c. cinereus* and *S. c. jacksoni* (2N = 66, FN = 70). The karyogram of *leucogaster,* however, is like that of the latter two taxa with respect to diploid number, FN, and perhaps morphological characteristics of the chromosomes. Nonetheless, *leucogaster* is considered to be specifically distinct from *S. cinereus* (Ivanitskaia & Kozlovskii 1985, Pavlinov & Rossolimo 1987, van Zyll de Jong 1991). A significant distinguishing character, as shown by Iudin (1969, 1971), is the glans penis of *S. beringianus* Iudin (= *S. leucogaster*), which differs from that of *S. cinereus* in being rounded and smooth, described by Iudin (1969:29) as having ". . . a massive, globular, rounded crown," with an apparent corona, and lacking the ventral extension typical of the glans of *S. cinereus.*

Definition of karyotypes can be expected to clarify the affinities of *pribilofensis* and *ugyunak.* We examined the glans penis of only one specimen of *S. pribilofensis,* dissected from an animal preserved in formalin, and it was not suitable for detailed comparison. Some indications exist that *ugyunak* will be found to represent a subspecies of *cinereus.* A converse possibility was indicated in the vicinity of the Mackenzie Delta, Northwest Territories (Canada), where *cinereus* and *ugyunak* appeared to be associated with taiga and tundra, respectively, with no reported evidence of intergradation (Martell & Pearson 1978). With reference to *S. c. cinereus,* Youngman (1975:41) remarked that "Shrews of this subspecies become smaller in a cline from the central Yukon to the northern part of the Territory, where they intergrade with the smaller *S. c. ugyunak,*" and evidence for intergradation of *ugyunak* with *cinereus* and possibly with *hollisteri* was reported by Bee & Hall (1956) in northern Alaska. Twenty-three specimens collected by us along the northern margin of the Brooks Range, between about lat. 67°57′N and 68°20′N (encompassing taiga as well as tundra) were designated *S. c. ugyunak*; body-measurements and cranial dimensions of them were interpreted as indicating intergradation with *S. c. cinereus.* The medial tines of the incisors of those specimens were like those of the latter taxon. (The data concerning *ugyunak* will be reported elsewhere.)

Analysis of morphometric data may define precisely the degree of difference existing among taxa, but does not necessarily provide a basis for establishing taxonomic rank. As well, insular species may present unusual difficulties if conclusions are derived solely from macromorphological data, without consideration of potentiality for genetic drift and of the rate at which morphological divergence may have taken place. The small mammals on St. Lawrence Island, with the possible exception of the varying lemming there, *Dicrostonyx exsul* Allen, have been isolated for only about 10,000 years or less; that island was the last of the Beringian highlands to become separated from the continents by rising sea level at the end of the Pleistocene period (Hopkins 1959, 1976). In addition to the shrew and the varying lemming, the indigenous terrestrial mammals of the island (excluding the arctic fox, *Alopex lagopus* (L.), which immigrates and emigrates freely on the sea-ice) consist of the northern red-backed vole, *Clethrionomys rutilus* (Pallas); the northern vole, *Microtus oeconomus* (Pallas); and the arctic ground squirrel, *Citellus parryi* (Richardson). The mammalian faunas of the other Beringian islands (not including the upper Aleutian Islands) are more depauperate: a single species, *Microtus abbreviatus* Miller, on the St. Matthew Islands; the brown lemming, *Lemmus sibiricus* (Kerr), on St. George Island and *Sorex pribilofensis* on St. Paul Island (Pribilof Islands), and *L. sibiricus* and *Dicrostonyx vinogradovi* Ognev, on Vrangel' Island. With the exception of the varying lemmings, *S. pribilofensis,* and *S. jacksoni* (about which questions have remained) all of the small mammals on the Beringian Islands are recognized as being only subspecifically distinct from their precursors on the continents. All but the brown lemmings are characterized in part by larger size, most strongly defined in the voles. *Microtus abbreviatus* on the St. Matthew Islands is not only much larger than any of the continental subspecies (Alaska and NW Canada), but it exhibits the greatest degree of phenotypic divergence among the insular taxa mentioned (Rausch & Rausch 1968). *Microtus oeconomus* on St. Lawrence Island also is very large (TL up to at least 210 mm); only *M. o. koreni* Allen, inhabiting the valleys of the Kolyma and Indigirka Rivers, in Chukotka, approaches it in size. The red-backed vole on St. Lawrence Island (TL up to at least 155 mm) is larger than subspecies of *Clethrionomys rutilus* in either Chukotka or Alaska, approaching the northeastern Siberian red-grey vole, *C. rufocanus* (Sundevall) in size. Comparisons have shown that the karyotypes of *S. cinereus, L. sibiricus, M. abbreviatus,* and *M. oeconomus* are indistinguishable from those of conspecifics on the continents (*L. sibiricus* and *M. oeconomus* are holarctic). *Clethrionomys rutilus* is also indistinguishable karyotypically, except that chromosomal polymorphism, involving a Robertsonian rearrangement, was observed among animals collected at one locality (Sevuokuk Mountain) on St. Lawrence Island, possibly indicating that chromosomal evolution is taking place (Rausch & Rausch 1975b). Like *C. rutilus* in Alaska and Chukotka, *C. rutilus* on St. Lawrence Island has a metacentric Y-chromosome (Vorontsov et al. 1978). When the arvicolids were crossed with respective conspecifics from the Alaskan mainland, the offspring were found to be interfertile for numerous generations (Rausch & Rausch 1968, 1975a, 1975b, and unpubl.). Intergrades were bred within each successive generation. Such breeding was carried to about the 30th generation in the case of *C. rutilus albiventer* × *C. r. dawsoni,* and to at least several generations with the other species. With successive generations, the offspring of *M. abbreviatus fisheri* Merriam × *M. a. muriei* Nelson, from the Alaskan mainland, increasingly resembled the latter in size and cranial characteristics (R. L. Rausch, unpubl.). Such investigations involving *S. c. jacksoni* have not been attempted, since shrews are comparatively difficult to breed in captivity. Relative to the biological species-concept, we conclude that none of the aforementioned species, with exceptions as noted, is reproductively isolated.

The varying lemmings on the Beringian Islands, *D. exsul* on St. Lawrence Island, and *D. vinogradovi* on Vrangel' Island, are karyotypically distinct (Rausch 1977, Kozlovskii & Khvorostianskaia 1978). Both are restricted to habitat at higher elevations. On St. Lawrence Island, the wet tundra that covers 60% of the surface-area is occupied by the northern vole and the shrew, and the lowlands of Vrangel' Island are inhabited by brown lemmings. The limitation of varying lemmings to areas of higher elevation on the two islands may be attributable to the competitive superiority of the northern vole and the brown lemming, respectively (Rausch & Rausch 1975a). Among the species on the Beringian islands, *Dicrostonyx* spp. may have been the most ancient colonizers of the highlands that are now islands. Lemmings of the genus *Praedicrostonyx* evidently spread into eastern Beringia more than a million years ago, where they were replaced by *Dicrostonyx* (subgenus *Misothermus*) in pre-Mindel time (Zazhigin 1976). *Dicrostonyx* (subgenus *Dicrostonyx*) first appeared in deposits of Riss age. The degree of karyotypic diversity among Recent varying lemmings and the vast extent of their geographic distribution in the Nearctic (including apparently all of the islands of the Canadian Arctic Archipelago as well as Greenland) are indicative of long isolation of the respective populations. Of the small mammals on the Beringian islands, probably only the varying lemmings had been long established in restricted habitat by the time the mammals of the other species were separated from continental populations at the end of the last glacial period.

In insular populations, phenotypic changes sufficient to permit characterization of subspecies may take place comparatively rapidly [cf. Degerbøl (1939) for *Apodemus sylvaticus islandicus* Thienemann; Huxley (1943) for *Mus musculus* L.; and Cameron (1958) for mammals on Newfoundland]. All of the small mammals on islands within the area of Beringia were described originally as independent species. The period of time elapsing since their separation has been sufficient to mark most of those taxa as different, but only infraspecifically so, from mainland populations. With the exception of the varying lemmings, and possibly *Sorex pribilofensis,* none is known to have become reproductively isolated during the relatively brief interval since the end of the Pleistocene epoch.

Acknowledgments

Many of the shrews used in this study were collected by the late Dr. Francis H. Fay, in connection with our investigation of the epidemiology of alveolar hydatid disease on St. Lawrence Island. There, the hospitality and assistance of the Siberian Yupik residents greatly facilitated our work. At the Arctic Health Research Center, collections were made by Dr. Francis S. L. Williamson, and specimens were provided also by Mr. Donald Hartbauer, the late Dr. Christine Heller, Mr. Leonard Peyton, and Mr. Davis Rhodes, and at the Alaska Native Medical Center, by Dr. Joseph Wilson. Mr. L. Alan LeMaster and Mrs. Shirley LeMaster kindly provided space for laboratory work at Gakona. Mr. Warren Matumeak, Dr. Thomas F. Albert, and other members of the Department of Wildlife Management, North Slope Borough, Barrow, Alaska, gave support in connection with field-work. At the University of Washington, Ms. Gladys Crespo generously advised concerning karyological procedures. We express our sincere thanks for these contributions.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):729–747. 1995

Taxonomy of the genus *Lycalopex* (Carnivora: Canidae) in Argentina

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Abstract.—Previously treated as species of *Pseudalopex,* Argentine members of the genus *Lycalopex* (*L. griseus, L. gymnocercus,* and *L. culpaeus*) are examined to clarify the taxonomic status of each named form. Principal components analyses of 26 cranial measurements of 151 adult specimens and 11 pelage characters of 111 specimens, clearly distinguish *L. culpaeus* from the other two taxa. *Lycalopex griseus* and *L. gymnocercus* show clinal variation in cranial measurements and pelage characters. Qualitative cranial characters, traditionally used as diagnostic for *L. griseus* and *L. gymnocercus,* revealed great nongeographic variation. We conclude that *L. griseus* and *L. gymnocercus* are conspecific, and should be known as *L. gymnocercus.* Therefore, we recognize only two species of the genus *Lycalopex* (*L. culpaeus* and *L. gymnocercus*) in Argentina. We also use this opportunity to review synonymies of the recognized species in *Lycalopex.*

Although the taxonomic status of South American canids has been reviewed at length, classification at generic and subgeneric levels has not been completely resolved (Berta 1988, Kraglievich 1930, Langguth 1975). Three of the living Argentine foxes (*Lycalopex culpaeus, L. gymnocercus,* and *L. griseus*) have been alternatively included in the genera: *Pseudalopex* Burmeister, 1856 (Cabrera 1931, 1932, 1940; Thomas 1914a; Berta 1987, 1988; Nowak 1991; Wozencraft 1993), *Dusicyon* Hamilton-Smith, 1839 (Cabrera 1958, Corbet and Hill 1991, Clutton-Brock et al. 1976, Langguth 1969, Osgood 1934, Simpson 1945, Wozencraft 1989), or *Canis* Linnaeus, 1758 (Kraglievich 1930, Langguth 1975, Van Gelder 1978). Their inclusion in each of these genera was based on the degree of comparability with *D. australis* (Kerr, 1792), type species of genus *Dusicyon,* as determined from studies of external, cranial, and dental characters. Cabrera (1931, 1932) and Berta (1987, 1988) suggested that *culpaeus, gymnocercus,* and *griseus* were sufficiently different from *D. australis* to place them in the genus *Pseudalopex,* an arrangement followed by Wozencraft (1993). Cabrera (1931, 1958) considered *Lycalopex* Burmeister, 1854 (type species *Canis vetulus* Lund) separate from *Pseudalopex* Burmeister, 1856 (type species *Canis magellanicus* Gray). However, Berta (1987, 1988) and Wozencraft (1993) treated them as congeneric, but used *Pseudalopex* for the genus. Corbet and Hill (1991) also treated them as congeneric, but used *Dusicyon* for the genus. We follow Berta and Wozencraft in treating *Lycalopex vetulus* as congeneric with species previously assigned to *Pseudalopex,* but use *Lycalopex* as the valid generic name because it has two-years priority.

The taxonomic status of Argentine foxes has rarely been evaluated since their original descriptions. Three living species of genus *Lycalopex* currently are recognized in Argentina: the culpeo fox, *L. culpaeus,* which inhabits mainly grasslands (pampas) and deciduous forests from southern Patagonia to Ecuador; the patagonian gray fox, *L. griseus,* which occurs from Atacama, Chile, and Santiago del Estero, Argentina, south to Tierra del Fuego, and is sympatric with *L. culpaeus* in part of its range; and the pampas gray fox, *L. gymnocercus,* which inhabits the humid grasslands (pampas) in southern Brazil, northern Argentina, Uruguay, Paraguay, and eastern Bolivia (Cabrera & Yepes 1940, Cabrera 1958, Nowak 1991, Wozencraft 1993). However, information on distributional limits of *L. griseus* and *L. gymnocercus* in central Argentina, especially in the provinces of La Pampa, Córdoba, and San Luis, is scanty (Kraglievich 1930, Cabrera 1932).

Clutton-Brock et al. (1976) concluded that *L. culpaeus* and *L. gymnocercus* were phenetically close, and suggested that they should be considered conspecific because of cranial and pelage similarities. The skull of *L. griseus* has little to distinguish it from that of *L. culpaeus* except for smaller size and lack of an interparietal crest.

Our objectives in this paper are to analyze geographic variations of dental, cranial, and pelage characters and to evaluate the taxonomic relationships of *L. culpaeus, L. gymnocercus,* and *L. griseus.* We also use this opportunity to correct several errors, omissions, and misallocations of names discovered during our research, and to provide a synonymy that includes first usage of unique name combinations applied to the recognized species in *Lycalopex.*

Materials and Methods

We examined 151 skulls and 111 skins (see Appendix 1) deposited in the following collections: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN) and Instituto Miguel Lillo de Tucumán (IML).

We used only specimens of adults with intact skulls and complete data in the statistical analyses. We considered specimens to be adult if the basisphenoid-basioccipital suture was closed and the permanent dentition was complete. We measured 30 cranial and dental characters with a dial caliper to the nearest 0.1 mm on each skull, with bilateral characters always measured on the left side.

Measurements are defined as follows: 1) condylobasal length: distance from anterior edge of premaxillae to posteriormost surface of occipital condyles; 2) palatal length: distance from anterior margin of premaxillae to anteriormost point on posterior edge of palate; 3) minimum rostral length: distance from anterior margin of premaxillae to anteriormost orbital margin; 4) facial length: distance from anterior edge of premaxillae to posterior end of nasal bones; 5) bullar length: from sharp anterior end of tympanic bulla diagonally to posterior margin adjacent to paroccipital process; 6) maxillary toothrow length: alveolar length of upper toothrow including canine and second upper molar; 7) P4–M2 length: alveolar length of upper toothrow including fourth upper premolar and second upper molar; 8) minimum rostral height: rostral height behind canines; 9) height of braincase: height measured at right angle to basisphenoid, excluding sagittal crest; 10) interorbital constriction: least distance between orbits; 11) postorbital constriction: least distance across constriction just posterior to postorbital processes; 12) rostral width at canines: width across the rostrum at canines, measured from outer margins of alveoli; 13) rostral width at first upper molars: width across the rostrum at first upper molars, measured from outer margins of alveoli; 14) zygomatic breadth: greatest distance across outer margins of zygomatic arches; 15) mastoidal width: greatest distance across mastoid processes; 16) braincase width; greatest width across parietals; 17) width across occipital condyles: greatest distance between outer margins of occipital condyles; 18) width between postglenoid processes: least distance between inner margins of postglenoid processes; 19) P4 length: greatest alveolar length of fourth upper premolar; 20) P4 width: greatest alveolar width of fourth upper premolar; 21) ml length: greatest alveolar length of first lower molar; 22) ml width: greatest alveolar width of first lower molar; 23) rostral height at P2-P3: rostral height measured between second and third upper premolars; 24) mandibular length: length of mandible from anteriormost part of mandibular symphysis to posteriormost part of articular process; 25) mandibular toothrow length: alveolar length of lower toothrow including canine and third lower molar; 26) m1–m3 length: alveolar length of lower molars; 27) alveolar length of upper canine: greatest alveolar length of upper canine; 28) nares length: distance from anterior margin of premaxillae to anteriormost margin of nasal bones; 29) width across postorbital processes: greatest distance across outer margins of postorbital processes; 30) length between postorbital constriction and postorbital processes: least distance measured along sagittal suture. The last four measurements were not included in statistical analyses due to their high individual variability.

We grouped collecting sites of gray foxes into six OTUs, each representing a geographically discrete region (Fig. 1, Appendix 1). One specimen from La Paz, Mendoza, coded as unknown, was assigned to the central-western (CWT) OTU using a stepwise discriminant-function analysis with a probability of 61%. All specimens of *L. culpaeus* were included in a single OTU.

Sexual dimorphism was assessed only in the gray fox CCT OTU (19 ♂♂, 14 ♀♀) by multivariate analysis of variance (MANOVA) and discriminant-function analysis. Samples for the other taxa were too small to evaluate for dimorphism.

The mean and standard deviation of each measurement were calculated for each OTU. Principal component analysis was done using NT-SYS programs (Rohlf 1992) to assess phenetic overlap among individuals. Each character was standardized to a mean of zero and a standard deviation of one.

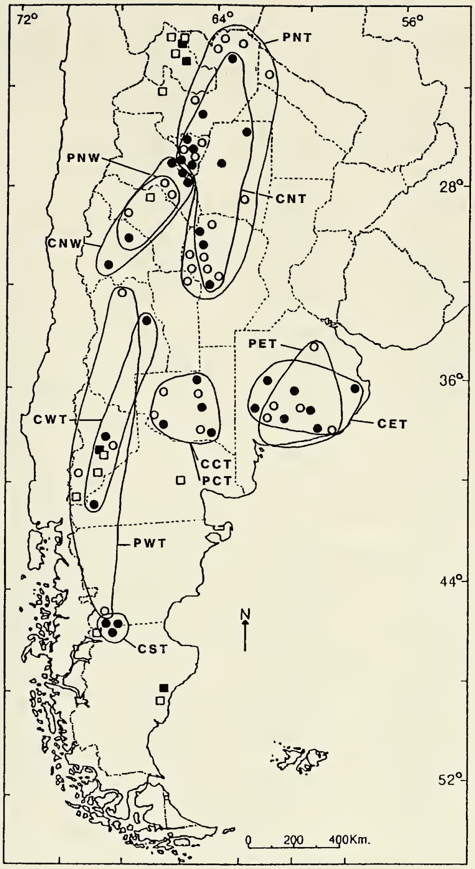

Fig. 1. Map of Argentina showing collecting sites for specimens listed in Appendix 1. Squares indicate culpeo foxes; circles or dots, gray foxes; solid symbols correspond to specimens used in cranial analyses; open symbols indicate specimens used in pelage analysis. Abbreviations refer to OTUs, which are identified in Appendix 1.

Environmental factors vary greatly over the ranges of latitude (approximately 24°) and elevation (sea level to over 3000 meters) represented by the samples analyzed. Therefore, to determine if variation in size was associated with environmental factors, a second principal component analysis was performed using the means of measurements for each OTU. Pearson's correlation coefficients were calculated between the first principal component scores and latitude, longitude, elevation, mean annual temperature, and average annual rainfall. Since each OTU comprised more than one collecting site, weighted means were calculated for each environmental factor.

Kraglievich (1930) used two cranial characters (crests on the skull and distance between postorbital constriction and postorbital processes) to distinguish *gymnocercus* from *patagonicus* (= *griseus* of authors). He believed that the presence of a sagittal crest and a long interorbital region distinguished *gymnocercus* from *patagonicus,* which he identified as having a lyriform sagittal area and a short distance between postorbital constriction and postorbital processes. We examined geographic and nongeographic variation of both characters in a sample of 81 specimens representing areas from which only the presence of *gymnocercus* had been cited. We scored three possible conditions for each character as follows: Temporal ridges, A) fused to form a well-developed sagittal crest, B) not fused and enclosing a narrow lyriform sagittal area, or C) not fused and enclosing a wide lyriform sagittal area; distance between postorbital constriction and postorbital processes: A) long (10.0–15.0 mm), B) medium (7.0–9.0 mm) or C) short (4.0–6.0 mm).

We analyzed geographic variation in 11 pelage characters (as described by Cabrera 1932) with color determinations made under natural light. Characters were scored as follows: A) chin spot: absent = 0, poorly marked = 1, very dark = 2; B) thigh spot: absent = 0, poorly marked = 1, very dark = 2; C) dorsal longitudinal band: absent = 0, poorly marked = 1, very dark = 2; D) underparts: brownish = 0, cream = 1, gray = 2; E) sides: reddish = 0, brownish = 1, gray = 2; F) upperparts: reddish = 0, gray = 1, brownish = 2; G) dorsal guard hairs banded (agouti): fine = 0, intermediate = 1, thick = 2; H) length of dorsal guard = hairs: short = 0, medium = 1, long = 1; I) ears: reddish = 0, pale brown = 1, dark brown = 2; J) head: reddish = 0, gray = 1, brownish = 2; K) thigh: reddish = 0, brownish = 1, gray = 2. Specimens were grouped into six OTUs, each representing a geographically discrete region (Fig. 1, Appendix 1). We used principal component analysis to evaluate phenetic overlap.

We also examined the microscopic structure of dorsal guard hairs taken from 48 specimens including both gray and culpeo foxes. Samples were first washed in an alcohol-ether solution (1:1) and then bleached for 24 hours in hydrogen peroxide. Then hairs were washed with fresh water, fixed to a glass slide with a thin layer of vinilic glue, and examined at 320 diameters. Type and disposition of cuticular scales and the type of medulla follow the nomenclature adopted by Chehébar & Martín (1989).

Results

Cranial characters.—Multivariate analysis of variance (MANOVA) of the gray fox CCT OTU revealed no significant sexual dimorphism ($P = 0.62$; $n = 33$) in 20 of the 26 measurements analyzed. Discriminant analysis showed an overlap between sexes with females being more variable.

Skulls of *L. culpaeus* (CCU OTU) clearly are larger than those of the other groups, which are all gray foxes (see Table 1 for means and standard deviations). Braincase width (16) was one of the more important measurements for separating gray and culpeo foxes. The skulls of the gray fox OTUs are not only smaller, but show little variation except for size increase toward the east and northeast, suggesting that variation is clinal.

All variables in the principal components analysis had positive correlations on component I, which indicates a general size factor (Table 2). The second component was bipolar, with both positive and negative loadings. The first component (Fig. 2) clearly separated *L. culpaeus* (CCU) from the gray foxes (*griseus* and *gymnocercus*). The OTUs of gray foxes overlapped with a general increase in size from west to east.

Table 1.—Cranial measurements for Argentine culpeo and gray foxes. Mean and one standard deviation (in parentheses) for each sample (OTU; sample acronym over sample size) measured. Measurements (left column) defined in text; OTUs identified in Appendix 1 under specimens examined for cranial analysis.

	CCU 58	CST 7	CWT 14	CNW 8	CCT 33	CET 15	CNT 16
1	164.66	122.69	122.83	122.98	138.79	141.53	125.91
	(7.13)	(4.15)	(4.12)	(8.90)	(5.44)	(7.56)	(2.86)
2	85.87	64.80	65.11	64.49	71.95	72.79	64.90
	(3.92)	(3.36)	(2.29)	(5.70)	(2.92)	(3.56)	(2.22)
3	73.59	54.09	53.74	52.39	60.49	61.24	53.81
	(4.50)	(3.04)	(2.45)	(4.93)	(3.19)	(3.77)	(2.32)
4	81.36	60.00	59.91	57.03	68.21	68.81	59.01
	(4.65)	(3.72)	(3.43)	(6.52)	(2.72)	(4.77)	(2.90)
5	20.66	18.44	17.90	18.39	18.92	19.76	19.91
	(1.02)	(1.07)	(1.19)	(0.73)	(1.25)	(0.93)	(0.97)
6	20.99	15.19	14.83	15.64	17.60	17.97	16.24
	(1.53)	(0.92)	(1.05)	(1.44)	(1.25)	(1.18)	(1.13)
7	43.66	38.19	38.19	37.88	40.15	40.10	38.03
	(1.20)	(0.76)	(1.21)	(2.75)	(1.15)	(1.57)	(1.80)
8	24.99	20.00	18.84	19.16	21.79	22.66	20.44
	(1.67)	(1.03)	(1.37)	(1.86)	(1.35)	(1.66)	(0.75)
9	73.66	58.66	58.32	57.06	63.01	63.50	57.93
	(2.81)	(1.66)	(1.72)	(4.09)	(2.42)	(2.91)	(1.91)
10	30.42	25.71	25.34	25.76	27.41	27.85	26.40
	(1.29)	(0.86)	(1.22)	(1.69)	(1.12)	(1.22)	(1.05)
11	16.52	12.97	12.84	12.79	13.79	14.19	13.19
	(0.87)	(0.42)	(0.71)	(0.91)	(0.77)	(0.57)	(0.66)
12	7.86	6.06	5.98	6.46	6.92	7.00	6.66
	(0.49)	(0.28)	(0.51)	(0.49)	(0.44)	(0.35)	(0.37)
13	16.77	13.73	13.62	13.40	14.88	15.11	14.00
	(0.83)	(0.40)	(0.89)	(1.31)	(0.71)	(0.98)	(0.73)
14	7.01	5.67	5.70	5.78	6.20	6.25	5.84
	(0.37)	(0.20)	(0.36)	(0.42)	(0.32)	(0.42)	(0.31)
15	128.61	95.40	94.35	93.61	106.57	108.78	96.79
	(6.10)	(4.27)	(3.51)	(8.38)	(4.40)	(5.85)	(2.59)
16	83.51	65.14	64.94	63.81	70.55	71.01	65.44
	(3.30)	(2.05)	(2.29)	(5.02)	(2.81)	(3.33)	(1.93)
17	29.58	24.71	24.58	25.03	26.53	27.06	25.50
	(1.12)	(0.98)	(1.14)	(1.66)	(1.28)	(1.10)	(0.91)
18	28.15	23.04	21.94	21.48	25.51	26.47	23.19
	(1.94)	(1.41)	(1.45)	(2.50)	(1.55)	(2.30)	(1.61)
19	26.55	25.33	24.19	23.65	25.18	25.53	24.19
	(1.86)	(1.28)	(1.35)	(1.25)	(1.68)	(1.67)	(1.65)
20	27.51	19.21	18.67	19.75	22.50	23.20	20.59
	(1.84)	(1.11)	(0.91)	(2.05)	(1.26)	(1.73)	(0.97)
21	46.70	36.74	35.07	37.25	40.39	42.00	38.72
	(1.80)	(1.51)	(1.76)	(2.45)	(1.95)	(2.09)	(0.97)
22	88.79	64.27	63.27	65.06	73.59	75.53	67.60
	(5.32)	(2.52)	(2.09)	(5.71)	(3.54)	(4.46)	(2.09)
23	54.75	42.49	41.95	42.00	46.62	48.13	44.53
	(2.50)	(1.43)	(1.10)	(2.89)	(1.88)	(2.99)	(1.23)
24	51.88	44.66	44.30	44.05	46.76	46.93	44.58
	(1.48)	(0.94)	(0.86)	(1.65)	(1.42)	(1.97)	(0.91)
25	29.79	23.34	23.59	23.95	26.02	25.93	24.35
	(1.63)	(1.18)	(1.41)	(2.08)	(1.48)	(1.39)	(0.92)
26	38.48	31.47	31.22	31.85	34.32	34.53	33.13
	(1.39)	(0.96)	(0.80)	(1.47)	(1.59)	(1.78)	(1.21)

Table 2.—Character loadings of cranial variables of Argentine culpeo and gray foxes ($n = 151$) on the first two principal components. Measurements defined in text.

	Component			Component	
Variable	I	II	Variable	I	II
1	0.211	−0.037	14	0.193	−0.103
2	0.209	−0.042	15	0.210	−0.026
3	0.205	−0.041	16	0.208	−0.059
4	0.206	0.021	17	0.197	−0.143
5	0.149	0.022	18	0.184	0.286
6	0.197	0.012	19	0.108	0.885
7	0.191	0.111	20	0.206	0.029
8	0.192	−0.228	21	0.205	−0.012
9	0.208	−0.060	22	0.206	0.064
10	0.198	−0.132	23	0.206	0.003
11	0.199	−0.107	24	0.203	0.078
12	0.184	−0.250	25	0.197	−0.096
13	0.194	−0.109	26	0.200	0.024
			% variance	84.68	3.26

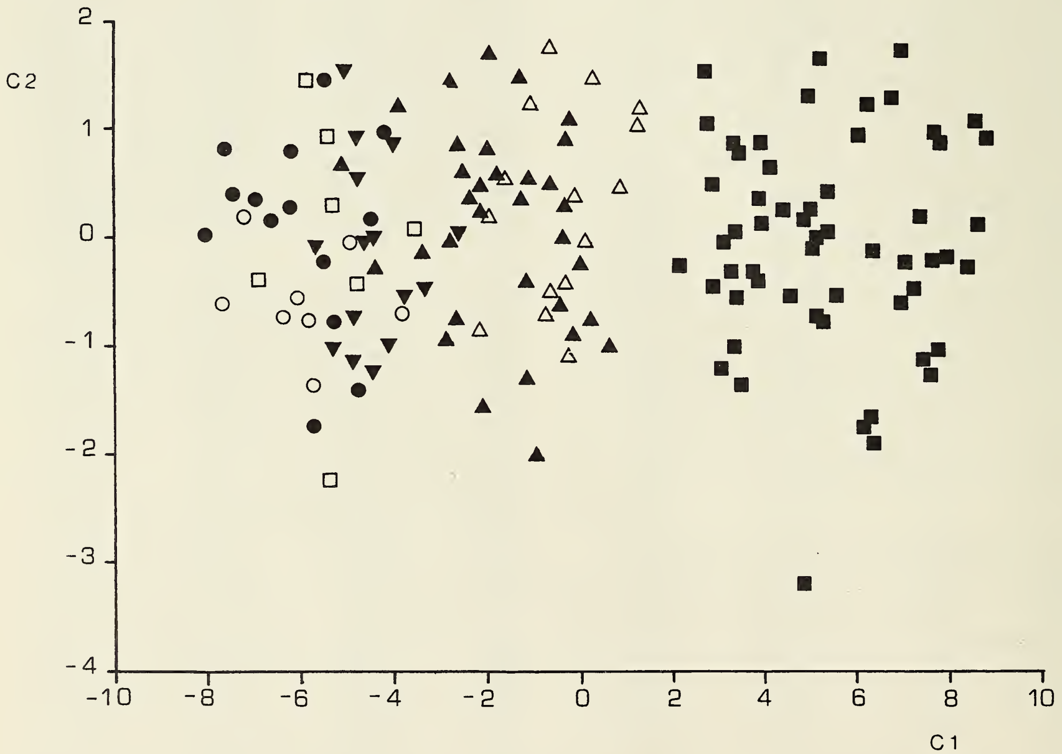

Fig. 2. Distribution of 151 specimens of Argentine foxes based on cranial data on the first two principal components. Symbols represent OTUs, identified in Appendix 1 under cranial analysis, as follows: ■—CCU; □—CST; ●—CWT; ○—CNW; ▲—CCT; △—CET; ▼—CNT.

Table 3.—Argentine gray foxes from areas where only *gymnocercus* was believed to occur, segregated on the basis of three developmental conditions of temporal ridges and three comparative lengths of interorbital region of the skull. Development of temporal ridges: A, fused into sagittal crest; B, not fused and enclosing narrow lyriform sagittal area; C, not fused and enclosing wide lyriform sagittal area. Distance in midline from plane of interorbital constriction to plane of postorbital processes: A, long (10.0–15.0 mm); B, medium (7.0–9.0 mm); C, short (4.0–6.0 mm).

Condition	Temporal ridges	Interorbital distance
A	15 (19%)	33 (41%)
B	23 (28%)	20 (25%)
C	43 (53%)	28 (34%)
Total	81	81

Table 4.—Character loadings of coded pelage variables of Argentine foxes ($n = 111$) on the first two principal components.

Variable	PC I	PC II
A	0.392	−0.010
B	0.355	−0.201
C	0.118	0.548
D	−0.173	0.108
E	0.318	−0.313
F	0.234	−0.281
G	0.195	0.326
H	0.217	0.551
I	0.354	0.068
J	0.372	0.159
K	0.414	−0.173
% of variance	43.00	14.81

The La Pampa OTU (CCT) was the most variable (Fig. 2), spanning the gap between the western OTUs and the Buenos Aires sample (CET).

In the analysis based on means of gray fox OTUs, the first component explained 90.9% of the variance. As all variables had a positive loading, component I represents a general size factor. First component scores showed a significant positive correlation with rainfall ($r = 0.90$; $P < 0.05$) which increases toward the northeast.

Cranial characters of Argentine gray foxes are highly variable. Our analysis (Table 3) of the development of temporal ridges and length of interorbital region, once considered diagnostic for separating *griseus* from *gymnocercus,* shows that these cranial features have little or no value for distinguishing among gray foxes.

Pelage characters.—Principal components analysis of pelage characters showed high variation among the groups (Table 4, Fig. 3) with the first two components explaining only 57.8% of the variance. However, these results are in agreement with the principal component analysis based on cranial characters; in both analyses the culpeo foxes (*culpaeus*) are clearly separated from the gray foxes (*griseus* and *gymnocercus*).

The *L. culpaeus* group differs from the other groups in the completely white chin and the reddish thigh lacking a posterior dark spot. Patterns of gray fox pelage characteristics can be correlated with geographic areas represented by the OTUs (Table 5).

Microscopic examination of guard hairs revealed no differences in either the type of medulla or the type and arrangement of cuticular scales. The medulla is segmented and scales are lanceolate and imbricated in all skins examined.

Discussion and Conclusions

We found no significant sexual dimorphism in gray foxes; small samples sizes precluded testing for sexual dimorphism in culpeo foxes. The absence of sexual dimorphism has been reported in other canids (Waithman & Roest 1977, Gingerich & Winkler 1979).

Multivariate analyses of both cranial and pelage characters confirm that *L. culpaeus* differs significantly from gray foxes in Argentina. These differences support species status for *L. culpaeus* and argue against the Clutton-Brock et al. (1976) conclusion that culpeo and gray foxes are phenetically close and might be conspecific.

Gray foxes, however, show clinal variation in skull size correlated with increasing annual precipitation. Gray foxes also are

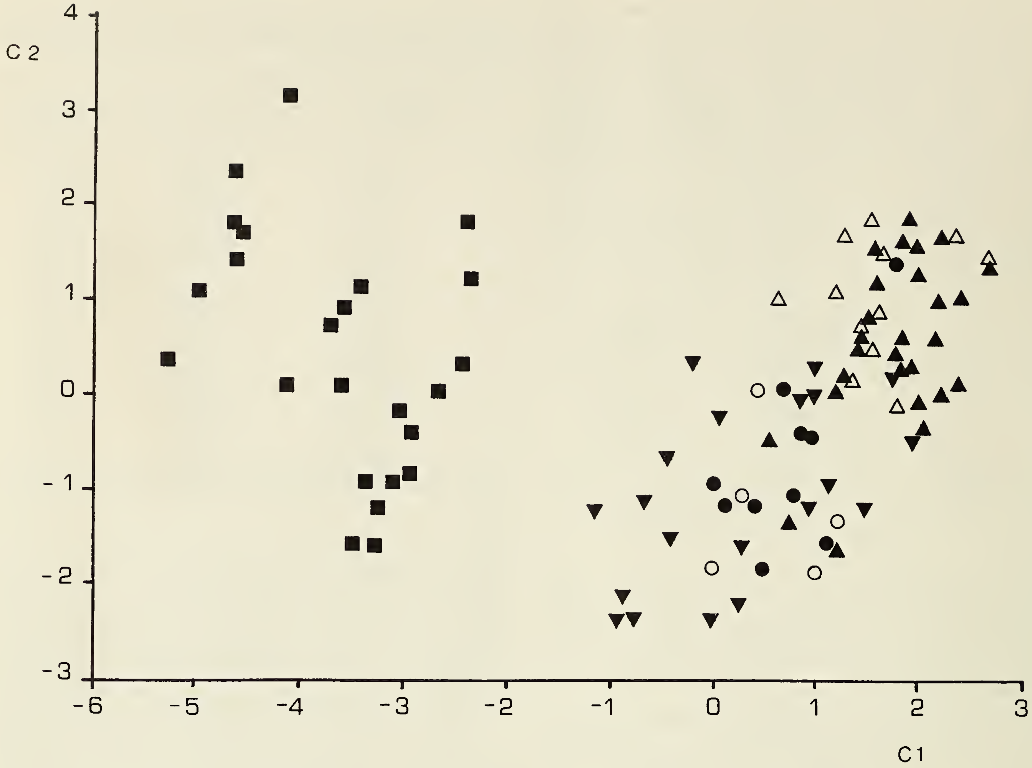

Fig. 3. Distribution of 111 specimens of Argentine foxes based on pelage characters on the first two principal components. Symbols represent OTUs, identified in Appendix 1 under pelage, as follows: ■—PCU; △—PET; ○—PNW; ▼—PNT; ●—PWT; ▲—PCT.

Table 5.—Qualitative pelage characteristics of Argentine gray foxes. Pelage characters described in text; OTUs identified in Appendix 1 under specimens examined for pelage analysis; OTU acronym followed by sample size in parentheses.

Character	PNW (6)	PWT (9)	PNT (25)	PET (14)	PCT (30)
Chin spot	Very dark	Variable-dark	Very dark	Very dark	Very dark
Thigh spot	Very dark	Variable-dark	Very dark	Very dark	Very dark
Dorsal band	Absent–poorly marked	Absent–poorly marked	Absent–poorly marked	Very dark	Variable
Underparts	Brownish	Cream	Brownish-cream	Cream	Brownish-cream
Sides	Brownish	Brownish-gray	Brownish-gray	Brownish	Brownish
Upperparts	Brownish	Brownish	Brownish	Brownish	Brownish
Agouti	Fine–medium	Fine–very fine	Fine–medium	Thick–medium	Variable
Guard hair length	Variable	Variable	Variable	Variable	Variable
Ears	Reddish	Dark brown	Reddish-pale brown	Pale brown	Variable-brown
Head	Reddish	Brownish	Reddish-brownish	Brownish	Brownish
Thigh	Reddish	Reddish	Brownish	Brownish	Brownish

smaller when sympatric with *L. culpaeus.* Data on geographic variation and clinal trends in size of canids are scarce. Fuentes & Jaksic (1979) found clinal variation in size from north to south in *L. culpaeus* and *L. griseus* in Chile, and suggested that progressive increments of habitat overlap towards the south were compensated by progressively greater differences in body size and in mean prey size.

We found the cranial characters used by Kraglievich (1930) to distinguish *L. gymnocercus* from *L. griseus* to be highly variable even within the same population. Kraglievich (1930:51) claimed that *gymnocercus* frequently has an extensive sagittal crest and a greater distance between the interorbital region and postorbital processes than has *patagonicus* (= *griseus* of authors). We scored three possible conditions for each of these two cranial characters in 81 gray foxes previously identified as *gymnocercus* from areas where only *gymnocercus* had been assumed to occur. Our results (Table 3) showed high individual and geographic variation indicating that the characters have little or no taxonomic value for discriminating among gray foxes. Kraglievich (1930) also considered postorbital constriction (measurement 11) to be narrower in *gymnocercus* than in *patagonicus* (= *griseus* of authors), but our analysis revealed relatively little variation when all groups of gray foxes are compared (Table 1).

Most of the morphological differences ascribed to the named forms of gray foxes had been based on type specimens, which for *griseus* and *gymnocercus* come from localities approximately 3500 km apart. Some of these characters, once considered diagnostic, have not proven useful for taxonomic purposes. For example, in accord with Clutton Brock et al. (1976), our results suggest that the absence of a sagittal crest in canids may be associated with small size.

Chromosomal analyses of these species (Gallardo & Formas 1975, Vitullo & Zuleta 1992) show a 2N = 74, NF = 76 karyotype with all-acrocentric autosomes. This karyotype, considered primitive for South American canids, does not distinguish among these species.

Because our samples of gray foxes showed clinal variation in size and color pattern as well as considerable nongeographic variation in qualitative characters considered diagnostic by previous workers, we conclude that gray foxes of Argentina are conspecific. *Lycalopex gymnocercus* is the oldest available name for the gray foxes of Argentina.

Taxonomy

Lycalopex Burmeister, 1854

Synonyms.—

Canis: Molina, 1782:293 (not *Canis* Linnaeus, 1758).

Vulpes: Martin, 1837:11 (not *Vulpes* Frisch, 1775).

Procyon: Fischer, 1814:178 (not *Procyon* Storr, 1780).

Dusicyon Hamilton-Smith, 1839:248 (part; described as a section of *Chaon* Hamilton-Smith, 1839).

Cerdocyon Hamilton-Smith, 1839:259 (part; described as a section of *Chaon* Hamilton-Smith, 1839).

Lycalopex Burmeister, 1854:95 (described as a section of *Canis* Linnaeus); type species *Canis vetulus* Lund, 1842a, by subsequent designation (Thomas 1914a: 352).

Pseudalopex Burmeister, 1856:24 (described as a section of *Canis* Linnaeus); type species *Canis magellanicus* Gray, 1837a (= *Vulpes magellanicus* Gray, 1837b), by subsequent designation (Thomas 1914a:352).

Thous: Gray, 1869:514 (part; not *Thous* Hamilton-Smith, 1839).

Lupulus: Trouessart, 1897:304 (part; not *Lupulus* Blainville, 1830).

Nothocyon: Wortman and Matthew, 1899: 124 (part; not *Nothocyon* Matthew, 1899).

Pseudolopex Philippi, 1903:157 (incorrect subsequent spelling of *Pseudalopex* Burmeister, 1856).

Pseudolycos Philippi, 1903:157; proposed as a subgenus of "unsere grösseren Füchse" (our larger foxes [Chilean]); no species mentioned.

Eunothocyon J. A. Allen, 1905:152; type species *Canis sladeni* Thomas, 1904, by original designation.

Angusticeps Hilzheimer, 1906:114 (proposed as a subgenus of *Canis* Linnaeus, 1758); type species *Canis* (*Angusticeps*) *reissi* Hilzheimer, 1906, by monotypy.

Viverriceps Hilzheimer, 1906:116 (*lapsus* for *Angusticeps*; not *Viverriceps* Gray, 1867).

Microcyon Trouessart, 1906:1186 (proposed as a subgenus of *Speothos* Lund, 1839a); type species *Speothos riveti* Trouessart, 1906, by original designation.

Lycalopex culpaeus (Molina, 1782)

Synonyms.—

Canis culpaeus Molina, 1782:293; type locality "Chili," restricted to "Santiago province" by Cabrera (1931:62).

C[*anis*]. *Vulpes chilensis* Kerr, 1792:144; type locality "Chili." Based exclusively on *Canis culpaeus* Molina.

C[*anis*]. *Magellanicus* Gray, 1837a:88 (*nomen nudum*).

Vúlpes magellánica Gray, 1837b:578; type locality "Magellan's Straits" [= Port Famine; Gray 1843:61], Magellanes, Chile.

Cerdocyon Magellanicus: Hamilton-Smith, 1839:266 (name combination).

Canis (*Pseudalopex*) *lycoides* Philippi, 1896:542 (p. 2 in reprint); type locality "insulis Tierra del Fuego" [= Bahía Felipe; Wolffsohn 1921:514], Magellanes, Chile.

[*Canis* (*Lupulus*)] *magellanicus*: Trouessart, 1897:306 (name combination).

Canis montanus Prichard, 1902:260; type locality "South-eastern Patagonia." Preoccupied by *Canis montanus* Marsh, 1871.

Canis amblyodon Philippi, 1903:158; type locality "provincia Valparaiso," Chile.

Canis albigula Philippi, 1903:159; type locality "provinciis centralibus," Chile.

[*Canis* (*Cerdocyon*)] *magellanicus*: Trouessart, 1904:233 (name combination).

[*Canis* (*Cerdocyon*)] *lycoïdes*: Trouessart, 1904:234 (name combination).

[*Canis* (*Cerdocyon*)] *prichardi* Trouessart, 1904:234 (new name for *Canis montanus* Prichard, 1902).

Canis (*Angusticeps*) *reissii* Hilzheimer, 1906:116; type locality "Quito," Pichincha, Ecuador.

Speothos Riveti Trouessart, 1906:1185; type locality "Alchipichi, province de Pichincha (Equateur), altitude de 2101^{m}."

Canis (*Cerdocyon*) *magellanicus Riveti*: Trouessart, 1910:12 (name combination).

C[*anis*]. *Riveti*: Cabrera, 1912:63 (name combination).

Ps[*eudalopex*]. *c*[*ulpaeus*]. *magellanicus*: Thomas, 1914a:357 (name combination).

Ps[*eudalopex*]. *c*[*ulpaeus*]. *culpaeus*: Thomas, 1914a:357 (name combination).

Ps[*eudalopex*]. *lycoides*: Thomas, 1914a: 357 (name combination).

Ps[*eudalopex*]. *c*[*ulpaeus*] *reissii*: Thomas, 1914a:357 (name combination).

Pseudalopex culpaeus andina Thomas, 1914a:357; type locality "Esperanza, near Mt. Sajama, Province of Oruro [La Paz], Bolivia. Alt. 4000 m."

Pseudalopex culpaeolus Thomas, 1914a: 359; type locality "Santa Elena," Soriano, Uruguay. Considered a composite (skin of *P. culpaeus*; skull of *P. gymnocercus*) by Langguth (1967) who selected the skin as lectotype, thus treating the taxon as an objective synonym of *P. inca* Thomas, 1914a, and a subjective synonym of *P. culpaeus andina* Thomas, 1914a.

Pseudalopex inca Thomas, 1914a:361; type locality "Sumbay, Arequipa, Peru. Alt. 4000 m." Considered a composite (skin of *P. gymnocercus*; skull of *P. culpaeus*) by Langguth (1967) who selected the skull as lectotype, thus treating the taxon as an objective synonym of *P. culpaeolus* Thomas, 1914a, and a subjective synonym of *P. culpaeus andina* Thomas, 1914a.

Canis culpaeus reissi: Osgood, 1914:172 (name combination).

Pseudalopex smithersi Thomas, 1914b:573; type locality "Sierra de Cordoba," Cordoba, Argentina; restricted by Cabrera (1958:232) to Pampa de Achala, 2200 m.

Canis culpaeus andinus: Osgood, 1916:211 (name combination).

Pseudalopex magellanicus: Lönnberg, 1919:1 (name combination).

Pseudalopex culpaea Thomas, 1921:385 (unjustified emendation of gender termination for *culpaeus*).

Pseudalopex reissii: Lönnberg, 1921:23 (name combination).

Canis ferrugineus Huber, 1925:9; type locality "la Cordillera [de los Andes], entre low ríos Mendoza, Atuel, Neuquén y Collun-Curá," Argentina.

[*Canis* (] *Pseudalopex*[)] *gymnocercus culpaeola*: Kraglievich, 1930:52; (name combination).

[*Canis* (] *Dusicyon*[)] *lycoides*: Kraglievich, 1930:58; (name combination).

[*Canis* (] *Dusicyon*[)] *culpaeus magellanicus*: Kraglievich, 1930:58; (name combination).

[*Canis* (] *Dusicyon*[)] *culpaeus andinus*: Kraglievich, 1930:59; (name combination).

[*Canis* (] *Dusicyon*[)] *culpaeus reissii*: Kraglievich, 1930:59; (name combination).

[*Canis* (] *Dusicyon*[)] *culpaeus Riveti*: Kraglievich, 1930:60; (name combination).

[*Canis* (] *D*[*usicyon*)]. *smithersi*: Kraglievich, 1930:60; (name combination).

[*Canis* (] *Dusicyon*[)] *inca*: Kraglievich, 1930:61; (name combination).

Pseudalopex culpaeus andina: Cabrera, 1931:63 (name combination).

Pseudalopex culpaeus reissii: Cabrera, 1931:63 (name combination).

Pseudalopex culpaeus smithersi: Cabrera, 1931:63 (name combination).

Pseudalopex culpaeus magellanica: Cabrera, 1931:63 (name combination).

Pseudalopex culpaeus lycoides: Cabrera, 1931:63 (name combination).

Dusicyon (*Dusicyon*) *culpaeus*: Osgood, 1934:49 (name combination).

Canis magellanicus priscus Spillmann, 1938:387 (*nomen nudum*).

Dusicyon culpaeus andinus: Osgood, 1943: 64 (name combination).

Dusicyon culpaeus lycoides: Osgood, 1943: 66 (name combination).

Dusicyon culpaeus magellanicus: Osgood, 1943:65 (name combination).

Dusicyon [(*Dusicyon*)] *culpaeolus*: Cabrera, 1958:229 (name combination).

Dusicyon [(*Dusicyon*)] *culpaeus reissii*: Cabrera, 1958:232 (name combination).

Dusicyon [(*Dusicyon*)] *culpaeus smithersi*: Cabrera, 1958:232 (name combination).

Dusicyon [(*Dusicyon*)] *inca*: Cabrera, 1958: 235 (name combination).

Comments.—*Lycalopex culpaeus* occurs from the Andes of Colombia to Tierra del Fuego, is widely distributed in Patagonia, but is not known from Paraguay, Uruguay, or Brazil. The species has not been revised since Cabrera's (1958) catalog in which he recognized five subspecies in addition to the nominate form. Langguth (1967) presented convincing arguments that *Pseudalopex culpaeolus* and *P. inca,* both described by Thomas (1914a), were based on composites. Langguth reduced both names to the synonymy of *Pseudalopex* (= *Lycalopex*) *culpaeus.*

Lycalopex gymnocercus (Fischer, 1814)

Synonyms.—

Canis lagopus Molina, 1782:272; type locality "Arcipelago di Chiloe," Chiloé, Chile. Preoccupied by *Canis lagopus* Linnaeus, 1758.

Procyon gymnocercus Fischer, 1814:178; based solely on "L'Agourachay" of Azara (1801:317); therefore, type locality is Paraguay; restricted by Cabrera (1958: 235) to vicinity of Asunción.

Can[*is*]. *brasiliensis* Schinz, 1821:220; type locality "Brasilien und Paraguay." Based solely on "L'Agourachay of Azara (1801: 317); therefore, restricted type locality is vicinity of Asunción, Paraguay (Cabrera 1958:235).

Canis Azarae s. *Brasiliensis*: Rengger, 1830:143 (name combination).

C[*anis*]. *griseus* Gray, 1837a:88 (*nomen nudum*).

Vulpes fulvipes Martin, 1837:11; type locality "island of Chiloe," restricted by Darwin (*in* Waterhouse 1839) to "sea-beach at the southern point of the island," near San Pedro channel, Chiloé, Chile.

Vúlpes gríseus Gray, 1837b:578; type locality "Magellan," Magellanes, Chile.

Cerdocyon fulvipes: Hamilton-Smith, 1839: 257 (name combination).

C[*anis*]. *protalopex* Lund, 1839a:223 (*nomen nudum*).

Canis protalopex Lund, 1839b:32 (*nomen nudum*).

Canis protalopex Lund, 1840:54, text to plate 28 (fig. 9); type locality "Rio das Velhas," Lagoa Santa, Minas Gerais, Brazil.

Canis [(*Pseudalopex*)] *gracilis* Burmeister, 1861:406; type locality "die buschige Pampa in den Umgebungen Mendozas," Mendoza, Argentina.

Canis patagonicus Philippi, 1866:116; type locality "Magellans Strasse," Magellanes, Chile.

Pseudalopex griseus: Gray, 1869:512 (name combination).

Thous fulvipes: Gray, 1869:514 (name combination).

Canis azarae fossilis Gervais and Ameghino, 1880:36 (*nomen nudum*).

Canis Azarae m. *fossilis* Ameghino, 1889: 298; type locality "Rio Lujan y Cañada de Rocha en los partidos de Mercedes y Lujan, provincia de Buenos Aires," Argentina. Preoccupied by *Canis familiaris fossilis* Pictet, 1853.

Canis Azarae, m. *antiguus* Ameghino, 1889:298; type locality "Rio Lujan en los partidos de Mercedes y Lujan, provincia de Buenos Aires," Argentina.

Canis azarae (var. *fulvipes*): Mivart, 1890a: fig. 25 (name combination).

[*Canis* (*Thous*)] *griseus*: Trouessart, 1897: 307 (name combination).

[*Canis* (*Thous*)] *gracilis*: Trouessart, 1897: 308 (name combination).

Canis domeykoanus Philippi, 1901:168 (p. 4 in reprint); type locality "Provincia de Copiapó," Chile.

Canis rufipes Philippi, 1901:168 (p. 4 in reprint); type locality not given, assumed to be Chile. Most likely a *lapsus* for *Canis fulvipes* (Martin, 1837).

Canis maullinicus Philippi, 1903:158; type locality "provincia Llanquihue ad occidentem lacus Llanquihue, loco 'Nueva Braunau," Chile.

Canis trichodactylus Philippi, 1903:158; type locality "provincia Valdivia," Chile.

Canis torquatus Philippi, 1903:159; type locality "Puerto Montt," Llanquihue, Chile.

[*Canis* (*Cerdocyon*) *azarae*] *protalopex*: Trouessart, 1904:233 (name combination).

[*Canis* (*Cerdocyon*) *azarae*] *antiguus*: Trouessart, 1904:233 (name combination).

[*Canis* (*Cerdocyon*) *azarae*] *fulvipes*: Trouessart, 1904:233 (name combination).

[*Canis* (*Cerdocyon*)] *griseus*: Trouessart, 1904:234 (name combination).

[*Canis* (*Cerdocyon*) *griseus*] *gracilis*: Trouessart, 1904:234 (name combination).

[*Canis* (*Cerdocyon*)] *domeykoanus*: Trouessart, 1904:234 (name combination).

Cerdocyon griseus: J. A. Allen, 1905:155 (name combination).

Pseudalopex azarica Thomas, 1914a:360; type locality "Mar del Plata, S. E. Buenos Ayres," Argentina.

Canis (*Pseudalopex*) *gymnocercus*: Osgood, 1915:143 (name combination).

Pseudalopex domeykoanus: Cabrera, 1917: 27 (name combination).

Canis Domeycoanus: Wolffsohn, 1918:61 (incorrect subsequent spelling of *domeykoanus* Philippi).

Pseudalopex zorrula Thomas, 1921:383; type locality "Chumbicha, Catamarca[, Argentina]. Alt. 500 m."

P[*seudalopex*]. *domeycoanus*: Wolffsohn, 1921:514 (incorrect subsequent spelling of *domeykoanus* Philippi).

C[*anis*]. *cinereo argenteus*: Larrañaga, 1923:344 (not *Canis cinereo argenteus* Schreber, 1775).

C[*erdocyon*]. *t*[*hous*]. *brasiliensis*: G. M. Allen, 1923:56 (name combination).

[*Canis* (] *Pseudalopex*[)] *patagonicus gracilis*: Kraglievich, 1930:50 (name combination; however, *gracilis* has priority over *patagonicus*).

[*Canis* (] *Pseudalopex*[)] *patagonicus zorrula*: Kraglievich, 1930:51 (name combination).

[*Canis* (] *Pseudalopex*[)] *gymnocercus attenuatus* Kraglievich, 1930:54; type locality "los Estados brasileños de Río Grande del Sur, Paraná y tal vez Matto Grosso."

Pseudalopex gymnocercus gymnocercus: Cabrera, 1931:64 (name combination).

Pseudalopex gymnocercus antiguus: Cabrera, 1931:64 (name combination).

Pseudalopex gracilis zorrula: Cabrera, 1931:65 (name combination).

Pseudalopex gracilis domeykoanus: Cabrera, 1931:65 (name combination).

Pseudalopex gracilis patagonicus: Cabrera, 1931:65 (name combination).

Pseudalopex fulvipes: Cabrera, 1931:66 (name combination).

Dusicyon (*Dusicyon*) *gymnocercus*: Osgood, 1934:49 (name combination).

Dusicyon (*Dusicyon*) *griseus*: Osgood, 1934:49 (name combination).

Dusicyon griseus domeykoanus: Osgood, 1943:69 (name combination).

Dusicyon griseus maullinicus: Osgood, 1943:70 (name combination).

Dusicyon fulvipes: Osgood, 1943:71 (name combination).

Ducicyon griseus domeicoanus Mann, 1950:5 (incorrect subsequent spellings of *Dusicyon* Hamilton-Smith, 1839 and *domeykoanus* Philippi, 1901).

Dusicyon [(*Dusicyon*)] *griseus gracilis*: Cabrera, 1958:233 (name combination).

Dusicyon [(*Dusicyon*)] *gymnocercus antiguus*: Cabrera, 1958:234 (name combination).

Comments.—*Lycalopex gymnocercus* occurs from southern Bolivia and Brazil to Tierra del Fuego. Previously considered to represent two species, *gymnocercus* was the name used for the northern and northeastern populations; *griseus,* for the western and southern populations. Kraglievich (1930: 49) used the name *Canis* (*Pseudalopex*) *patagonicus* Philippi, 1866, for the taxon currently known in the literature as *Pseudalopex griseus* (Gray) because he, along with Cabrera (1931), believed *Canis griseus* Gray (1837a) to be preoccupied by *Canis griseus* Boddaert, 1784. However, Gray's name is a *nomen nudum*; the correct original name combination is *Vulpes griseus* Gray (1837b) a junior synonym of *Lycalopex gymnocercus.* Instead of *patagonicus,* Cabrera (1931:65) used *Pseudalopex gracilis* Burmeister, 1861, as the earliest available name for the taxon he later (1958:233) called *Dusicyon griseus* (= *Lycalopex gymnocercus*). Because we have not attempted a complete revision of *L. gymnocercus,* we are reluctant to identify any populations as representing subspecies. Nevertheless, the name *griseus* Gray is available for the southernmost Argentine and Chilean population and *fulvipes* Martin is the appropriate name for the Chiloé Island and adjacent mainland population, which until recently had been considered a separate species.

Canis azarae fossilis has been attributed to Gervais and Ameghino (1880:36); however, the taxon was not described in that publication, hence it is a nomen nudum because the references to Bravard are not valid indications, since Bravard's work was never actually published (Simpson 1940). The name dates from Ameghino (1889) and is preoccupied. Wozencraft (1993:284) included [*Canis*] *entrerianus* Burmeister, 1861, under *Pseudalopex gymnocercus,* but the type is a male *Cerdocyon thous* (see Thomas 1914a:359, footnote; Cabrera 1931:61; Berta 1982).

Lycalopex sechurae (Thomas, 1900)

Synonyms.—

Canis sechurae Thomas, 1900:148; type locality "Sullana," Piura, Perú.

[*Canis* (*Cerdocyon*)] *sechurae*: Trouessart, 1904:234 (name combination).

Pseudalopex sechurae: J. A. Allen, 1916: 122 (name combination).

[*Canis* (] *Pseudalopex*[)] *sechurae*: Kraglievich, 1930:51 (name combination).

Dusicyon (*Dusicyon*) *sechurae*: Osgood, 1934:49 (name combination).

Comments.—*Lycalopex sechurae* is monotypic and restricted in distribution to the coastal desert and arid inter-Andean valleys of northwestern Perú and southern Ecuador. Its southern limits in western Perú are not known. Osgood (1914) recorded it in Depto. La Libertad, and it may occur farther south along the Pacific coast.

Lycalopex vetulus (Lund, 1842)

Synonyms.—

Canis azarae: Lund, 1837:324 (not *Canis azarae* Wied, 1824).

Canis vetulus Lund, 1842a:5; type locality "*Rio das Velhas's* Floddal," Lagoa Santa, Minas Gerais, Brazil.

Canis fulvicaudus Lund, 1843:20; type locality "Rio das Velhas's Floddal," Lagoa Santa, Minas Gerais, Brazil.

Vulpes vetulus: Gerrard, 1862:88 (name combination).

[*Lycalopex fulvicaudus*] var. 1. *chilensis* Gray, 1869:511; type locality "Chiloe," Chile. According to Thomas (1904:236), the type locality is wrong.

Canis parvidens Mivart, 1890a:76; type locality "Brazil."

Canis urostictus Mivart, 1890a:81; type locality "Brazil."

[*Canis* (*Thous*)] *parvidens*: Trouessart, 1897:308 (name combination).

[*Canis* (*Thous*)] *urostictus*: Trouessart, 1897:308 (name combination).

Nothocyon urostictus: Wortman and Matthew, 1899:125 (name combination).

Nothocyon parvidens: Wortman and Matthew, 1899:126 (name combination).

Canis sladeni Thomas, 1904:235; type locality "Santa Anna de Chapada," Matto Grosso, Brazil.

[*Canis* (*Nothocyon*)] *parvidens*: Trouessart, 1904:235 (name combination).

[*Canis* (*Nothocyon*)] *urostictus*: Trouessart, 1904:235 (name combination).

E[*unothocyon*]. *sladeni*: J. A. Allen, 1905: 152, footnote (name combination).

E[*unothocyon*]. *urostictus*: J. A. Allen, 1905:152, footnote (name combination).

E[*unothocyon*]. *parvidens*: J. A. Allen, 1905:152, footnote (name combination).

Canis (*Eunothocyon*) *vetulus*: Ihering, 1911:206 (name combination).

Canis Vitulus Huber, 1925:1 (incorrect subsequent spelling of *Canis vetulus* Lund, 1842a).

Lycalopex vetulus: Kraglievich, 1930:43 (name combination).

[*Lycalopex*] *vetulus fulvicaudus*: Kraglievich, 1930:43 (name combination).

Dusicyon (*Lycalopex*) *vetulus*: Osgood, 1934:49 (name combination).

P[*seudalopex*]. *vetulus*: Berta, 1987:458 (name combination).

Comments.—*Lycalopex vetulus* is monotypic and found only in Brazil, although Berta (1987) mentioned a fossil from Argentina. Mivart's names *Canis parvidens* and *C. urostictus* have been cited from his report in the Proceedings of the Zoological Society of London (1890b); however, that paper was published in August 1890 (Duncan 1937) after his monograph on the Canidae, which was listed in volume 12(8) of Nature Novitates for May 1890.

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Appendix 1

List of specimens included in the statistical analyses of craniometry and pelage. OTU acronyms for cranial analyses start with the letter C; those for pelage character analysis start with a "P." Museum acronyms: Museo Argentino de Ciencias Naturales, MACN; Instituto Miguel Lillo, Tucumán, IML.

Craniometric Analysis

Lycalopex culpaeus (*culpeo fox*).—CCU ($n = 58$). (MACN) JUJUY, Abra Blanca (2): 38.039, 4.041; Lizoite (1): 41.055. NEUQUEN, Catán-Lil (53): 15138–15142, 15147, 15151–15154, 15167, 15169, 15171, 15173–15177, 15181, 15183–15184, 15188, 15190–15192, 15194–15196, 15204, 15207–15208, 15211, 15220, 15221, 15223–15227, 15231, 15235–15236, 15238–15240, 15243–15244, 15247–15248, 15250–15253. SANTA CRUZ, San Julián (2): 19221–19222.

Lycalopex gymnocercus (*gray fox*).—CST (7). (MACN) CHUBUT, Lago Blanco (1): 224; Río Mayo (2): 20207–20208. (MACN) SANTA CRUZ, Río Robles (2): 15692, 16321; (IML) SANTA CRUZ (2): 421–422.

CWT (14). (MACN) MENDOZA, La Paz (1): 1737. (MACN) NEUQUEN, Zapala (1): 14902. (MACN) RIO NEGRO, Pilcaniyeu (4): 20205–20206, 20276, 20278; General Roca (8): 24.050, 24.052–24.054, 24.066, 24.079–24.081.

CNW (8). (MACN) CATAMARCA, Andalgalá (3): 50.419–50.420, 50.432; Salar de Pipanaco (1): 51.170; Singuil (1): 53.002; (IML) CATAMARCA, Belén (1): 895. (MACN) SAN JUAN, Ischigualasto (1): 13781. (IML) SAN JUAN, Valle Fértil (1): 1178.

CCT (33). (MACN) LA PAMPA, Caleu-Caleu (15): 13327, 13331, 13337, 15748–15752, 15754, 49.139, 49.148–49.149, 49.159–49.160, 49.167; Carro Quemado (11): 16120, 16127, 16130, 16136, 16140–16141, 16145, 16147–16150; General Acha (7): 50.489, 50.492–50.493, 50.495–50.496, 50.499, 50.502.

CET (15). (MACN) BUENOS AIRES, (1): 285; Puerto Quequén (1): 14409; Bolívar (2): 15363–15364; Coronel Suárez (4): 15387–15390; Balcarce

(4): 24.133, 24.143, 24.148, 24.156; Azul (1): 26.028; Punta Médano (1): 26.163; Juárez (1): 54.133.

CNT (16). (MACN) CORDOBA, La Paz (1): 29.035; Pampa de Olaén (1): 39.191; Soto (1): 39.194. (MACN) JUJUY, (1): 32.252. (MACN) SALTA, Metán (1): 14323; Dragones (1): 36.480. (MACN) SANTIAGO DEL ESTERO, Cerro Quemado (2): 30.210–30.211; (IML) SANTIAGO DEL ESTERO, La Banda (1): 908; Giménez (1): 959. (MACN) TUCUMAN, Tapia (1); 26.129; Monteros (1): 28.182; (IML) TUCUMAN, Trancas (2): 192, 495; Tafí del Valle (2): 545, 836.

Specimens Analyzed for Pelage Characters

Lycalopex culpaeus (*culpeo fox*).—PCU (27). (MACN) RIO NEGRO, Valcheta (1): 14546; El Manso (1): 16419. (MACN) NEUQUEN, Aluminé (2): 13473, 13475; Catán-Lil (8): 15021–15024, 15030, 16169, 16171, 19223. (MACN) SANTA CRUZ, Puerto San Julián (3): 19221–19222, 50.449. (MACN) CHUBUT, Valle Lago Blanco (1): 207. (MACN) LA RIOJA, Velazco (1): 34.316. (MACN) JUJUY, Cochinoca (1): 39.493; Lizoite (2): 41.055–41.056; Santa Catalina (2): 41.164–41.165. (MACN) TIERRA DEL FUEGO, Río Grande (3): 50.480–50.482. (MACN) SALTA, San Antonio de los Cobres (2): 26.189–26.190.

Lycalopex gymnocercus (*gray fox*).—PET (14). (MACN) BUENOS AIRES, Puerto Quequén (1): 14409; Bolívar (1): 15363; Sierra de La Ventana (9): 36.046–36.050, 36.052–36.055; Rocha (2): 39.713, 39.715; Juárez (1): 54.133.

PNW (6). (MACN) SAN JUAN, Ischigualasto (1): 13781. (MACN) LA RIOJA, Villa Unión (1): 34.562. (MACN) CATAMARCA, Andalgalá (3): 50.419–50.420, 50.432; Singuil (1): 53.002.

PNT (25). (MACN) CORDOBA, (1): 31.195; Bialet Masse (1): 39.190; Soto (1): 39.194; La Paz (1): 29.035; Valle de Los Reartes (1): 25.166; Sobremonte (1): 13299; Sierra de Achala (1): 25.110. (MACN) CHACO, (1): 30.206. (MACN) SALTA, Aguaray (1): 36.228; Metán (2): 14319, 14323; Dragones (2): 36.180, 36.479; Río Caraparí (1): 36.477. (MACN) SANTIAGO DEL ESTERO, Colonia Dora (1): 42.011. (MACN) FORMOSA, Ingeniero Juárez (5): 47.133–47.136, 47.138. (MACN) SAN LUIS, Chacabuco (1): 14707; Chosmes (1): 49.224. (MACN) TUCUMAN, Burruyacú (1): 30.150; Tapia (1): 26.129; Monteros (1): 28.182.

PWT (9). (MACN) MENDOZA, (2): 38.002–38.003; Capital (1): 17827. (MACN) NEUQUEN, Catán-Lil (1): 17828; Junín de Los Andes (1): 38.223. (MACN) CHUBUT, Valle Lago Blanco (4): 209–212.

PCT (30). (MACN) LA PAMPA, Lihuel-Calel (1): 15601; Limay-Mahuida (1): 16357; Caleu-Caleu (14): 49.134–49.136, 49.148, 49.159, 49.167, 49.174–49.181; General Acha (14): 50.483–50.488, 50.492, 50.494, 50.498, 50.501, 50.503–50.505, 50.507.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):748–750. 1995

A new genus of the Compositae: *Paramiflos* (Espeletiinae) from Colombia

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Abstract.—Paramiflos is a new genus from the high Andes of Colombia that belongs to the subtribe Espeletiinae of the Compositae. It differs significantly from the related genus *Espeletiopsis* and all the other genera of Espeletiinae in the structure of the involucre, which has the outer phyllaries sharply different from the inner phyllaries.

During a study of all the taxa of the Espeletiinae, while trying to place the old species *Espeletia glandulosa* within the genus *Espeletiopsis,* special attention was paid to the uncommon structure of its involucre. Almost all the features characteristic of this species agree with other species of *Espeletiopsis,* except for the structure of the phyllaries, which are of two types. The sterile (outer) ones are fewer (only 5–7), broad, herbaceous, green, and nearly glabrous. They are distinct from the fertile (inner) phyllaries subtending the ray florets, which differ in their smaller size and in their shape. The latter are scarious, loosely clasping, and partially surround the floret. The contrast in these phyllaries distinguishes *E. glandulosa* not only from *Espeletiopsis,* but from all other genera of Espeletiinae. The involucral arrangement resembles rather that seen in *Smallanthus* Mackenzie (a segregate of *Polymnia* in the subtribe Melampodiinae. Because of these differences, here is established a new genus, *Paramiflos.* The name means "flower of the páramo," the environment that is characteristic of the high tropical Andes.

Paramiflos Cuatrecasas, gen. nov.

Caulirosula trunco erecto brevi, foliis linearibus copiosissimis conferte rosulatis. Folia viridia coriacea angustissima marginibus revolutis. Plantae pachycaules universaliter glanduliferae. Inflorescentiae plures simultaneae axillare prodientes, quam folia duplo longiores vel ultra; axis erectus rigidus superne ramosus, ramis ramulisque alternis bracteatis in corymbo dispositis; pars inferior indivisa nuda ebracteata vel bractea singula distali. Capitula radiata circulo ligularum amplo, 20–35 mm diametro. Involucrum 13–16 mm diametro, cum 5–7 phyllariis exterioribus herbaceo-membranaceis ovato-ellipticis vel obovatis vel oblongis attenuatis acutis, valde inaequalibus saepe asymmetricis 10–18 mm longis 7–11 mm latis, cum phyllariis interioribus satis distinctis bene discretis; aliquando 1–3 phyllariis similaribus sed minoribus intermediis cum phyllariis exterioribus. Phyllaria interiora herbacea uniformiter subverticillata, plerumque biseriata subaequalia, elliptica acuta, dorso rigido convexo marginibus scariosis, 7–8 mm longa, 3–4 mm lata, flores femineos vel fructus amplectentia. Flosculi radii feminei corolla ligulata lutea, tubulo piloso et glandulifero. Fructus nigrescens trigonus faciebus laevibus. Flosculi disci pseudohermaphroditi corolla tubulosa lutea pentamera parce pilosa et glandulifera; antherae 1.8–2 mm longae, basi breviter sagittatae; stylo apice conico bilobato papilloso, ovario sterile. Grana pollinia sphaeroidalia, sphaeroidale-subprolata, sphaerodale prolata, (23.5)27–31 μm pol. diametro, (23)24–27 μm aeq. diametro, spinis 4.5 μm longis, numero 12.

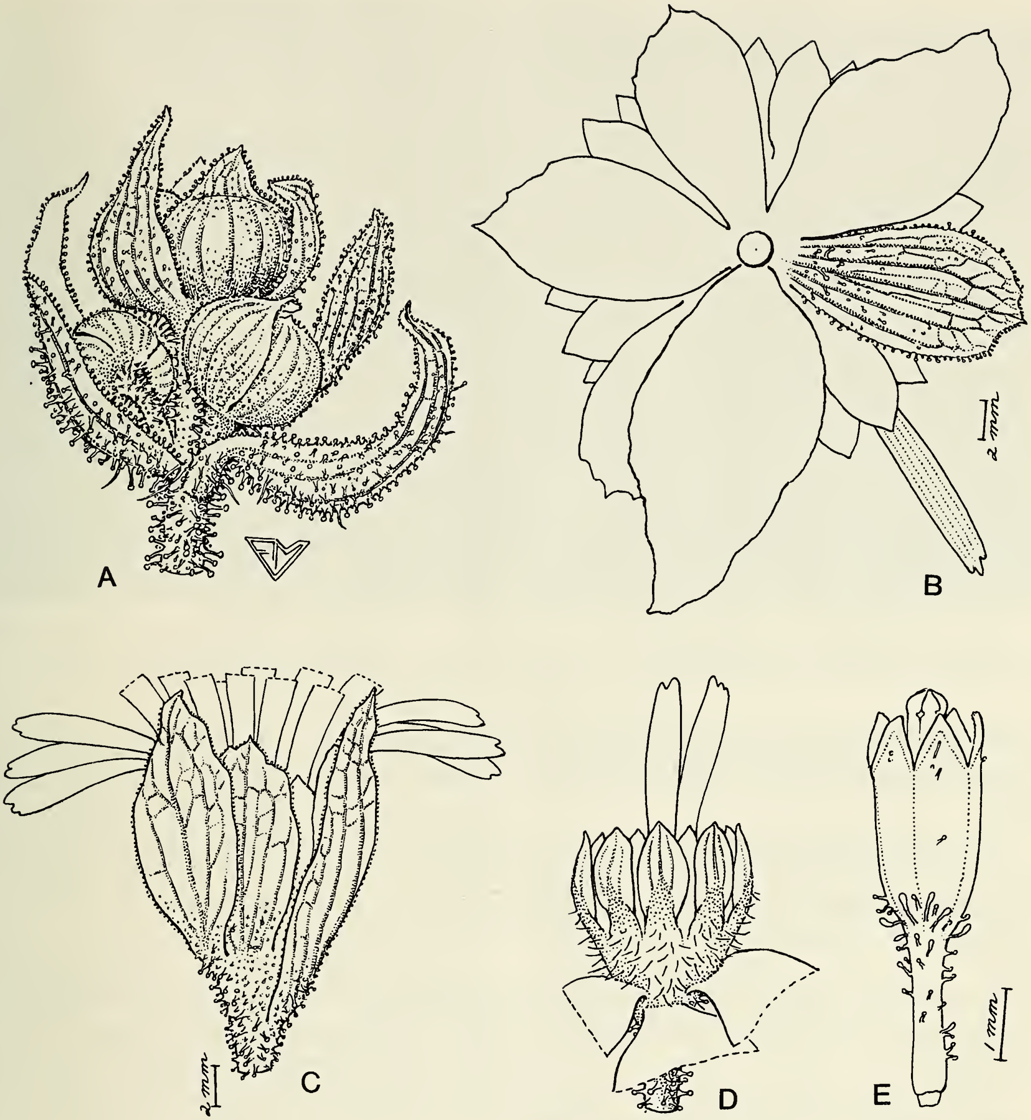

Fig. 1. *Paramiflos glandulosus* (Cuatrecasas) Cuatrecasas. A. Terminal part of inflorescence branchlet supporting three flower buds. B. Extended involucrum, abaxial view. C. Capitulum. D. Row of inner phyllaries with the outer phyllaries removed. E. Disk flower.

Type: *Espeletia glandulosa* Cuatrecasas [≡*Paramiflos glandulosus* (Cuatrecasas) Cuatrecasas].

Paramiflos glandulosus
(Cuatrecasas) Cuatrecasas, comb. nov.
Figs. 1, 2

Espeletia glandulosa Cuatrecasas, Revista Acad. Colomb. Cienc. 3:434, f. 17, 18, 23, pl. III. 1940. Type: Colombia: Boyacá: Alto de Canutos, Páramo de Guantiva, south side, 3000 m elev., 3 Aug 1940, *Cuatrecasas 10360* (holotype COL; isotypes F, US).

Espeletiopsis glandulosa (Cuatrecasas) Cuatrecasas, Phytologia 35(1):55. 1976.

Distribution.—Subpáramo and páramo

Fig. 2. Photographs of *Paramiflos glandulosus* at El Bosque, in a páramo close to Alto de Canutos, 3250 m elevation, in Boyacá, Cordillera Oriental, Colombia. Cuatrecasas photos C-1683 and I-3863.

habitats of the Eastern Cordillera of the Andes in the Department of Boyacá, Colombia.

Discussion.—Paramiflos glandulosus as first published was distinguished by the caulirosulous habit, with dense, linear, very narrow, stiff leaves; by monochasial, corymbose, deciduous, axillary inflorescences with ebracteate scapes; by bright yellow heads; and by the general glandulosity of the plant.

Later, because of some of these characteristics, the species was transferred to *Espeletiopsis* (Cuatrecasas, 1976). More recently, I realized that the structure of the involucre in this species differs substantially from the one common in that genus and in all other Espeletiinae.

In *E. glandulosa* as described, the involucre has 5–7 discretely separate, herbaceous outer phyllaries that are different in shape and size from the pseudoverticillate inner phyllaries that are more like the receptacular pales. This arrangement is otherwise unknown in *Espeletiopsis* and the other genera of Espeletiinae, which have a gradual and progressive change from the outermost phyllaries to the inner phyllaries and the receptacular pales.

The distinctive structure observed in *P. glandulosus* is similar to one already known in some other genera of the Compositae, e.g., *Smallanthus* (Melampodiinae). However, the characteristic alternate leaves and bracts (not frondose), the triangular non-striate, non-furrowed blackish achenes, the pachycaulous and caulirosular life-form of the plant, and the decidous, monochasial, axiallary infloresences clearly define *Paramiflos* as a new genus of Espeletiinae close to *Espeletiopsis*.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(4):751–752. 1995

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Applications published in the *Bulletin of Zoological Nomenclature*

The following Applications were published on 30 June 1995 in Vol. 52, Part 2 of the *Bulletin of Zoological Nomenclature.* Comment or advise on any of the 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.

2900 *Porites* Link, 1807, *Galaxea* Oken, 1815, *Mussa* Oken, 1815 and *Dendrophyllia* Blainville, 1830 (Anthozoa, Scleractinia): proposed conservation.

2903 *Tropidoptera* Ancey, 1889 (Mollusca, Gastropoda): proposed designation of *Endodonta wesleyi* Sykes, 1896 as the type species.

2946 PLUTONIINAE Bollman, 1893 (Arthropoda, Chilopoda) and PLUTONIINAE Cockerell, 1893 (Mollusca, Gastropoda): proposed removal of homonymy.

2910 *Cubaris murina* Brandt, 1833 (Crustacea, Isopoda): proposed conservation of both the generic and specific names.

2884 *Xerammobates* Popov, 1951 (Insecta, Hymenoptera): proposed designation of *Ammobates* (*Xerammobates*) *oxianus* Popov, 1951 as the type species.

2945 *Melissodes desponsa* Smith, 1854 and *M. agilis* Cresson, 1878 (Insecta, Hymenoptera): proposed conservation of the specific names.

2810 *Rhabdomeson* Young & Young, 1874 (Bryozoa): proposed designation of *Rhabdomeson progracile* Wyse Jackson & Bancroft, 1995 as the type species.

2951 *Nectria* Gray, 1840 (Echinodermata, Asteroidea): proposed designation of *Nectria ocelleta* Perrier, 1875 as the type species.

2850 *Phyllophis carinata* Günther, 1864 (currently *Elaphe carinata*; Reptilia, Serpentes): proposed conservation of the specific name.

2879 *Aptornis* Owen, [1848] (Aves): proposed conservation as the correct original spelling.

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 30 June 1995 in Vol. 52, 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.

1803 *Robulina nodosa* Reuss, 1863, (currently *Lenticulina nodosa*; Foraminiferida): neotype confirmed as the name-bearing type.

1804 *Cristellaria humilis* Reuss, 1863 (currently *Astacolus humilis;* Foraminiferida): neotype replaced by rediscovered lectotype, and *Rotalia schloenbachi* (currently *Notoplanulina*? *schloenbachi*; Foraminiferida): placed on the Official List.

1805 *Doris grandiflora* Rapp, 1827 (currently *Dendrodoris grandiflora*) and *Doridopsis guttata* Odhner, 1917 (currently *Dendrodoris guttata*) (Mollusca, Gastropoda): specific names conserved.

1806 *Ammonites nodosus* (currently *Ceratites nodosus*; Cephalopoda, Ammonoidea): specific name attributed to Schlotheim, 1813, and a lectotype designated.

1807 *Johnstonia* Quatrefages, 1866 (Annelida, Polychaeta): conserved.

1808 *Mastotermes darwiniensis* Froggatt, 1897 and *Termes meridionalis* Froggatt, 1898 (currently *Amitermes meridionalis*) (Insecta, Isoptera): neotypes retained following rediscovery of syntypes.

1809 *Bruchus* Linnaeus, 1767, *Ptinus* Linnaeus, 1767 and *Mylabris* Fabricius, 1775 (Insecta, Coleoptera): conserved.

1810 *Cryptophagus* Herbst, 1792, *Dorcatoma* Herbst, 1792, *Rhizophagus* Herbst, 1793 and *Colon* Herbst, 1797 (Insecta, Coleoptera): conserved as the correct original spellings, and *Lyctus bipustulatus* Fabricius, 1792 ruled to be the type species of *Rhizophagus.*

1811 COLYDIIDAE Erichson, 1842 (Insecta, Coleoptera): given precedence over CERYLONIDAE Billberg, 1820 and ORTHOCERINI Blanchard, 1845 (1820); and *Cerylon* Latreille, 1802: *Lyctus histeroides* Fabricius, 1792 designated as the type species.

1812 ELMIDAE Curtis, 1830 (Insecta, Coleoptera): conserved as the correct original spelling, and the gender of *Elmis* Latreille, 1802 ruled to be feminine.

1813 *Alestes* Müller & Troschel, 1844 (Osteichthyes, Characiformes): conserved.

1814 *Catharacta antarctica lonnbergi* Mathews, 1912 (currently *Catharacta skua lonnbergi*) and *Catharacta skua hamiltoni* Hagen, 1952 (Aves, Charadriiformes): subspecific names conserved.

INFORMATION FOR CONTRIBUTORS

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