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MORPHOLOGICAL AND ECOLOGICAL VARIATION IN *OTOPTEROPUS CARTILAGONODUS* KOCK, 1969 (MAMMALIA: CHIROPTERA: PTEROPODIDAE) FROM LUZON, PHILIPPINES

Luis A. Ruedas, John R. Demboski, and Rogelio V. Sison

Abstract.—Morphological variation in twenty-four characters of the skull, eight wing bones, and five characters of external morphology, as well as ecological data, are examined in the pteropodid bat, *Otopteropus cartilagonodus*, heretofore only known from six specimens. This study examines *O. cartilagonodus* from three populations: Zambales Mountains ($n = 38$), Mount Isarog ($n = 46$), and Isabela Province ($n = 1$). In the Zambales population, marked sexual dimorphism was found in five cranial characters associated with the feeding apparatus, as well as in overall length. Only two characters differed between sexes in the Mount Isarog population. The Zambales and Mount Isarog populations differed significantly in 21 out of 37 mensural characters, as well as in reproductive timing and embryonic development. From the segregation of sexes along an elevational gradient in the Zambales population, it is hypothesized that bats of this population may reduce intersexual competition by displaying distinct trophic and habitat preferences. This pattern of altitudinal segregation was not as marked in the Mount Isarog population. The structured, geographically and morphologically cohesive populations of *O. cartilagonodus* represent an ideal organism for elucidation of zoogeographic relationships among the different regions of the island of Luzon.

The pteropodid bat fauna of the Philippines currently is known to comprise twenty-four species in 15 genera (Heaney et al. 1987, Heaney 1991, Ingle & Heaney 1992). Of the 15 species of Pteropodidae endemic to the Philippines, only *Otopteropus cartilagonodus* Kock, 1969, is restricted to the island of Luzon. Until recently, only six specimens of this species were known: five from the Cordillera Central Mountains of northwestern Luzon (Kock 1969), and one from the Sierra Madre Mountains, northeastern Luzon (Mudar & Allen 1986). An additional reported specimen (University of Michigan Museum of Zoology no. 156689) was misidentified, and actually represents *Haplonycteris fischeri* (Heideman et al. 1993; LAR, pers. obs.). More recently, Heideman et al. (1993) reported on the reproductive timing and early development of this species based on a sample of seven males and twenty-two females from Mount Isarog, southern Luzon Island. The specimens forming the basis of that report now are at the United States National Museum, and form part of the basis for this report.

Recently, an inventory of the fauna of the Philippines was undertaken jointly by the Cincinnati Museum of Natural History (CMNH), the National Museum of the Philippines (NMP), and the University of the Philippines at Los Baños (UPLB), to provide baseline data on the distribution and conservation status of major vertebrate groups in the Philippines and to promote the conservation of centers of biological diversity. A portion of that survey was carried out along an elevational gradient in west central Luzon Island. During that time, several specimens of *O. cartilagonodus* were secured, allowing us the opportunity to examine morphological and ecological variation in this species in greater detail than heretofore possible. We also examined some ecological factors that may influence intraspecific altitudinal zonation in the species.

Methods

Field studies in the Zambales Mountains were conducted from 17 February to 8 March 1992. The Zambales were chosen as a study area because the fauna was relatively unknown (only studies by Johnson 1962 and Ripley & Marshall 1967 are known to us, both conducted in the foothills of the Zambales Mountains in and around the former Clark Air Force Base), and because they constitute a large, "insular" mountain, presently isolated from the other montane areas of Luzon. In addition, Dickerson (1924) suggested that the Zambales Mountains may have constituted an island separated from Luzon for much of the Tertiary and Quaternary.

Mist nets were set up along an elevational gradient extending from 125 m to 1900 m. Forty standard 12 m four-rung 25 mm mesh mist nets were used at each of three sites and run for seven consecutive nights; *O. cartilagonodus* were caught at two of these sites (described below). At both sites, a single "wall net" was set, consisting of four (Site 1) and three (Site 2) superimposed nets extending from ground level to the top of the canopy. At Site 1, an additional three sets were "doublehigh" nets, consisting of two superimposed nets. Mist nets were checked for bats and birds at dawn, every three to four hours during the course of the day, at dusk, and at least twice at two-hour intervals after dusk.

Twenty-four cranial measurements of *O. cartilagonodus* were taken to the nearest 0.01 mm using a Fowler Max-Cal digital caliper (measurements defined by Freeman 1981). These included greatest length of skull (GLS), length of rostrum (ROSL), length of palate (PALL), length of maxillary toothrow (MAXTL), length of upper molariform row (UPMOLL), rostral breadth (ROSW), least interorbital breadth (IOB; = postorbital breadth, POST ORB, of Freeman 1981), zygomatic breadth (ZB), breadth of braincase (BB), height of braincase (HB), breadth between upper canines (INTCB), breadth between M2 (INTMB), width between anterior pterygoids (APTB), width between posterior pterygoids (PPTB), height of upper canine (HUPCAN), length of M3 (M3L), width of M3 (M3W), length of dentary (DENTL), condylocanine length (CONCANL), condyle to m1 (CONM1), length of lower toothrow (MNDTOOTH), moment arm of masseter (MAMASTR), thickness of dentary (DENTTHK), and height of lower canine (HTLWRCAN). Wing bone measurements (described by Ruedas & Bickham 1992), included forearm length (FA), length of metacarpals of digits two through five (D2M through D5M), and length of proximal phalanges of digits two through five (D2P1 through D5P1). External measurements included total length, length of hind foot, length of ear, and weight.

Statistical analyses were carried out using the Statistical Analysis Software, version 6.03 (SAS Institute, Inc. 1988a, 1988b). Standard univariate statistics were obtained using the UNIVARIATE procedure; pairwise comparisons were evaluated using the TTEST procedure. The significance of the moment statistics (skewness, g_1; and kurtosis, g_2) was calculated by hand using the method of Sokal and Rohlf (1981:174–175).

Species diversity was measured using the Shannon diversity index, H' (Shannon 1948). Differences between diversity indices of the two sites were evaluated using the t test approach of Hutcheson (1970) for the Shannon formula, as described by Zar (1984). Community similarity was examined using the Horn index of community overlap (Horn 1966, Brower & Zar 1984).

Evenness of abundance of species was calculated as the ratio of the Shannon index, H', to the maximum possible diversity, H'_{max} (Pielou 1969). These measures of diversity and community similarity (heterogeneity indices sensu Peet 1974) are preferred herein over species abundance models because they are distribution independent (Magurran 1988, Peet 1974; but see Graham 1983 for a contrasting opinion).

Specimens Examined

Otopteropus cartilagonodus.—Philippines: Luzon Island; Camarines Sur Province; 4 km N, 18 km E Naga, Mt. Isarog, 13°40'N, 123°20'E, 475 m; external and cranial characters of 4 males (U.S. National Museum of Natural History [USNM] 573439, 573444–573446) and 6 females (USNM 573440–573443, 573447, 573448); external characters of 1 male (USNM 573684) and 2 females (USNM 573680, 573682). Philippines, Luzon Island; Camarines Sur Province; 4 km N, 21 km E Naga, Mt. Isarog, 13°40'N, 123°22'E, 1350 m; external and cranial characters of 1 female (USNM 570503), external characters of 1 female (USNM 573713) and 2 males (USNM 573712, 573715). Philippines: Luzon Island; Camarines Sur Province; 5 km N, 20 km E Naga, Mt. Isarog, 13°40'N, 123°21'E, 900 m; external characters of 3 males (USNM 573694, 573696, 573704) and 20 females (USNM 573685–573693, 573695, 573697–573703, 573705–573707). Philippines: Luzon Island; Camarines Sur Province; 4.5 km N, 20.5 km E Naga, Mt. Isarog, 13°40'N, 123°22'E, 1125 m; external characters of 4 females (USNM 573708–573711). Philippines: Luzon Island; Camarines Sur Province; 4 km N, 21.5 km E Naga, Mt. Isarog, 13°40'N, 123°22'E, 1550 m; external characters of 1 male (USNM 573715). Philippines: Luzon Island; Camarines Sur Province; 4 km N, 22 km E Naga, Mt. Isarog, 13°40'N, 123°22'E, 1750 m; external characters of 1 male (USNM 573716). Philippines: Luzon Island; Isabela Province; 3 km W mouth of Blos River, 17°30'N, 122°10'E, elev. 50 m (precise locality illustrated in Fig. 1, Mudar & Allen 1986:220; external and cranial characters of 1 female (University of Michigan Museum of Zoology [UMMZ] 156972). Philippines: Luzon Island; Zambales Province; Zambales Mountains, 15°35'N, 120°09'E, 1140 m; external and cranial characters of 7 females (National Museum of the Philippines/Cincinnati Museum of Natural History field numbers [NMP/CMNH] 22, 39, 75, 139, 140, 148, 149); external characters of 3 females (NMP/CMNH 45, 106, 141). Philippines: Luzon Island; Zambales Province; Zambales Mountains, 15°30'N, 120°08'E, 1500 m; external and cranial characters of 3 females (NMP/CMNH 354, 388, 407) and 9 males (NMP/CMNH 304, 312, 356, 362, 364–366, 390, 391); external characters of 4 females (NMP/CMNH 321, 332, 389, 408) and 12 males (NMP/CMNH 302, 307, 314, 318, 322, 335, 336, 355, 357, 363, 378, 409). These specimens will be assigned permanent museum numbers as soon as the division of specimens between CMNH and NMP takes place.

Specimens from the National Museum of the Philippines were examined by RVS, but the measurements are not included to maintain consistency of measurer and instrument. Specimens are identified by collection date because of lack of museum number, as follows: Luzon Isl.; Laguna Prov.; Balian; 1 female (col. 16 Jul 1964). Luzon Isl.; Nueva Viscaya Prov.; Dalton; 1 male (col. 20 Apr 1966), 4 females (col. 20 and 21 Apr 1966; 3 Jun 1970; 29 Oct 1970). Luzon Isl.; Quezon Prov.; Real, National Botanic Garden (University of the Philippines Land Grant); 2 males (3 and 8 Jun 1974). Three specimens (two males, one female) were collected at this last site by Andres L. Dans and Pedro L. Alviola, III, in May 1983, but were lost during a fire at the University of the Philippines at Los Baños on 10 May 1990 (A. L. Dans, in litt.). One additional male was collected during May 1992 by two students of A. L. Dans in Luzon Isl.; Cagayan Prov.; Mount Cetaceo, Sierra Madre, elev. 1500 m (A. L. Dans, in litt.) The exact whereabouts of this specimen are unknown.

The type series was not examined, but includes the holotype (Senckenberg Museum, Frankfurt [SMF] No. 28462, male) and three paratypes (SMF 28852–28854, 2 males, 1 female) from Philippines: Luzon Island; Mountain Province; Sitio Pactil; paratype, SMF 35750, female, Luzon Island: Abra Province; Massisiat Resthouse; and paratype, SMF 35749, female, "Philippines," no specific locality. No elevations, latitude, or longitude are noted in the description.

Study Sites

Specimens from Mount Isarog were collected by L. R. Heaney and his coworkers. These sites are described and illustrated by Goodman & Gonzales (1990) and Rickart et al. (1991); one *O. cartilagonodus* from that locality is illustrated in Heaney & Rickart (1990). The collection locality of the single specimen from Isabela Province (UMMZ 156972), also collected by L. R. Heaney, is described by Mudar & Allen (1986). The Zambales Mountains specimens were collected by LAR and JRD and coworkers.

The Zambales Mountains (Fig. 1) are an isolated mountain range encompassing approximately 6960 km^2 in west central Luzon. Including the volcanoes of the Bataan Peninsula, the Zambales extend approximately 200 km in length, running about 20° west of due north; the southern end (Bataan Peninsula) begins approximately 55 km west of the city of Manila, across Manila Bay. The greatest width of the range is about 60 km. To the east, the Zambales Mountains are isolated from the Cordillera Central (the nearest mountain range) by the extensive plains of Tarlac, also known as the Great Valley of Luzon, a wide expanse of alluvial, fluviatile, lacustrine and other sedimentary deposits (including beach and coralline), now consisting primarily of rice fields. To the west and north, the mountains end in the South China Sea; to the south, they separate Subic Bay from Manila Bay.

Rainfall patterns in the area display clearly demarcated dry and wet seasons. Data collected between 1951 and 1970 in Iba, a coastal town in the Zambales Province near the study area, indicate rainfall maxima in late July or August (ca. 1025 mm monthly average) and minima in late January or February (ca. 20 mm monthly average; data from Philippine Council, 1977).

Site 1.—Zambales Mountains, 15°35′N, 120°09′E, 1140 m. Sampled 17 to 26 Feb 1992. The altitudinal transect at this site was situated along a steep South facing ridge of Mount Apoy between 1050 m and 1265 m. During our stay at this camp, nighttime low temperatures averaged 10°C, while daytime highs rarely exceeded 23°C. This site was characteristic of the tropical moist deciduous forest type of Whitmore (1984), specifically, tropical lower montane rain forest; toward the top end of the transect were found elements transitional to a mossy forest type. Relatively untouched forest begins in the area only above approximately 1030 m (LAR, pers. obs.); below this elevation, extensive thickets of bamboo and other secondary growth predominate. The forest had two stories, but moving from the lower to higher elevations, the canopy gradually decreased in height above ground from 15–16 m to 11–13 m, and the subcanopy became increasingly broken and less conspicuous. Due to the high number of tree falls and boulders (the latter often 4–5 m wide) at either end of the transect, the canopy at the extremes of the transect was broken and uneven, while the canopy between the extremes was closed and continuous. Vegetation varied depending on exactly where the nets were set. Nets set along a ridge near the camp (ca. 1170 m) were in a moderately to dry habitat, with volcanic ash from the explosion of Mount Pinatubo in

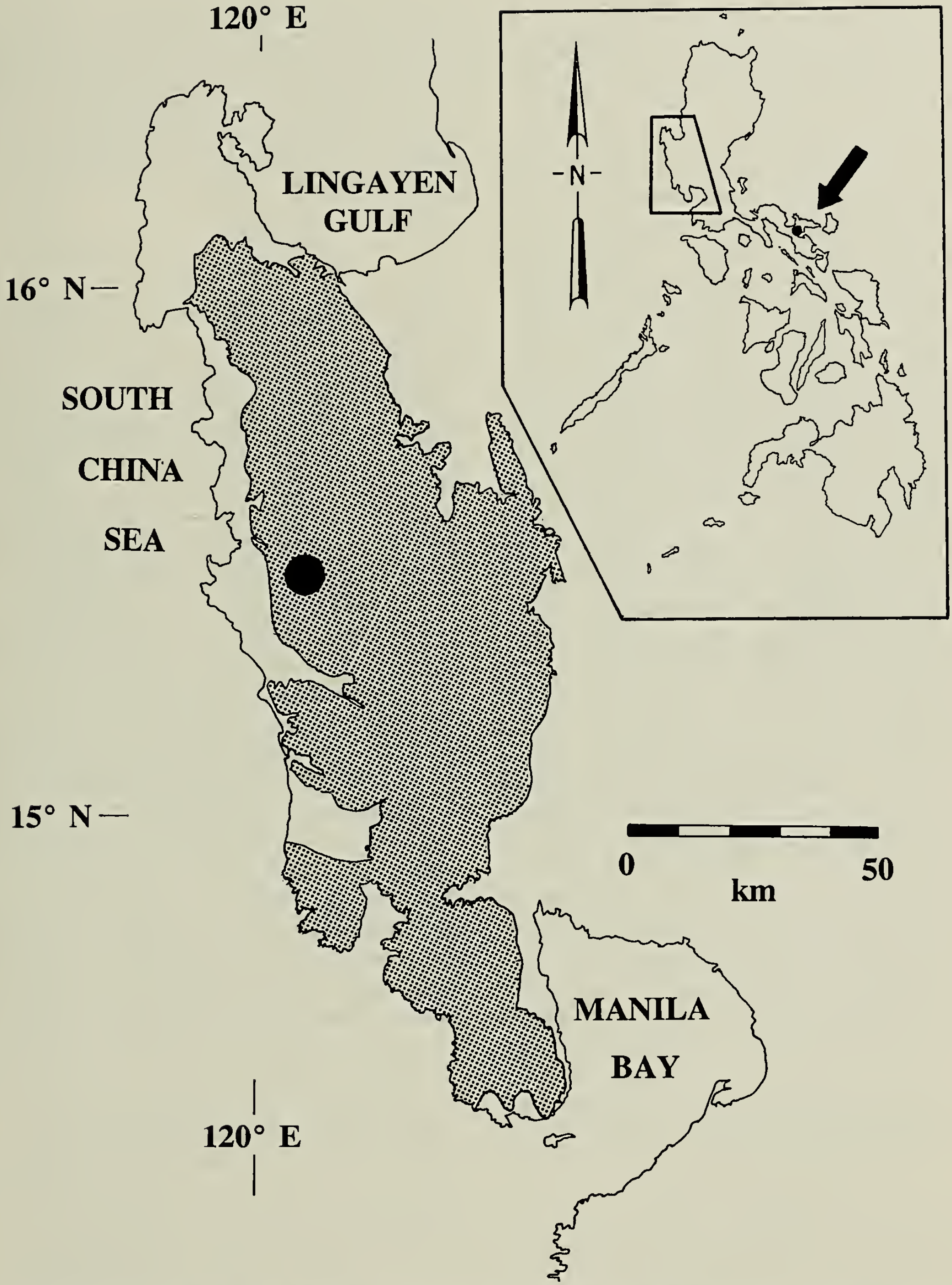

Fig. 1. Map of the geological assemblage constituting the Zambales Mountains (stippled area); the solid circle marks the study area. Inset map shows the Zambales area (box) in relation to the remainder of Luzon Island and the Philippines, with the arrow pointing to Mount Isarog, where the sample of *Otopteropus cartilagonodus* from the National Museum of Natural History originated.

1991 covering much of the ground and vegetation (1–2 cm thick layer). The driest portion of the site was covered almost entirely by grasses (Poaceae); several charred upright tree trunks showed the area once had other vegetation, but had since been burned to grassland. Toward the east, the area was less dry, and trees of the families Myrtaceae, Lauraceae, and Tiliaceae predominated; these had a maximum height of approximately 9 m, with a diameter at breast height (dbh) no greater than 50 cm, and usually less than 30 cm. Proceeding downhill from the camp (S) trees increased slightly in stature. There were some, though not many, epiphytic orchids, particularly above 1250 m; some climbing bamboos, and shrubby, herbaceous undergrowth in the wooded areas northeast of the camp. Below 1100 m there was abundant rattan, a climbing spiny palm (*Calamus*) used in manufacturing furniture, and the gathering of which is the livelihood for many people in the area; the area cannot be said, therefore, to be wholly undisturbed. Sampling effort was 240 net nights.

Site 2.—Zambales Mountains, 15°30′N, 120°08′E, 1500 m. Sampled 11 to 18 March 1992. Nighttime lows at this site averaged 12.6°C (range: 10.3°–14.0°), while daytime highs averaged 22.5°C (range: 19.8°–24.0°). As with Site 1, this site is in the broad category of tropical moist deciduous forest type of Whitmore (1984); however, at this elevation, the vegetation was more characteristic of tropical upper montane rain forest. This site was very dry, especially as it was visited near the height of the dry season in the Zambales Mountains. Ashfall from the 1991 Mount Pinatubo explosion covered the ground to a depth of 2–4 cm and coated much of the vegetation. Canopy height varied from less than 5 m to approximately 11 m; no trees exceeded 70 cm dbh: in fact, few were greater than 50 cm dbh. Predominant trees were of the families Fagaceae, Myrtaceae, Magnoliaceae, and Pinaceae, although other families also were represented to a lesser extent. Many epiphytic orchids were present at this site, as well as epiphytic ferns. Not much bamboo or other secondary vegetation was found; in addition, there were many dead branches, and a thick cover of leaf litter on the ground. This site was sampled for 200 net nights.

Results

Morphological variation.—Results of morphometric analyses of the Zambales Mountains population are summarized in Table 1 for cranial mensural characters that did not differ significantly between the two sexes. Those cranial characters that did differ are summarized in Table 2. Using a probability level of $\alpha = 0.05$, the expected number of sexually dimorphic characters would have been between one and two for 24 characters examined; five were found. All of these are directly or indirectly involved in the feeding apparatus. Length of rostrum, length of M3, and length of mandible from condyle to canine, all affect the mechanical force applied during mastication. Posterior pterygoid breadth influences the maximum size of food particles able to be ingested. An additional note with respect to sexual dimorphism in this population is that all cranial characters are larger in male *O. cartilagonodus*; the remaining sexually dimorphic character, height of braincase, is larger in females of the species. This last character may offset partially the size advantage of males over females in mastication related measurements by influencing the mechanics of the masseter muscle.

Wing bone measurements are summarized in Table 3; no sexual dimorphism was found in any of these mensural characters. External measurements are summarized in Table 4. Of these, only total length displayed significant sexual dimorphism, with females being somewhat longer than males.

Mensural characters of the Mount Isarog population are summarized in Tables 5–7. Only two cranial measurements differed be-

Table 1.—Standard univariate statistics for cranial characters (in millimeters; abbreviations defined in text) of *Otopteropus cartilagonodus* from the Zambales Mountains. Characters displaying sexual dimorphism are summarized in Table 2. (Other abbreviations are: $\bar{X}$ mean; *SE,* standard error; *W,* results of the Shapiro-Wilk test for normality [N, normal; *, $0.05 > P > 0.01$; **, $0.01 > P > 0.001$; ***, $P < 0.001$]; g_1, skewness statistic [n.s., not significant]; g_2, kurtosis statistic.)

Character	$\bar{X}$	*SE*	Range	*W*	g_1	t_{g1}	g_2	t_{g2}
GLS	23.02	± 0.107	22.2–23.8	N	0.257	n.s.	−0.652	n.s.
PALL	11.35	± 0.072	10.9–11.9	N	−0.046	n.s.	−1.308	n.s.
MAXTL	6.56	± 0.042	6.2–6.8	N	−0.493	n.s.	−0.672	n.s.
UPMOLL	5.33	± 0.039	5.0–5.6	N	−0.655	n.s.	−0.440	n.s.
ROSW	5.52	± 0.956	5.0–6.1	N	0.323	n.s.	−0.716	n.s.
IOB	4.20	± 0.051	3.7–4.6	N	−0.224	n.s.	−0.100	n.s.
ZB	14.49	± 0.079	13.9–15.3	N	0.692	n.s.	0.504	n.s.
BB	10.65	± 0.058	10.2–11.2	N	0.435	n.s.	−0.040	n.s.
INTCB	2.09	± 0.034	1.8–2.4	N	0.123	n.s.	−0.633	n.s.
INTMB	4.84	± 0.054	4.4–5.2	N	−0.253	n.s.	−0.930	n.s.
APTB	3.90	± 0.036	3.7–4.2	N	0.157	n.s.	−1.030	n.s.
HUPCAN	1.85	± 0.071	1.2–2.3	N	−0.335	n.s.	−0.370	n.s.
M3W	0.90	± 0.018	0.7–1.0	*	−1.472	**	4.325	***
DENTL	16.43	± 0.088	15.7–17.6	*	1.385	**	3.855	***
CONM1	13.26	± 0.093	12.7–14.1	N	0.406	n.s.	−0.722	n.s.
MNDTOOTH	6.64	± 0.043	6.3–6.9	N	−0.523	n.s.	−0.991	n.s.
MAMASTR	7.18	± 0.079	6.5–7.8	N	−0.545	n.s.	−0.075	n.s.
DENTTHK	1.93	± 0.029	1.6–2.2	N	−0.128	n.s.	0.797	n.s.
HTLWRCAN	1.66	± 0.046	1.2–2.1	*	−0.001	n.s.	3.034	**

tween males and females in this population: zygomatic breadth ($P = 0.0085$) and posterior pterygoid breadth ($P = 0.0090$). With respect to the wing bones, the only one found to differ between the sexes was the first phalanx of digit 5 ($P = 0.0053$). Ear length was the only external character found to differ between the sexes ($P = 0.0117$), despite considerable overlap in the ranges.

Mensural characters of the single specimen from Isabela Province (UMMZ 156972) are reported in Table 8. Because this sample consists of a single specimen, statistical comparisons between this and the other two populations were not carried out.

Geographic variation.—Considerable differences in morphology exist between the two populations of *O. cartilagonodus* examined herein: 21 out of the 37 characters examined differed significantly between Zambales and Isarog populations. With respect to non-sexually dimorphic characters of the skull, significantly different characters include interorbital breadth ($P = 0.0000$),

Table 2.—Standard univariate statistics for sexually dimorphic mensural cranial characters of *Otopteropus cartilagonodus* from the Zambales Mountains. (Character abbreviations as in text; other abbreviations as in Table 1.)

	Males			Females		
Character	$\bar{X}$	*SE*	Range	$\bar{X}$	*SE*	Range
ROSL	10.67	± 0.116	10.0–11.1	10.12	± 0.118	9.7–10.7
HB	8.93	± 0.098	8.8–9.8	9.34	± 0.102	8.8–9.8
PPTB	3.48	± 0.048	3.3–3.7	3.27	± 0.058	3.0–3.6
M3L	1.12	± 0.022	1.1–1.2	1.04	± 0.020	0.9–1.1
CONCANL	15.82	± 0.105	15.4–16.3	15.50	± 0.096	15.1–16.0

Table 3.—Wing bone measurements, in millimeters, for *Otopterops cartilagonodus* from the Zambales Mountains. (Character abbreviations as in text; other abbreviations as in Table 1.)

Character	$\bar{X}$ *SE*	Range	*W*	g_1	t_{g1}	g_2	t_{g2}
D2M	22.41 ± 0.138	20.1–24.1	N	−0.433	*	0.864	n.s.
D2P1	5.23 ± 0.055	4.6–5.8	*	−0.012	n.s.	−1.274	n.s.
D3M	32.88 ± 0.173	30.0–35.2	N	−0.467	n.s.	0.500	n.s.
D3P1	24.78 ± 0.161	22.1–26.9	N	−0.361	n.s.	0.919	n.s.
D4M	30.58 ± 0.183	27.2–33.5	N	−0.076	n.s.	2.046	**
D4P1	17.82 ± 0.145	15.0–19.9	N	−0.453	n.s.	1.985	**
D5M	32.25 ± 0.181	28.3–34.0	*	−1.103	**	3.769	***
D5P1	15.44 ± 0.106	14.0–16.4	N	−0.576	n.s.	−0.388	n.s.

height of upper canine (*P* = 0.0000), length of dentary (*P* = 0.0052), length of condyle to M1 (*P* = 0.0001), length of mandibular toothrow (*P* = 0.0000), and height of lower canine (*P* = 0.0047). In sexually dimorphic characters, females differ between the two populations in length of rostrum (*P* = 0.0005), zygomatic breadth (*P* = 0.0003), posterior pterygoid breadth (*P* = 0.0370), and condylocanine length (*P* = 0.0201), while males differ in posterior pterygoid breadth only (*P* = 0.0397). Every wing bone measurement differs significantly between the two populations (FA, D2M, D3M, D4M, D4P1, D5M, *P* = 0.0000; D3P1, *P* = 0.0093; D5P1, females, *P* = 0.0000, males, *P* = 0.0005). Finally, with respect to external characters, the two populations differ in length of hind foot (*P* = 0.0001), mass (*P* = 0.0001), and total length (females, *P* = 0.0001, males, *P* = 0.0091). The specimen from Isabela Province (Table 8) is closest to Mount Isarog specimens rather than to Zambales specimens in all characters examined, albeit without statistical confirmation.

Ecological notes.—Thirty-eight specimens of *O. cartilagonodus* were collected in mist nets set near Sites 1 and 2. Ten individuals, all females, were collected at Site 1 in seven nets set between 1130 and 1235 m. Four were caught in two nets, set at 1140 m and 1180 m; the remaining six were caught singly. All individuals were flying between 125 and 270 cm above the ground when captured. Of these ten females, nine were pregnant, with embryos averaging 9.22 mm in crown rump length (mode, 12 mm; range 5–13 mm; *SE*, ± 0.969).

At Site 2, 15 males and 9 females were collected. Two nets, set at 1579 m, and 1613 m, each caught two; one net set at 1594 m resulted in three; remaining bats were caught singly in nets at elevations between 1365 m

Table 4.—Standard external measurements for *Otopterops cartilagonodus* from the Zambales Mountains. Total length was the only external measurement found to be sexually dimorphic. (Mass expressed in grams; all other measurements in millimeters; abbreviations as in Table 1.)

Character	$\bar{X}$ *SE*	Range	*W*	g_1	t_{g1}	g_2	t_{g2}
Hind foot	10.66 ± 0.102	9–12	***	−0.294	n.s.	0.189	n.s.
Ear length	13.80 ± 0.150	11–16	***	−0.646	n.s.	1.887	*
Forearm	44.55 ± 0.213	41–47	N	−0.835	*	0.864	n.s.
Mass	13.55 ± 0.099	12–15	*	−0.025	n.s.	0.192	n.s.
Total length							
Females	69.47 ± 0.515	65–74	N	0.088	n.s.	−0.344	n.s.
Males	68.10 ± 0.350	66–70	*	−0.092	n.s.	−1.422	n.s.

Table 5.—Standard univariate statistics for mensural cranial characters of *Otopteropus cartilagonodus* from Mt. Isarog (specimens at the U.S. National Museum of Natural History, U.S.N.M.), in millimeters. (Abbreviations are as in Table 1.)

Character	$\bar{X}$ *SE*	Range	*W*	g_1	t_{g1}	g_2	t_{g2}
GLS	23.18 ± 0.123	22.4–23.9	N	−0.374	n.s.	0.723	n.s.
ROSL	10.79 ± 0.078	10.4–11.1	N	−0.454	n.s.	−1.625	n.s.
PALL	11.89 ± 0.077	11.4–12.3	N	−0.364	n.s.	−0.134	n.s.
MAXTL	6.76 ± 0.112	6.2–7.5	N	0.518	n.s.	0.976	n.s.
UPMOLL	5.45 ± 0.068	5.0–5.7	N	−1.271	n.s.	0.921	n.s.
ROSW	5.72 ± 0.140	5.1–6.5	N	0.232	n.s.	−0.878	n.s.
IOB	3.73 ± 0.071	3.4–4.0	N	0.006	n.s.	−1.606	n.s.
BB	10.85 ± 0.094	10.2–11.2	N	−1.144	n.s.	0.897	n.s.
HB	9.52 ± 0.091	9.0–10.2	N	0.844	n.s.	1.485	n.s.
INTCB	2.20 ± 0.045	1.9–2.4	N	−0.802	n.s.	0.361	n.s.
INTMB	4.77 ± 0.064	4.4–5.1	N	−0.081	n.s.	−0.779	n.s.
APTB	3.81 ± 0.027	3.7–4.0	N	0.944	n.s.	2.110	n.s.
HUPCAN	2.53 ± 0.077	2.0–2.8	N	−0.759	n.s.	0.466	n.s.
M3L	1.09 ± 0.016	1.0–1.1	N	−0.503	n.s.	−1.168	n.s.
M3W	0.91 ± 0.021	0.8–1.0	N	0.675	n.s.	0.309	n.s.
DENTL	16.89 ± 0.124	16.2–17.7	N	0.172	n.s.	0.706	n.s.
CONCANL	16.10 ± 0.141	15.0–16.6	N	−1.128	n.s.	1.947	n.s.
CONM1	13.92 ± 0.114	13.1–14.5	N	−0.828	n.s.	1.247	n.s.
MNDTOOTH	7.03 ± 0.068	6.7–7.5	N	0.421	n.s.	0.768	n.s.
MAMASTR	7.23 ± 0.079	6.6–7.6	N	−1.112	n.s.	1.552	n.s.
DENTTHK	1.91 ± 0.045	1.7–2.2	N	0.300	n.s.	−0.372	n.s.
HTLWRCAN	1.90 ± 0.053	1.6–2.3	N	0.612	n.s.	0.516	n.s.
ZB (females)	15.10 ± 0.086	14.8–15.5	N	0.066	n.s.	0.385	n.s.
ZB (males)	14.51 ± 0.180	14.2–15.0	N	1.635	n.s.	2.999	n.s.
PPTB (females)	3.09 ± 0.043	2.9–3.3	N	0.360	n.s.	−0.701	n.s.
PPTB (males)	3.30 ± 0.035	3.2–3.4	N	−1.414	n.s.	1.500	n.s.

Table 6.—Wing bone measurements, in millimeters, for the *Otopteropus cartilagonodus* from Mt. Isarog (specimens at the U.S.N.M.); 33 females and 8 males comprise the sample. The only measurement differing at $\alpha = 0.05$ was that of the first phalanx of digit 5 (D5P1; $P = 0.0053$); however, D3M, D3P1, and D4P1 all had P values between 0.05 and 0.10. (Character abbreviations as in text; other abbreviations as in Table 1.)

Character	$\bar{X}$ *SE*	Range	*W*	g_1	t_{g1}	g_2	t_{g2}
D2M (♀)	23.94 ± 0.183	21.4–25.8	N	−0.038	n.s.	−0.170	n.s.
D2M (♂)	23.44 ± 0.529	21.1–25.5	N	−0.346	n.s.	0.382	n.s.
D3M (♀)	34.56 ± 0.191	32.3–36.7	N	−0.123	n.s.	−0.739	n.s.
D3M (♂)	33.78 ± 0.333	32.6–35.1	N	0.016	n.s.	−1.702	n.s.
D3P1 (♀)	25.45 ± 0.143	23.8–27.2	N	−0.045	n.s.	−0.673	n.s.
D3P1 (♂)	24.82 ± 0.277	23.5–25.8	N	−0.688	n.s.	−0.412	n.s.
D4M (♀)	32.98 ± 0.181	30.0–35.2	N	−0.402	n.s.	1.059	n.s.
D4M (♂)	32.56 ± 0.469	30.8–34.7	N	0.351	n.s.	−0.673	n.s.
D4P1 (♀)	19.28 ± 0.188	17.7–23.9	***	2.509	***	10.050	***
D4P1 (♂)	18.55 ± 0.245	17.5–19.4	N	−0.279	n.s.	−1.210	n.s.
D5M (♀)	33.48 ± 0.214	31.0–35.3	N	−0.206	n.s.	−0.803	n.s.
D5M (♂)	33.09 ± 0.389	31.6–35.0	N	0.502	n.s.	−0.072	n.s.
D5P1 (♀)	17.12 ± 0.120	15.8–18.8	N	0.149	n.s.	0.498	n.s.
D5P1 (♂)	16.36 ± 0.177	15.6–17.2	N	0.281	n.s.	0.593	n.s.

Table 7.—Standard external measurements for *Otopteropus cartilagonodus* from Mt. Isarog (specimens at the U.S.N.M.); 40 females and 14 males comprise the sample. Ear length was the only external measurement found to be sexually dimorphic ($P = 0.0117$). (Mass expressed in grams; all other measurements in millimeters; abbreviations as in Table 1.)

Character	$\bar{X}$ *SE*	Range	*W*	g_1	t_{s1}	g_2	t_{s2}
Total length							
Females	74.67 ± 0.989	65–87	N	0.196	n.s.	−0.861	n.s.
Males	72.28 ± 1.348	65–79	N	−0.175	n.s.	−1.422	n.s.
Hind foot							
Females	13.78 ± 0.494	11–20	***	1.058	**	−0.658	n.s.
Males	12.88 ± 0.670	11–19	***	1.931	**	2.892	*
Ear length							
Females	14.00 ± 0.095	12–15	***	−0.753	*	2.789	***
Males	13.21 ± 0.260	12–15	N	0.089	n.s.	−1.026	n.s.
Forearm							
Females	48.75 ± 0.256	44–52	N	−0.190	n.s.	0.650	n.s.
Males	47.86 ± 0.404	45–51	N	0.124	n.s.	0.494	n.s.
Mass							
Females	15.98 ± 0.245	13–19	N	0.109	n.s.	−0.706	n.s.
Males	16.36 ± 0.360	15–20	*	1.615	**	3.369	**

and 1643 m. At this site bats were flying between 30 and 210 cm above the ground when caught. Only three of the nine females were pregnant; two embryos measured 8 and 14 mm, the third female was fluid preserved intact and determined to be pregnant by external inspection (fide JRD). All males captured exhibited abdominal testes; habit-

Table 8.—Measurements of the single specimen of *Otopteropus cartilagonodus* (UMMZ 156972) from Isabela Province, Luzon Island, Philippines. (Mass expressed in grams, all other measurements in millimeters.)

Cranial measurements

Greatest length of skull	23.3	Anterior pterygoid breadth	3.7
Length of rostrum	10.7	Posterior pterygoid breadth	3.0
Length of palate	12.2	Height of upper canine	2.6
Length of maxillary toothrow	7.2	Length of M3	1.0
Length of upper molariform row	6.1	Width of M3	0.9
Rostral breadth	4.8	Length of dentary	17.7
Interorbital breadth	3.5	Condylocanine length	15.7
Zygomatic breadth	15.4	Condyle to m1	14.3
Breadth of braincase	10.9	Length of mandibular toothrow	6.7
Height of braincase	9.4	Moment arm of masseter	7.8
Breadth between upper canines	2.2	Thickness of dentary	2.0
Breadth between M3	4.8	Height of lower canine	2.0

Wing bone measurements

D3M 32.6	D4M 31.3	D5M 32.3
D3P1 26.0	D4P1 18.7	D5P1 16.3
FA 47.6		

External measurements (from specimen label)

Total length	70	Length of hind foot	11
Length of ear	14	Mass	17

ually, this would indicate the organism is not breeding, however, many bats are able to move their testes in and out of their abdominal cavity, apparently at will. For 14 males where such data were taken, testes measurements averaged 3.3 by 2.4 mm.

A single net set for one night just below Mt. High Peak (15°29'N, 120°07'E) at ca. 1900 m caught four male *O. cartilagonodus* with abdominal testes, averaging 3.2 by 2.5 mm. The nighttime low at this camp reached at least 7°C.

Geographic variation.—The altitudinal segregation of sexes found in the Zambales sample was not present in the sample from Mount Isarog, as no statistically significant differences were found between capture elevations in males versus females. The trend, however, was for a greater number of females than males at the lower elevations: three males and twenty females were captured at 900 m, only females at 1125 m, one female and two males were captured at 1350 m, but only males of the species were captured at 1550 and 1750 m (one at each elevation). The two populations also appear to differ in reproductive timing. Heideman et al. (1993) found that the Mount Isarog sample displayed synchrony of embryological development, with small uterine swellings in March, and 15–20 mm embryos in females captured in May; they extrapolated birth dates in late May or June. In contrast, the sample from the Zambales Mountains (collected mid-February to early March) contains a mixture of pregnant and nonpregnant females with embryos from 5 to 14 mm in crown rump length.

Other chiropteran species.—An additional 12 species of bats were collected in the same two localities where *O. cartilagonodus* was found to be present (Table 9). The Shannon diversity index for the chiropteran fauna of Site 1 was $H'_1 = 0.648$, while that for Site 2 was $H'_2 = 0.585$. The t test for the Shannon formula (Hutcheson 1970), indicated there was no significant difference between species diversities at the two sites ($P \gg 0.05$). Because diversity indices usually are not calculated for particular subsections of a fauna (Chiroptera in this instance), we calculated the relative diversity, or evenness, J', as a proportion of H'_n to the theoretical maximum value for H', or $H'_{n\,max}$, thereby yielding a value constrained between 0 and 1. For Site 1, $H'_{1\,max} = 1.079$, while for Site 2, $H'_{2\,max} = 0.845$. Thus, for Site 1, $J'_1 = 0.600$, while for Site 2, $J'_2 = 0.692$. The Horn index of community similarity ("community overlap"), R_0, also constrained between 0.0 (when the two communities under consideration have no species in common) and 1.0 (when species compositions and relative abundances are identical between the two sites) calculated for Sites 1 and 2 was $R_0 = 0.637$; the overlap between the chiropteran faunas of the two sites was thus on the order of 64%.

Table 9.—List of bats caught at the two localities where *Otopteropus cartilagonodus* also were captured[1].

Species	Site: Site 1, Zambales, 1100 m (*n*)	Site 2, Zambales, 1500 m (*n*)
Rhinolophidae		
Rhinolophus arcuatus	59	39
Rhinolophus subrufus	36	2
Rhinolophus philippinensis	1	3
Hipposideros bicolor	0	1
Vespertilionidae		
Myotis muricola	2	20
Murina cyclotis	1	1
Pteropodidae		
Cynopterus brachyotis	1	0
Eonycteris spelaea	1	0
Haplonycteris fischeri	1	0
Macroglossus minimus	1	0
Otopteropus cartilagonodus	10	24
Ptenochirus jagori	5	0
Rousettus amplexicaudatus	19	0

[1] Four *O. cartilagonodus* and two *R. arcuatus* that were caught in a net set at 1900 m are not included in the totals.

What may not readily be apparent from these indices is that there is at least one major difference between the two sites, that being in the abundances of three species:

Myotis muricola, Rhinolophus subrufus, and *Rousettus amplexicaudatus.* This last species is particularly noteworthy because it previously has been associated with disturbed areas, either natural or anthropogenic (Heideman & Heaney 1989). Its presence at Site 1 reinforces our perception of this site as disturbed, either by rattan gathering, or by the Mount Pinatubo ashfall, or a combination of both factors. The few known specimens of *R. subrufus* have been collected from caves (Heaney et al. 1987); their presence at Site 1 but not Site 2 may be more indicative of the proximity of a cave, rather than of any specific habitat preference.

Discussion

With respect to morphological variation, we found that 21 out of the 37 mensural characters examined in the Zambales and Isarog populations differed significantly between the two populations. They are most readily separated by forearm length (Isarog, 45–52 mm; Zambales, 41–46 mm), and length of upper and lower canines. The differences in dental characters may be indicative of differences in diet. There also are marked differences in reproductive timing and embryonic development between the Zambales and Isarog samples. Although the two populations constitute readily identifiable clusters of individual organisms (sensu Cracraft 1983, McKitrick & Zink 1988), we prefer at this time not to make any hard and fast taxonomic decision with respect to *Otopteropus,* since this might obscure the fact that we still know very little about the biology of these bats, which still are known from very small samples. We were unable to examine the type series, although from measurements provided in Kock (1969), the holotype and adult paratypes most closely resemble the specimens from Mount Isarog than the geographically closer Zambales specimens. The specimen from Isabela Province also is most similar to the Isarog and type series. The specimens from the Cordillera Central and Sierra Madre Mountains are closer in multivariate morphological space to the Mount Isarog population (based on the available material) than they are to the Zambales population.

In our Zambales Mountain study population of *O. cartilagonodus* we found a greater number of sexually dimorphic mensural characters in the skull than expected by chance alone. All differences found were in characters that affect the feeding apparatus, and thereby potentially trophic behavior as well; these may also impact male competition in this probably harem-polygynous species. Although there is sexual dimorphism in characters associated with feeding and mastication, there is no difference in mass between the sexes, and only a slight (but significant) difference in total length. Four of the five dimorphic characters of the skull were larger in males than females; however, males are significantly smaller than females in overall length. Because there is no difference in mass between the sexes, and only the difference in overall length is very small, we hypothesize that the intersexual differences in masticatory characters affect (or are affected by) food preferences, rather than resulting from an overall size component.

Latitudinal species succession, or succession of species with temperature variation is a long known phenomenon (Fleming 1973, McCoy & Connor 1980, Rapoport 1982, Pianka 1983). Recently, however, more attention has been paid to an expected corollary of this phenomenon, that is, to elevational zonation of species. The underlying processes controlling this phenomenon remain unclear because of the extensive variation in geographic, taxonomic, and trophic parameters (Terborg 1971, Heaney et al. 1989, Patterson et al. 1989, Rickart et al. 1991). One reason for the uncertainty underlying the patterns and processes of altitudinal distribution may be that most research has focused on faunal subsets, such as mammals (Heaney et al. 1989, Heaney & Rickart 1990), small mammals (Patterson et al. 1989, Rickart et al. 1991), bats (Graham 1983), or birds (Goodman & Gonzales 1990; Terborgh 1971, 1977), rather than on individual species. It is possible that the different faunas, and indeed, different species within a faunal assemblage, may be prescribed by a specific paradigm governing different factors, or characteristics, of their elevational distribution and, consequently, altitudinal patterns of replacement. Furthermore, in habitats considered less "heterogeneous" (where there may be fewer resources available to species), there may be mechanisms for reducing intraspecific competition (or intersexual competition); this sort of intraspecific zonation may be a confounding variable when it comes to examining the elevational distribution of taxa and faunas.

We found such an apparent segregation of sexes by habitat along an elevational gradient. At lower elevations (ca. 1100 m), only females, most (90%) of them pregnant, were found. At elevations surrounding the 1500 m site, a ratio of 3 females to 8 males existed and only 30% of the females were pregnant. Within the confines of a limited sampling effort, only males were found at 1900 m. A major supposition here is that capture site is correlated with day roost site, which not always is the case in bats mist netted in the mountains. However, since the nets were set in recognizably discrete habitat types at each elevation (lower and upper montane forest), the hypothesis that intraspecific sexual segragation takes place may confidently be stated.

It has been remarked that in contrast to rodents, bats decrease in relative abundance and species richness with elevation (Graham 1983, Heaney et al. 1989, Heaney & Rickart 1990). Possibly, the metabolic demands imposed by flight on bats (Burton et al. 1989, McNab 1989), in contrast to other mammals, together with reduced availability of trophic resources for insectivorous and frugivorous organisms at higher elevations, may increase the competition for resources at these elevations.

Traditional definitions of competition divided this population phenomenon into exploitative (indirect, i.e., resource depletion) and interference competition (direct, i.e., fighting or predation [e.g., Park 1962]). An alternative taxonomy of competition was proposed by Schoener (1983). Here, "consumptive competition designates consumption of resources that deprives other individuals of those resources, whereas preemptive competition occurs when a unit of space is passively occupied by an individual, thereby causing other individuals not to occupy that space before the original occupant disappears" (Schoener 1988:256).

We hypothesize that *O. cartilagonodus* from the Zambales Mountains may reduce competition between sexes by two means: consumptive competition is reduced by adjusting to differences in food preferences (based on cranial morphometric data), and preemptive competition is reduced by adjusting habitat preferences between the sexes (based on capture data). A test of these hypotheses will necessitate further study involving examination of stomach contents from freshly captured individuals, and more extensive sampling along an elevational gradient. The data from Mount Isarog, currently under study by L. R. Heaney and coworkers may serve as an additional test of these hypotheses.

Clearly, the variation exhibited by this species is not a case of ordinary, clinal geographic variation. The data therefore lend themselves to a number of alternative hypotheses to be tested with respect to the relationships among the various populations. Given the exhibited pattern of morphological variation, it may well be that the Zambales population represents a long isolated population. Additional specimens will be needed to distinguish among competing hypotheses, including additional sampling from the Laguna and Batangas Provinces' montane areas, from which only a few specimens are known (and none closely scrutinized), as well as a greater number of specimens from the type locality (in Cordillera Central) and from the Sierra Madre Mountains. Until such a time as the regional populational differences are resolved, the structured, geographically and morphologically cohesive populations of *O. cartilagonodus* appear to represent an ideal study case for elucidation of zoogeographic relationships among different regions of the island of Luzon.

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CRYPTOPHOCA, NEW GENUS FOR *PHOCA MAEOTICA* (MAMMALIA: PINNIPEDIA: PHOCINAE), FROM UPPER MIOCENE DEPOSITS IN THE NORTHERN BLACK SEA REGION

Irina A. Koretsky and Clayton E. Ray

Abstract.—Review of relevant fossil and Recent material indicates that the fossil seal species *Phoca maeotica* Nordmann (1860) from Kishinev, Moldavia, earlier assigned to the Monachinae, actually belongs to the subfamily Phocinae. This species differs from all known seals and is placed in the separate genus *Cryptophoca. Cryptophoca maeotica* differs from other seals in its straight symphyseal region of mandible, position of mental protuberance between p^3 and p^4, rectangular greater trochanter of femur, and length of crest of greater tubercle of humerus extending ¼ length of humerus. Presence of these characters not only justifies the specific independence of the Moldavian seal, but also requires its placement in a separate genus, *Cryptophoca.*

Nordmann (1860:313–326) described the species *Phoca maeotica* on the basis of dissociated postcranial bones extracted from material originally assigned by Eichwald (1850) to his *Phoca pontica.* Nordmann suggested the close affinity of this large seal with monk seals. Later, Trouessart (1898–1899, 1904), never questioning this relationship, transferred the species to the genus *Monatherium,* belonging to the subfamily Monachinae. However, the taxonomic position of this species has since been questioned. For instance, some systematists (Grigorescu 1977, Kellogg 1922, McLaren 1960, de Muizon 1992) classified (on the basis of the size of the distal epiphysis of femur) *Phoca maeotica* with the monachine seals, whereas others (Alekseev 1924, 1926; Bogachev 1927; Kirpichnikov 1961; Ray 1977; Savage & Russell 1983) considered it to be a phocine seal, or did not mention the placement of this species (de Muizon 1982).

In recent years, discoveries of cranial and postcranial remains of *Phoca maeotica* in the northern Black Sea region have greatly augmented the classic collection of von Nordmann. Although several taxa of phocids occur in the same deposits with the nominal species *Phoca maeotica,* we feel confident in our assignment here of the mandible and humeri on the basis of similarity in size and morphology and analogy with modern phocids. Making use of all available material, we conclude that the Kishinev seal belongs to the subfamily Phocinae on the basis of length of the symphyseal part of the mandible to the anterior border of the alveolus of p2, presence of the mental protuberance; trochlear crest of the humerus not separated from coronoid fossa by distinct lip; different size of the femoral condyles, small difference in the width of proximal and distal epiphyses, and absence or poor development of intertrochanteric crest.

Furthermore, our study of the osteological remains of *Phoca maeotica* not only corroborates its specific distinctness, but also requires distinguishing it as a new genus, *Cryptophoca,* described here.

Morphometric analysis of the humeri, femora, and mandibles was carried out using the methods of Sergienko (1967), Burns & Fay (1970), Piérard (1971) and one of us

(Koretsky 1986). Although the question of sexual dimorphism must be kept in mind in all studies of fossil pinnipeds (Koretsky 1987, Van Bree & Erdbrink 1987), it could not be addressed meaningfully here because of the very limited material.

We are well aware of the recent intensive interest in pinniped phylogeny and classification, resulting in a currently unstable situation (e.g., Wozencraft 1989; Wyss 1988, 1989). Studies in progress by us and others will add much new information in the near future. Meanwhile, we feel that it would be premature and unproductive to address these broad questions in the present paper of very limited scope and objectives.

Family Phocidae Gray, 1825
Subfamily Phocinae Gill, 1866
Cryptophoca, new genus

Type species.—Phoca maeotica Nordmann, 1860:321, pl. 23, figs. 8, 9.

Diagnosis.—Lower canine and p1 very large (Fig. 1a, b), p1 single-rooted; symphyseal part straight, its inner part thickened from anterior alveolus of p2 to canine; mental protuberance located between p3 and p4. Deltoid crest up to ¼ of humeral length, not reaching radial fossa and proximal border is widest part (Figs. 2a, b; 4a, b); lesser tubercle of humerus located on same level as proximal border of deltoid crest; head round. Femur with almost rectangular greater trochanter; trochanteric fossa deep and open; head of femur big (Figs. 3a, b; 4c, d), situated on relatively narrow, short neck; smallest width of diaphysis shifted toward proximal epiphysis; greatest breadth across condyles 20.0%–21.0% of bone length; proximal epiphysis narrower than distal by 2.0%–8.0%.

Comparison.—The genus *Cryptophoca* differs from other known seals by: straight shape of symphyseal part of mandible (except for *Pagophoca*), smaller height of body of mandible under p2 (except for *Phoca, Halichoerus,* and *Pagophoca*); lower position of lesser tubercle of humerus relative to head and its location on same level with proximal border of deltoid crest (except for *Erignathus, Praepusa,* and *Monachopsis*); less developed spiral groove (except for *Erignathus, Pagophoca,* and *Monachopsis*); large rectangular greater trochanter (except for *Praepusa*); relatively smaller intercondylar width of femur (except for *Erignathus* and *Praepusa*); narrower neck of femur (except for *Phoca, Halichoerus, Pagophoca,* and *Praepusa*); peculiar shape of both humerus and femur (Table 1). Available material allows us to hypothesize that, based on similarities in the size and character of mandible and limb bones, this genus is closely related to *Pagophoca.*

In addition this genus differs distinctly from other genera as follows:

From *Phoca* by flattened body of mandible; mental protuberance not labially bent; greater length of p4 alveolus relative to m1, alveolus; larger diastemata between teeth; single-rooted p1. Relatively greater length of deltoid crest of humerus. Bigger size of intertrochanteric crest; relatively smaller condyles of femur.

From *Pusa* by larger dimensions; greater depth of body of mandible under p2; forward shifted mental protuberance. Absence of intertubercular grooves of humerus; large head; greater length of deltoid crest. Large swelling of intertrochanteric crest; deeper and wider trochanteric fossa, relatively larger head of femur.

From *Erignathus* by smaller dimensions; mental protuberance of mandible slightly pronounced, shifted forward and not labially bent. Relatively larger length of deltoid crest of humerus and latter's widening on proximal border; round shape of head. Large height of greater trochanter relative to femoral neck; smaller size of neck; relatively narrower proximal epiphysis.

From *Halichoerus* by greater mandible flattening; pronounced mental protuberance; double-rooted p2-m1. Lateral position of deltoid crest of humerus; absence of

Table 1.—Comparative diagnostic characters of the subfamily Phocinae: + = character present or similar; − = character absent or dissimilar; +− = character variable.

	Cryptophoca	*Histriophoca*	*Pagophoca*	*Phoca*	*Pusa*	*Halichoerus*	*Erignathus*	*Praepusa*
Mandible								
Location of chin prominence	+	+	−	−	−	−	−	+
Shape of symphyseal part	+	−	+	−	−	−	−	−
Alveolar part narrower than body	+	−	+	−	−	−	+	−
Diastemata present	+	+	+	−	+	−	+	−
Body thicker from p3 forward	+	+	−	+	−	+	−	−
Alveoli of p4 and m1 similar in size	+	+−	+−	−	+	+	+	+
Humerus								
Lesser trochanter located on same level as proximal part of crista deltoidea	+	−	−	−	−	−	+	−
Caput round	+	−	+	−	−	−	−	−
Crista deltoidea reaches fossa coronoidea	+	−	−	−	−	−	−	+
Femur								
Large rectangular greater trochanter	+	−	−	−	−	−	−	+
Relatively small intercondylar width	+	−	−	−	−	−	−	−

Fig. 1. *Cryptophoca maeotica.* Cast of the left mandibular ramus, without number. Tiraspol State Pedagogical Institute, Moldavia. a = labial aspect, b = occlusal aspect.

intertubercular groove; round head. Presence of intertrochanteric crest of femur.

From *Pagophoca* by forward-shifted mental protuberance. Lateral position of deltoid crest of humerus and its widening of proximal border. Deeper and wider trochanteric fossa of femur.

From *Praepusa* by far greater dimensions; larger height of body of mandible under p^2 to canine. Equal position of lesser tubercle

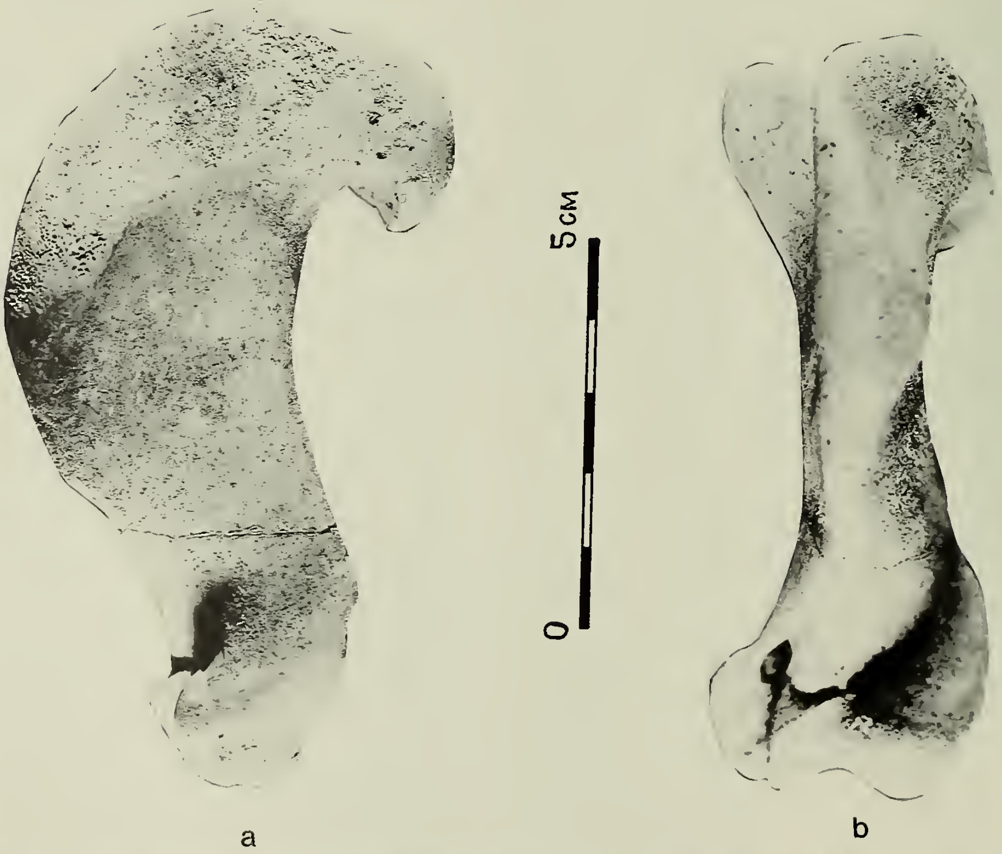

Fig. 2. *Cryptophoca maeotica.* Left humerus 64-530 from Kishinev. Institute of Zoology of Academy of Science of Ukraine, Kiev. a = lateral aspect, b = cranial aspect.

Table 2.—Means (±*SE*) and range for measurements (mm) of number in sample (*n*) of humeri from *Cryptophoca maeotica.*

Measurements	*n*	$\bar{X} \pm SE$	Range
Absolute length	5	107.1 ± 1.5	99.0–123.5
Length of deltoid crest	5	75.9 ± 0.7	73.0–80.0
Height of head	4	25.1 ± 0.2	24.0–28.0
Height of trochlea	4	20.1 ± 0.7	19.0–21.5
Width of head	4	25.0 ± 0.9	23.0–28.0
Width of deltoid crest	4	28.6 ± 0.2	28.0–30.0
Width of distal epiphysis	5	37.0 ± 1.8	30.0–45.0
Width of proximal epiphysis	7	34.2 ± 2.0	29.0–38.5
Width of trochlea distally	4	19.1 ± 0.6	18.0–20.0
Width of trochlea, frontal view	4	23.1 ± 0.8	22.0–25.0
Transverse width of diaphysis	5	14.5 ± 0.9	12.0–17.0
Thickness of proximal epiphysis	7	40.5 ± 1.8	33.8–46.0
Thickness of medial condyle	4	19.6 ± 0.6	18.5–20.5
Thickness of lateral condyle	4	17.4 ± 0.4	16.4–18.5
Diameter of diaphysis with deltoid crest	6	33.5 ± 1.6	29.0–38.0

of humerus and proximal border of deltoid crest; slightly bigger index of head width. Smallest width of femoral diaphysis shifted toward proximal epiphysis; relatively smaller width of proximal epiphysis, large but relatively more narrowly arranged condyles.

From *Monachopsis* by far bigger dimensions; double-rooted p2-m1 with large diastemata. Round head of humerus; short deltoid crest; higher and wider medial epicondyle. Deeper and more elongated trochanteric fossa of femur; relatively more narrow proximal epiphysis.

Distribution.—Middle Sarmatian (Upper Miocene) of the northern Black Sea region of the Ukraine and Moldavia.

Etymology.—From the Latin "crypticus," i.e., hidden, secretive; "phoca"—seal.

Cryptophoca maeotica (Nordmann, 1860)
Figs. 1–4, Tables 2–3

Phoca pontica Eichwald, 1850 (in part):210–218.—Eichwald, 1853 (in part):391–400.

Phoca Nordmann, 1858: pl. 23, figs. 1, 2, 8, 9, 10.

Phoca maeotica Nordmann, 1860 (in part): 320–321, 356–357.—Van Beneden, 1877: 26.—Toula, 1898:50.—Alekseev, 1924: 202.—Alekseev, 1926:138–143.—Savage & Russell, 1983:187, 292–294.

Monatherium maeoticum—Trouessart, 1897:380.—Trouessart, 1904:283.—King, 1964:131.—King, 1983:132.—Friant, 1947:50 (non pl. 1, fig. 2a–c).

Monotherium maeoticum—Kellogg, 1922: 114.—Kretzoi, 1941:353.—McLaren, 1960:50–52, 56–57, fig. 1e.—Grigorescu, 1976:407, 413–415, 417, fig. 5b.—de Muizon, 1982:202–205.

Monotherium maeotica—Grigorescu, 1976: 407.

"Monotherium" maesticum (sic)—de Muizon, 1992:37.

Lectotype.—Left femur N1815, Museum of Zoology, Helsinki, Finland; illustrated by Nordmann (1858: pl. 23, figs. 8, 9) as *Phoca* and described and named as *Phoca maeotica* in 1860. (Fig. 4c, d).

Type locality.—Moldavia (Kishinev), northern Black Sea region.

Geological age.—Upper Miocene, Middle Sarmatian (Bessarabian Formation).

Material examined.—Moldavia, Kishinev: Institute of Zoology of Academy of Sciences of Ukraine, Kiev (von Nordmann collection), collection 64—eight femora, a part of the material described by Nordmann

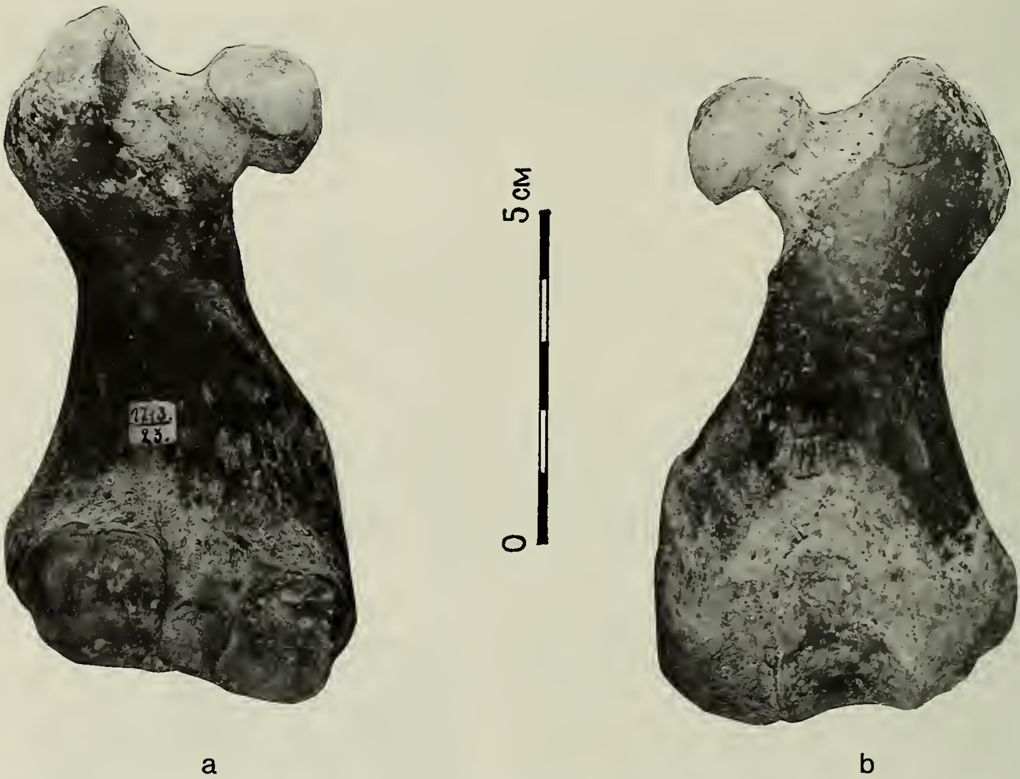

Fig. 3. *Cryptophoca maeotica.* Left femur 1713/23 from Kishinev. Paleontological Institute of Academy of Science of Russia, Moscow. a = caudal aspect, b = cranial aspect.

(1860)—three humeri, without numbers; Paleontological Institute of Academy of Sciences of Russia, Moscow, collection 1713—nine femora, 1713/1329 and 1713/1330—two incomplete rami of the mandible; Paleontological Museum of Odessa State University—five femora, the material described by Alekseev (1926); Tiraspol State Pedagogical Institute, Tiraspol—incomplete ramus of the left mandible, without number; Paleontological Department of Museum of Zoology, Helsinki, Finland (von Nordmann collection)—right humerus 1812 (illustrated by Nordmann, 1858: pl. 23, figs. 1, 2), proximal part of left femur N1816 (illustrated by Nordmann by 1858: pl. 23, fig. 10), left femur 1815 (illustrated by Nordmann, 1858: pl. 23, figs. 8, 9), six femora without numbers (not illustrated); cast of left femur National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S., 214979, Geological Museum of University of Bucarest, Romania 259/II,5c (Simionescu collection). Ukraine, Crimea, Kerchensky peninsula (Kamysh-Burun): Institute of Zoology Academy of Sciences Ukraine, collection 64—three femora.

Remarks.—McLaren (1960:56–57), working from literature, designated left femur N1815 as lectotype. Unfortunately, at some time subsequent to Nordmann's work the specimen was broken and the proximal half misplaced or lost. The breakage must have occurred prior to 1972, when the specimen was cataloged, as its number is affixed to the broken proximal surface. All recent efforts by the late Björn Kurtén and by Mikael Fortelius to locate the missing part have been unsuccessful. However, there are sev-

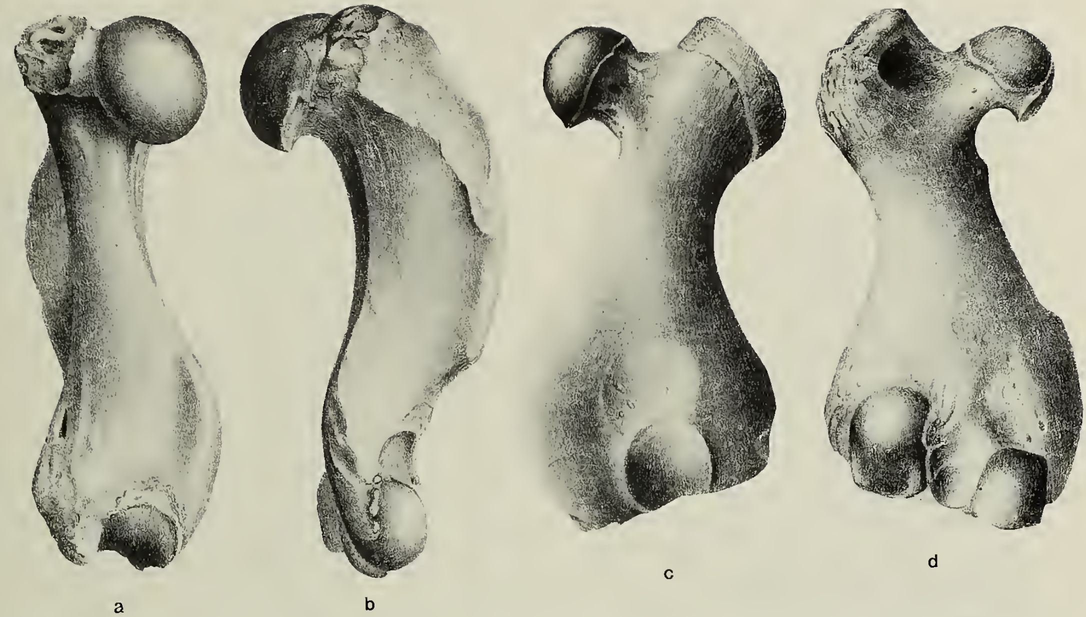

Fig. 4. a, b. *Cryptophoca maeotica.* Right humerus 1812 from Kishinev (from Nordmann, 1858: pl. 23, figs. 1, 2). Paleontological Department of Museum of Zoology, Helsinki. a = caudal aspect, b = lateral aspect; c, d. *Cryptophoca maeotica.* Lectotype, left femur 1815 from Kishinev (from Nordmann, 1858: pl. 23, figs. 8, 9). Paleontological Department of Museum of Zoology, Helsinki. c = cranial aspect, d = caudal aspect.

eral good illustrations of the intact femur and the distal half of the lectotype femur survives.

The Russian version of Eichwald's monograph, which we cite herein, was published in 1850, 3 years earlier than the German edition. For nomenclature it is very important, because western researchers seem to have been unaware of the Russian text. A few other elements (innominates, vertebrae and a radius) are not described here, but possibly pertain to this taxon.

Diagnosis.—As for the genus.

Description.—True seal close in size to the contemporary genus *Pagophoca.*

Mandible (Fig. 1). Not high, flat from lingual side. From labial side, body of mandible thickened in middle from level of anterior p2 alveolus to beginning of ascending ramus. All teeth arranged in alignment with the tooth row axis. Alveolar length of m1 smaller than that of p4; retromolar space shortened. Mental protuberance located between anterior alveolus of p3 and anterior alveolus of p4. Maximal depth of mandible between alveoli of p2 and p4. Symphyseal part straight and thick, i.e., the lower border of the mandible not elevated with respect to alveolus of canine. Alveolus of p1, similar to canine alveolus, is very large. Measurements of mandible: depth under m1—20.5–26 mm; depth under p2—18–19 mm; depth between p3-p4—20–24 mm; depth behind m^1—18.5–18.5 mm; alveolar length of row p1-p4—35.5–40 mm; alveolar length of row p1–m1—59 mm; alveolar length of p4—8–9 mm; alveolar length of m1—6–7 mm; length of diastema p4-m1—6.5–9 mm; thickness of mandible under m1—9–11 mm.

Humerus (Fig. 2, Table 2). Lesser tubercle of humerus slightly elongated and departing only slightly from basic axis (which is probably characteristic of all extinct true seals). Intertubercular groove only slightly discernible. Deltoid crest widest proximally. Deltoid tuberosity located along middle of

Table 3.—Means (±*SE*) and range for measurements (mm) of number in sample (*n*) of femora from *Cryptophoca maeotica.*

Measurements	*n*	$\bar{X} \pm SE$	Range
Absolute length	23	106.0 ± 2.4	93.0–138.0
Medial length	13	96.0 ± 3.2	87.0–110.4
Lateral length	12	92.9 ± 2.8	82.0–110.4
Length of medial condyle	19	18.8 ± 0.4	17.0–21.0
Length of lateral condyle	22	22.4 ± 0.5	18.0–26.5
Length of greater trochanter	23	26.9 ± 0.8	25.0–33.5
Intertrochanter length	9	31.2 ± 1.2	24.0–34.5
Height of head	17	20.0 ± 0.5	18.0–23.0
Height of articular area of patella surface	17	22.5 ± 0.7	18.5–25.0
Width of proximal epiphysis	23	51.8 ± 1.2	44.3–64.2
Width of distal epiphysis	25	53.4 ± 0.6	47.0–62.3
Width of condyles	23	43.3 ± 0.7	38.0–49.0
Width of greater trochanter	24	18.7 ± 0.4	16.0–22.0
Width of head	22	21.7 ± 0.5	18.5–25.0
Width of diaphysis	30	27.6 ± 0.4	23.0–33.0
Anteroposterior thickness of diaphysis	12	12.4 ± 0.6	12.0–17.0
Thickness of medial condyle	12	23.7 ± 0.7	21.0–27.5
Thickness of lateral condyle	15	26.1 ± 0.7	23.5–29.0
Distance between condyles	18	11.1 ± 1.3	8.0–12.0
Diameter of neck	22	16.2 ± 0.4	14.0–19.5

diaphysis. Radial fossa narrow and shallow. Epicondyles well developed. Medial epicondyle reaching distal part of deltoid crest; lateral epicondyle spreading from lower part of entepicondyloideum and ending below medial epicondyle. Spiral groove not pronounced.

Femur (Fig. 3, Table 3). Greater trochanter much higher than the head, approaching rectangular shape. Trochanteric fossa wide, deep, and open. Intertrochanteric crest located along middle part of femur, below trochanteric fossa. Smallest width of diaphysis shifted to proximal part of femur.

Distribution.—Upper Miocene, Middle Sarmatian (Bessarabian Formation) of the northern Black Sea region of Ukraine and Moldavia.

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A TAXONOMIC REVIEW OF *DENDROICA PETECHIA* (YELLOW WARBLER) (AVES: PARULINAE)

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Abstract.—The taxonomy and nomenclature of *Dendroica petechia* (Yellow Warbler), last discussed from the entire range of the species about 57 years ago, is reviewed. There are 43 recognizable subspecies based on geographic variation of plumage color and pattern of about 2500 specimens examined. Two new subspecies are named from populations of the migratory *aestiva* subspecies group of North America. New subspecies are also named that represent populations of the resident subspecies groups *erithachorides* of Middle and South American and *petechia* of the West Indies.

The Yellow Warbler, *Dendroica petechia,* comprises three groups of subspecies: the *aestiva* group is migratory and breeds in the Nearctic; the *petechia* group is resident in the West Indies; and the *erithachorides* group is resident on both coasts of Middle America and northern South America (A.O.U. [American Ornithologists' Union] 1983). The three groups were treated as separate species until Hellmayr (1935) combined the *petechia* and *erithachorides* groups, and Aldrich (1942) combined the *petechia* and *aestiva* groups. The A.O.U. (1944, 1945) combined all three groups as *D. petechia.* Lowery & Monroe (1968) recognized 34 subspecies in the combined groups of *D. petechia.* Olson (1980) named three additional subspecies from the *erithachorides* group.

Relatively recent discussions of geographic variation and taxonomy of *Dendroica petechia* have been limited to regional studies in North America (e.g., Phillips et al. 1964, Oberholser 1974, Raveling & Warner 1978, Godfrey 1986), Mexico (e.g., Parkes & Dickerman 1967), the Pacific coast of Middle America (Olson 1980), Panama (Wetmore et al. 1984), and islands off northern South America (e.g., Voous 1957, Phelps & Phelps 1950). Reviews of the entire species that discussed subspecific characters include Ridgway (1902) and Hellmayr (1935). These studies usually characterized subspecies of *D. petechia* on the basis of variation in plumage color and pattern; measurements were used secondarily in characterizing only a few subspecies. Peter's (1927) review of the subspecies of the *petechia* group included standard measurements, and Hellmayr (1935) provided measurements for some subspecies. Hellmayr usually characterized size in terms of such as "smaller," "averages slightly larger," and "slenderer." Raveling & Warner (1978) reported statistical differences in some measurements of specimens from North American populations, but, as with Hellmayr's measurements, means differed only 2–3 mm and ranges overlapped considerably. Broad patterns of geographic variation in size within the subspecies groups (Wiedenfeld 1991) suggest that measurements are of little use in identifying most subspecies.

The purpose of this study of *D. petechia* is to evaluate geographic variation and to determine the morphological limits of the subspecies. Color and pattern of breeding plumages of adult males and females form the basis for subspecific identifications. Other plumages, when known, are described, but these are less useful in characterizing populations than breeding plumages and are poorly represented in collections. Additional collecting is essential (see Winker et al. 1991) to document migration and winter distribution of subspecies of *D. petechia.*

Methods

About 2500 specimens from the breeding grounds of *D. petechia* were examined for variation in color. Measurements reported in the accounts include standard measurements of flight feathers, tarsi, and bill length (anterior edge of the nostril to the tip). Measurements are discussed where size is a useful taxonomic character. Evaluation of colors was by comparison of specimens in daylight conditions. Seasonally similar plumages were compared when possible. The color of the crown (excluding the chestnut or rusty color), back, and rump is described as darker (= more black), greener (less yellow), or the opposite, more yellow (= nearest Spectrum Yellow of Smithe [1975]). The yellow of the underparts is described according to observed intensity (brightness) and purity; the yellow of some subspecies is relatively dull (more white) while in some others it exhibits a greenish cast. The chestnut markings on the head and the ventral streaks on the underparts are characterized as dark or pale. The extent of chestnut markings was characterized on the basis of the relative amount on the head, throat, and breast, the relative width (wide vs. narrow) and density of ventral streaks. The character "chestnut areas" refers to all chestnut parts of the plumage. Color and pattern were determined subjectively and were characterized in terms relative to the populations being compared. This method served to verify many previously published taxonomic conclusions on *D. petechia.*

Each subspecies account includes its author, year and type locality. Locations of holotypes, when known, are indicated by abbreviation of museums (see Acknowledgments); abbreviations in parentheses indicate holotypes I examined. Other locations are indicated by a reference. The section "Subspecific characters" includes breeding plumages of adult male and female, with comparisons to geographically adjacent or morphologically similar subspecies. Nonbreeding plumages, when known, are mentioned for migratory species. "Distribution" includes breeding and winter ranges and localities of intergradation between adjacent subspecies. Winter ranges are included when they differ from those in Lowery & Monroe (1968). Maps show the breeding distributions of the subspecies in the *aestiva* group (Fig. 1) and in the *petechia* and *erithachorides* groups (Fig. 2). Use of subspecies groups in this paper is not meant to reflect historical relationships. "Specimens examined" are included as an abbreviated list by general locality and number examined. Few specimens were needed to characterize subspecies represented by populations with insular or linear ranges (e.g., *petechia* and *erithachorides* groups). The "Remarks" section includes discussions on nomenclature, synonymies, and geographic variation. The sequence of subspecies is only slightly modified from that by Lowery & Monroe (1968). A synopsis of the pattern of variation is presented at the end of each of the three subspecies groups.

Dendroica petechia aestiva subspecies group

Subspecies in the *aestiva* group differ from members of the *petechia* and *erithachorides* groups in generally lacking chestnut on the head except on the crown, where, if present, it is diffuse or concentrated on the feather shafts. Individuals in the *aestiva* group have more pointed wings than birds of the other groups.

Dendroica petechia rubiginosa (Pallas)

Motacilla rubiginosa Pallas, 1811:496 ("in insula Kodiak" = Kodiak Island, Alaska).

Subspecific characters.—Males nearest Yukon subspecies (named below) but darker and greener above. Compared with Mac-

Fig. 1. Approximate breeding ranges of subspecies in the *Dendroica petechia aestiva* subspecies group.

kenzie subspecies (see account below), males paler and more yellowish above; bill longer (see below). Compared with all subspecies in the *aestiva* subspecies group, males usually with greenish forehead. Females with greener (less yellow) crown and rump than Yukon subspecies; slightly greener above than Mackenzie subspecies.

Distribution.—Breeds from Unimak Island to Alaska Peninsula, Kodiak Island, and coastal British Columbia. Intergrades with Yukon subspecies along coastal Alaska (see below); intergrades with *morcomi* in British Columbia (Bella Coola, Vancouver Island and adjacent mainland). Migrates rarely east of the Rocky Mountains; individuals identified from Pennsylvania, Washington, D.C., Mississippi, and Florida (Parkes 1968).

Specimens examined.—Coastal Alaska (31); British Columbia (29).

Remarks.—Some migrants that were identified in the literature as *rubiginosa* may represent intergrades between *rubiginosa* and the next subspecies, or birds from Mackenzie District, Northwest Territories (named below). Further collecting and study of specimens in nonbreeding plumages from these northern populations are needed.

Dendroica petechia banksi, new subspecies

Holotype.—USNM 468183, adult male, Old Crow Village, Yukon Territory, Cana-

Fig. 2. Breeding ranges of subspecies of *Dendroica petechia* in the *petechia* and *erithachorides* subspecies groups: 1, *castaneiceps*; 2, *rhizophorae*; 3, *phillipsi*; 4, *xanthotera*; 5, *aithocorys*; 6, *iguanae*; 7, *aequatorialis*; 8, *jubaris*; 9, *peruviana*; 10, *aureola*; 11, *oraria*; 12, *rufivertex*; 13, *bryanti*; 14, *erithachorides*; 15, *gundlachi*; 16, *flaviceps*; 17, *eoa*; 18, *solaris*; 19, *chlora*; 20, *albicollis*; 21, *barthomelica*; 22, *melanoptera*; 23, *ruficapilla*; 24, *babad*; 25, *petechia*; 26, *alsiosa*; 27, *rufopileata*; 28, *aurifrons*; 29, *obscura*; 30, *cienagae*; 31, *paraguanae*; 32, *chrysendeta*; 33, *flavida*; 34, *armouri*.

da, collected 7 June 1957 by L. Irving and L. Peyton (original number 291).

Subspecific characters.—Males more yellow above, especially rump and forehead, than *rubiginosa*. Males paler and more yellow above than Mackenzie District subspecies (named below). Males similar to *amnicola* but more yellow above; slightly greener above than *morcomi;* chestnut streaks average darker and more prominent than *rubiginosa, amnicola* and *morcomi.* Females most similar to *amnicola* from central Canada but average slightly greener above. Males in fall plumage more yellow above than *rubiginosa.* Compared with *rubiginosa* and Mackenzie subspecies, females more yellow (less green) above.

Distribution.—Breeds (or probably breeds) from Old Crow to Selkirk, Yukon Territory, and in Alaska, along Yukon River (Charley River, Circle, Galena), north of the Arctic Circle (Kuguruok [= Canning] River, Umiat, Anaktuvuk, Sheenjek and Alatna rivers, Siruk Creek, Bettles), along Tanana River (Minto Lakes, Fairbanks, Tetlin), Kuskokwim River (Napaskiak, Bethel), interior Nushagak Peninsula, Lake Iliamna, and Anchorage. Intergrades with *rubiginosa* at Napaskiak (lower Kuskokwim River), Nushagak, New Iliamna, and near Anchor age. Migrant in southwestern Oregon (see Remarks).

Etymology.—For Richard C. Banks, colleague and friend, in recognition of his contributions to ornithology.

Specimens examined.—Alaska (21); Yukon Territory (34).

Remarks.—Oberholser (1897) characterized a specimen from Nushagak and one from Yukon River as slightly more yellow above than specimens from Kodiak Island, and Raveling & Warner (1978) remarked that the population from Arctic interior Alaska may represent an unnamed subspecies.

Dorsal color of breeding males ranges from brighter and more yellow in specimens from the Porcupine and upper Yukon rivers to duller and greener in birds from localities west and south of Fairbanks, Alaska. The duller and greener birds are still more yellow above than *amnicola* and neighboring subspecies. Males from north of the Brooks Range are still duller. Males from the type locality and Lake Iliamna have darker and more prominent ventral streaks than from elsewhere in the range of *banksi*. Specimens from Lake Iliamna that I identified as intergrades between *banksi* and *rubiginosa* were identified as intergrades between *amnicola* and *rubiginosa* by Williamson (see Williamson & Peyton 1962).

A specimen (UAM) from Tvativak Bay, Nushagak Peninsula, Alaska, collected 16 June, if actually breeding, is at the southwestern limit of the breeding range of *banksi*. The northern limit of *banksi* is based on specimens from north of the Brooks Range at Umiat (West & White 1966), Anaktuvuk (Irving 1960), the upper Sheenjek River (Kessel & Schaller 1960), and middle Noatak River (Kessel & Gibson 1978). Specimens from those localities are duller than most examples of *banksi* collected south of the Brooks Range. Additional specimens are needed to better determine the breeding range of *banksi*.

A migrant male (USNM 592840) from Brownsboro, Oregon, collected 13 May 1920, resembles breeding specimens of *banksi* in dorsal and ventral color.

Dendroica petechia parkesi,
new subspecies

Holotype.—CM 129401, adult male, Richards Island, Mackenzie Delta, Northwest Territories, Canada, collected 4 June 1942 by Arthur C. Twomey (original number 9864).

Subspecific characters.—Males darker green above than all other subspecies in the *aestiva* group. Compared with *banksi*, males much darker and greener above; chestnut streaks less prominent. Males near *rubiginosa* but greener above; forehead averaging more yellow. Compared to *amnicola*, males greener above; average duller yellow below; chestnut streaks average darker. Females greener than *banksi* and *amnicola*; average slightly paler yellow below in fall plumage. Bill, in males shorter (6.9–7.9, mean 7.55, $n = 24$) than *rubiginosa* (7.6–8.6, mean 8.29, $n = 10$), and similar to *banksi* (7.5–8.3, mean 7.84, $n = 11$).

Distribution.—Breeds in Northwest Territories from Mackenzie River Delta to Arctic Red River, Ft. Simpson, Ft. Providence, Ft. McPherson, Ft. Norman, Rae, Reliance, Ft. Resolution, Hay River, and provisionally, northeastern Manitoba (Ft. York). Intergrades (?) with *amnicola* at Ft. Providence and Hay River south of Great Slave Lake. Parkes (1968) identified a specimen from Massachusetts with the Mackenzie Delta population (= *parkesi*).

Specimens examined.—Northwest Territories (21); Manitoba (6).

Etymology.—For Kenneth C. Parkes, who first discussed the distinction of the new subspecies.

Remarks.—Parkes (1968) commented that birds from the interior of Alaska to the west coast of Hudson Bay represented an unnamed subspecies. Ramos & Warner (1980) believed that the range given by Parkes (1968) included two unnamed subspecies, one from Alaska (= *banksi*) and the other from Northwest Territories and prairie provinces.

There is some geographic variation in *parkesi*, with a reduction of green color from northwest to southeast. Specimens from the Mackenzie River Delta are the darkest above, with about one-half having greenish foreheads. Males from Ft. Simpson are slightly more yellow above, and females are paler above than specimens from the Mackenzie River Delta. Two of five specimens from Ft. Providence resemble *amnicola* in dorsal color; specimens from Hay River, south of Ft. Providence, are, however, greener above. Males from the west coast of Hudson Bay are slightly more yellow above but are definitely greener above than *amnicola.* Specimens from the northern prairie provinces are clearly *amnicola.*

Dendroica petechia amnicola Batchelder

Dendroica aestiva amnicola Batchelder, 1918:82 (Curslet, Newfoundland). MCZ

Subspecific characters.—Males near *parkesi* but more yellow and paler above; usually brighter yellow below. Compared to *banksi,* males darker (greener) above. Compared with *aestiva,* males darker and greener above, usually with greener foreheads. Females more yellow above than *parkesi* and greener above than *aestiva.* Males in fall plumage slightly paler above than those of *rubiginosa* and *parkesi.*

Distribution.—Breeds from northeastern British Columbia to central prairie provinces, Manitoba (Norway House), central Ontario, southeast to southern Quebec, New Brunswick, Newfoundland, and central Labrador. Intergrades (?; see above) with *parkesi* in southern District of Mackenzie (Ft. Providence). Intergrades with *aestiva* from central-northern Alberta to southern Manitoba, southern Quebec, and Nova Scotia.

Specimens examined.—Northwest Territories (7); British Columbia (5); Alberta (30); Saskatchewan (11); Manitoba (8); Ontario (43); Quebec (21); and Newfoundland (30).

Remarks.—Originally proposed for populations in Newfoundland, the name *amnicola* was generally considered a synonym of *aestiva* until Oberholser (1938), followed by the A.O.U. (1944), recognized *amnicola* for the subspecies occuring in most of Canada. Contrary to Oberholser (1974), the original description of *aestiva* was based on the pale southeastern subspecies, not the dark northeastern population now in *amnicola* (Browning 1990b). Oberholser (1974) also believed that *carolinensis* Latham, a name synonymized with *aestiva* by Hellmayr (1935), was a synonym of the northern subspecies, but *carolinensis* is indeterminate; it is doubtfully an example of *D. petechia.*

Geographic variation in back color of *amnicola* ranges from the brightest and most yellowish specimens from Newfoundland to greener birds from northeastern British Columbia, southern Mackenzie, and northern Alberta. Differences between the colors of the forehead and back of males vary geographically; both characters are greenish in 13% of the specimens from Newfoundland ($n = 15$), 17% of the birds from the southern Hudson Bay region, and about 25% of males from the prairie provinces. Raveling & Warner (1978) concluded that 90% of the males from the southern parts of the prairie provinces were "readily distinguishable" in back and head color from all other samples, and referred the prairie birds to *aestiva.* I concur.

Dendroica petechia aestiva (Gmelin)

Motacilla aestiva Gmelin, 1789:996 (in Gujana, aestate in Canada = Québec, Québec).

Sylvia flava Viellot, 1809:31, pl. 87, (on migration in the United States = New York, New York; fide Oberholser 1974: 1000)

Sylvia childrenii Audubon, 1831:180, (near Jackson, Mississippi).

?*Sylvia rathbonia* Audubon, 1831:333, (Gulf states, Mississippi, Louisiana, or Tennessee).

Dendroica aestiva ineditus J. C. Phillips, 1911:85 (Matamoros [Tamaulipas, Mexico]) fide A. R. Phillips (in litt.) and Ramos & Warner (1980). MCZ

Subspecific characters.—Both sexes, in all plumages, more intensely bright yellow below than other subspecies in the *aestiva* group. Compared with *amnicola,* both sexes paler (less greenish, more yellowish) above.

Compared to *morcomi,* both sexes more yellow above and below; males brighter yellow below. Compared with *sonorana,* both sexes greener above and brighter (not pale) yellow below; chestnut streaks more prominent. Paler males in fall plumage brighter with more yellowish rumps and crowns than other northern subspecies and *morcomi.*

Distribution.—Breeds from south-central Alberta to central Saskatchewan and southern Manitoba, southern Quebec, Prince Edward Island, Nova Scotia; east of Rocky Mountains from Montana to Colorado east to Kansas, central Oklahoma, all but western Texas, northern Arkansas, central Alabama, central Georgia, and central South Carolina. Intergrades with *amnicola* in central Alberta, southern Manitoba, southern Quebec, and Nova Scotia.

Specimens examined.—Alberta (7); Saskatchewan (6); Manitoba (21); Nova Scotia (31); Montana and Wyoming (16); Colorado (10); North and South Dakota (18); Nebraska (49); Oklahoma (8); Minnesota (41); New England (42); New York (54); New Jersey (11); Pennsylvania (11); Maryland and Virginia (25); Georgia and Carolinas (34); others (34).

Remarks.—Oberholser (1974) believed the name *aestiva* was based on the darker northern subspecies (*amnicola*) and used the name *flava* Vieillot for the paler southern subspecies. However, the basis of the earlier name *aestiva* clearly applies to the pale population (Browning 1990b). Based on Audubon's plates and descriptions (the types are missing), the name *childrenii,* and most probably *rathbonia,* are synonyms of *aestiva.* The name *inedita* was based on specimens collected in August and September. Griscom & Crosby (1926) and Hellmayr (1935) recognized *ineditus,* but Miller et al. (1957) and Lowery & Monroe (1968) synonymized the name with *morcomi.* A. R. Phillips (in litt.), who has examined the type of *ineditus,* concluded that the holotype is a migrant example of *aestiva,* and that the species does not breed west of Matamoros (contra Griscom & Crosby 1926). Paratypes (MCZ) from the original series of *ineditus* resemble specimens of *aestiva.*

Dorsally dark and greenish birds breed in southeastern Canada to Pennsylvania. There is a gradual north to south cline in reduction of dorsal green color and increased amount of yellow on the foreheads and backs of birds from Virginia to Georgia. Specimens from Nebraska, Kansas, and western Oklahoma are slightly brighter and less greenish above than specimens from the northeastern part of the breeding range and represent the end of a cline in coloration. A similar cline is represented by specimens from the northeast west to the prairie provinces and states. Specimens from Georgia resemble birds from Nebraska in reduction of green in their upper parts. Birds from Nebraska, collectively, are generally more intensely bright yellow above and have more yellowish rumps than do specimens of *morcomi, sonorana,* and *aestiva* from northeastern populations (Browning *in* Wetmore et al. 1984). Such specimens resemble the "*sonorana*" type characterized by Sutton (1967). A gradual west to east cline is also apparent from a large series of specimens collected at several localities across Nebraska, with specimens from northeastern Nebraska being less green above then birds from northwestern Nebraska. The Nebraska series, collectively, is slightly more yellowish above, with more yellow than green on the head, and resemble specimens from the southern prairie provinces in Canada and western Minnesota. Specimens from Nebraska resemble birds from Georgia in dorsal color. Geographic variation in *aestiva,* though considerable, is clinal and thus not diagnostic in recognizing additional subspecies in its range.

Johnston (1964) identified specimens from western Kansas as *morcomi* but specimens from western Kansas and eastern Colorado represent the end of a cline toward *morcomi,* with males being more greenish above and less yellow on the forehead than birds from other localities of the prairie states. Specimens of *aestiva* from central

Montana and Wyoming are also slightly paler and less greenish above than are those from the northeastern United States.

Dendroica petechia morcomi Coale

Dendroica aestiva morcomi Coale, 1887:82 (Fort Bridger, Utah [= Fort Bridger (Camp Scott), Uinta Co., Wyoming) fide Deignan 1961]). (USNM)

Subspecific characters.—Males near western populations of *aestiva* but greener above; duller yellow below. Compared to *brewsteri,* males darker and greener on back and rump; chestnut streaks average wider. Compared to *sonorana,* males greener above; ventral yellow with a greenish cast. Chestnut streaks average narrower than *parkesi, yukonensis,* and *amnicola.* Ventral yellow in males usually paler than *aestiva* and with a greenish cast compared to *sonorana.* Females dorsally paler yellow than *aestiva,* darker (less yellow) than *sonorana,* and less green than *aestiva*; ventrally brighter yellow than *sonorana* and *rubiginosa.* Specimens in fall plumage dorsally intermediate between *amnicola* and *aestiva* but nearer the latter; greener above than *sonorana.*

Distribution.—Breeds from interior British Columbia to eastern Washington, western Montana south to eastern California, Nevada (except extreme southern), northern Arizona, central New Mexico, and northwestern Texas. Intergrades with *rubiginosa* at Bella Coola, Vancouver Island, and adjacent mainland, western British Columbia; intergrades with *sonorana* in the Southwest (see beyond).

Specimens examined.—British Columbia (59); Washington (9); Oregon (30); California (7); Idaho/Wyoming (15); Nevada (5); Utah (18); northern Arizona and central New Mexico (20).

Remarks.—Specimens of *morcomi* from the northern Rocky Mountains, Utah, and the interior of British Columbia average slightly brighter yellow above than *morcomi* from elsewhere, but are greener above than *brewsteri.* Males from Vancouver Island and adjacent mainland (e.g., city of Vancouver) of British Columbia average slightly duller and greener on the back and forehead than other specimens of *morcomi.* The average dorsal color of males from Bella Coola, British Columbia, is intermediate in color between specimens from the Vancouver Island region and *morcomi* from central British Columbia. Females from most of British Columbia resemble others from the range of *morcomi.* I conclude that the populations from the Vancouver Island are intermediate in dorsal color between *morcomi* and *rubiginosa* but are closer to the latter, while birds from Bella Coola are likewise intermediate but are closer to *morcomi.*

Males from the northern Great Basin (e.g., Utah) are slightly more yellow (less greenish) above than most specimens of *morcomi* from the same latitudes or from higher elevations (e.g., east slopes of Sierra Nevada Mountains). Geographic variation is generally clinal from north to south, with darker and greener birds breeding to the north (Phillips et al. 1964). The zone of intergradation between *morcomi* and *sonorana* is wide and identifying specimens to either subspecies or as intergrades between them have been interpreted in different ways (see Behle 1948, Oberholser 1974, Behle 1985).

Dendroica aestiva brewsteri Grinnell

Dendroica aestiva brewsteri Grinnell, 1903: 72 (Palo Alto, California). (MVZ)

Subspecific characters.—Males near *morcomi* but definitely more yellow on the back; rump and forehead average more yellow; edges of secondaries and tertials more yellow (less greenish); chestnut streaks averaging thinner and sparser. Compared with western populations of *aestiva,* males greener above; chestnut streaks usually thinner and sparser. Many females resemble *morcomi,* but brightest yellow individuals more yellow than bright yellow examples of *morcomi.* Adult males in fall plumage, compared to *morcomi,* usually with ventral streaks absent or narrower; some fall males average more yellow above.

Distribution.—Breeds from western Washington to western Oregon, California west of the Cascade and Sierra Nevada ranges, and northwestern Baja California. Winters from Baja California to Nicaragua.

Specimens examined.—Washington (4); Oregon (10); California (34).

Remarks.—The subspecies *brewsteri* was recognized for many years while the name *morcomi* remained a synonym of *aestiva.* About the time *morcomi* became recognized as a subspecies distinct from *aestiva,* the name *brewsteri* became a synonym of *morcomi.* Because *brewsteri* is recognizable, and because the history of the names *brewsteri* and *morcomi* are closely related, a review of the usage of the two names follows.

When Grinnell (1903) described *brewsteri,* he also synonymized *morcomi* with *aestiva,* stating that the holotype of *morcomi* was an extreme example of *aestiva.* He characterized *brewsteri* as smaller in size, less brightly yellow, and with narrower chestnut streaks than in *aestiva,* and gave the breeding range of *brewsteri* as west of the Cascade and Sierra Nevada mountains from Oregon to southern California. Grinnell's comparative material of "*aestiva*" consisted of specimens from the Rocky Mountains and birds from the northeastern United States. The A.O.U. (1910, 1931) recognized *brewsteri* and included the populations from the Rocky Mountains (= *morcomi*) in the range of *aestiva.* Van Rossem (1931) and Dickey & van Rossem (1938) recognized both *brewsteri* and *morcomi,* characterized *brewsteri* of the Pacific coast as larger (contra Grinnell 1903) and having narrower breast streaks than *morcomi,* and gave the range of *morcomi* as from the eastern slopes of the Cascade and Sierra mountains to the Rocky Mountains. Gabrielson & Jewett (1940), without providing details, synonymized both *brewsteri* and *morcomi* with *aestiva.* Twomey (1942) reported that wing chord of *brewsteri* is not a useful subspecific character, but, on the basis of color, recognized *brewsteri* as the subspecies breeding in the Uinta Basin, Utah. Grinnell & Miller (1944) reported that specimens from east of the Sierra Nevada north of Mono Lake are intermediate between *brewsteri* and *morcomi.* The A.O.U. (1944) recognized *morcomi,* following Dickey & van Rossem (1938). However, Behle (1948: 77–78) reported that specimens from California and Utah are similar in size, dorsal color, and widths of chestnut streaks. He concluded that the topotypes of *brewsteri* and *morcomi* "are similar in their characters" and that "*brewsteri* appears to be [emphasis mine] a synonym of *morcomi.*" Aldrich (*in* Jewett et al. 1953) and the A.O.U. (1954), both of whom cited Behle (1948), synonymized *brewsteri* with *morcomi.*

The synonymy of *brewsteri* was thus based on comparisons of *brewsteri* with more yellowish specimens of *morcomi* typical of Utah and southwestern Wyoming. The taxonomic conclusion by A.O.U. (1954) did not account for geographic variation in *morcomi,* and the fact that the breeding range of *brewsteri* is isolated from the more yellowish examples of *morcomi* by darker and less yellowish populations of *morcomi* from the eastern slopes of the Cascade and Sierra Nevada mountains.

Grinnell & Miller (1944) included northeastern California as part of the breeding range of *brewsteri.* I did not examine specimens from that region, but specimens from adjacent Oregon belong to *morcomi.*

Dendroica petechia sonorana Brewster

Dendroica aestiva sonorana Brewster, 1888: 137 (Opusura [= Moctezuma], Sonora, Mexico). MCZ

Dendroica petechia hypochlora Oberholser, 1974:737 (3 mi north of Fort Whipple, near Prescott, Arizona). (USNM)

Subspecific characters.—Compared with other subspecies in the *aestiva* group, both sexes paler yellow above and below; males with dorsal chestnut streaks usually prominent; males with ventral chestnut streaks narrow, paler, and less prominent. Compared with *dugesi,* males with ventral chestnut streaks averaging more prominent; shorter wings (61.0–65.7, mean 63.1 (*n* = 14) in *sonorana* and 64.5–73.1, mean 68.6 (*n* = 10) in *dugesi.* Fall plumage greenish above but more yellowish above and more pure yellow below than *morcomi.*

Distribution.—Breeds from southeastern California, extreme southern Nevada, central Arizona, southern New Mexico, and western Texas south to northeastern Baja California, interior Nayarit, and Zacatecas. Intergrades with *morcomi* in northern and northeastern Arizona, Utah, New Mexico, and western Colorado; intergrades with *morcomi* and *aestiva* in southwestern Oklahoma.

Specimens examined.—California (6); Arizona (132); New Mexico (58); Colorado (7); Texas (24).

Remarks.—Oberholser (1974) named the populations from the area of intergradation with *morcomi* (above) *hypochlora.* The holotype of *hypochlora* most resembles specimens of *sonorana* (Browning 1978, 1990a).

Dendroica petechia dugesi Coale

Dendroica dugesi Coale, 1887:83 (Moro Leon [= Moroleón], Guanajuato, Mexico). (USNM)

Subspecific characters.—Males nearest *sonorana* but more greenish above; wings longer (see under *sonorana*). Females paler and grayer above than *sonorana.*

Distribution.—Breeds in Central Plateau of Mexico from southern San Luis Potosí to Hidalgo, Guanajuato, Michoacán, Guerrero, Morelos, and Puebla. Winters from Morelos to Puebla and Tlaxcala; reported in southern Veracruz (Ramos & Warner 1980).

Specimens examined.—Michoacán (6); Puebla (5); Durango (1); Guanajuato (1); Tlaxcala (1); Morelos (3); México (3).

Remarks.—The southern breeding range of *sonorana* and northern breeding range of *dugesi* are poorly known. Present information suggests the two ranges are disjunct, but *sonorana* and *dugesi* may come in contact somewhere in Zacatecas or San Luis Potosí.

Summary of *D. p. aestiva* group

Generally, males in the *aestiva* group from coastal Alaska and northern interior populations are greener (less yellow) above than birds from elsewhere. Males from the southwestern range of the *aestiva* group are paler yellow and much less green above than other populations. Ventral color is generally brighter and more purely yellow in southeastern populations, paler in southwestern birds, and slightly tinged with green in northern populations.

More specifically, the northern populations east of the Rocky Mountains from Canada (*parkesi* and *amnicola*) are darker and greener (less yellow) above than adjacent populations; *parkesi* is greener above than *amnicola.* Variation in dorsal color of birds from the eastern United States (*aestiva*) is clinal, with darker birds from the northeast and brighter and more yellowish birds from the southeast and prairie region. Except for the dark populations of coastal Alaska and British Columbia (*rubiginosa*), birds from west of the Rocky Mountains are generally darker and greener above in northern populations and paler and more yellow in southern populations. Birds from interior Alaska and Yukon Territory (*banksi*) are more yellow above than other northern populations and are darker and more greenish than birds of the northern intermountain United States and interior British Columbia (*morcomi*). Populations of western Washington to California (*brewsteri*) are more yellow above than *morcomi.* Southwestern populations (*sonorana*) are paler and more pure yellow (less greenish) above than the northern populations, and are smaller and slightly less greenish above than interior Mexican populations (*dugesi*).

Dendroica p. petechia group

Populations of the *petechia* group differ from birds of the *aestiva* group in having a generally well-defined chestnut crown and rounder wings. Birds of the *petechia* group differ from those of the *erithachorides* group in having the chestnut restricted to the crown, with the exception of the chestnut hooded birds from Martinique. Birds from Martinique are more similar in size to birds of the *petechia* group than to the *erithachorides* group. Birds of *petechia* group are usually found in mangroves.

Dendroica petechia rufivertex Ridgway

Dendroica petechia rufivertex Ridgway, 1885:21 (Cozumel Island, Yucatán [= Quintana Roo]). (USNM)

Subspecific characters.—Males near *gundlachi* above but chestnut streaks more extensive and darker. Females less heavily streaked below than *gundlachi.*

Distribution.—Resident on Cozumel Island, Quintana Roo, Mexico.

Specimens examined.—Cozumel Island (18).

Remarks.—The whitish plumages typical of most of the northern subspecies of the *petechia* group are apparently absent in this subspecies.

Dendroica petechia armouri Greenway

Dendroica petechia armouri Greenway, 1933:63 [= 68] (Old Providence Island). MCZ

Subspecific characters.—Males nearest *flavida* but forehead and throat yellow (not chestnut); ventral chestnut streaks more extensive. Compared with *rufivertex,* both sexes darker and less yellow above.

Distribution.—Isla Providencia, western Caribbean.

Specimens examined.—Isla Providencia (5).

Remarks.—The only female of *armouri* compared is similar to females of *rufivertex* and *flavida.* Bond (1950) reported *armouri* as the rarest resident on the island. Birds were not found there by Russell et al. (1979) and Tye & Tye (1991).

Dendroica petechia flavida Cory

Dendroica flavida Cory, 1887:179 (St. Andrew Island, Caribbean). FM

Subspecific characters.—Males nearest *rufivertex* but chestnut on crown reduced and ventral streaks wider. Compared to *armouri,* forehead and throat chestnut (not yellow) and rump greener. Females darker green than males of *flavida,* and some heavily marked with ventral chestnut streaks.

Distribution.—Isla Andrés, western Caribbean.

Specimens examined.—Isla Andrés (17).

Dendroica petechia eoa Gosse

Sylvicola eoa Gosse, 1847:158 (Crab Pond, Jamaica). BM

Dendroeca petechia e. *jamaicensis* Sundevall, 1870:608 (near Spanishtown, Jamaica). (USNM)

Dendroica auricapilla Ridgway, 1888:572 (Grand Cayman). (USNM)

Subspecific characters.—Males near *gundlachi* but slightly brighter (more yellow), especially above in fall plumage, with chestnut crown patch more extensive. Compared with *albicollis,* males slightly greener and darker above. Females greener above than *flaviceps.* Females in fall plumage duller above and below than *gundlachi.*

Distribution.—Jamaica and Cayman Islands.

Specimens examined.—Jamaica (31), Little Cayman (3), Grand Cayman Island (37).

Remarks.—Until Peters' (1927) study, birds from Jamaica were considered to represent nominate *petechia.* I follow Hellmayr (1935) and others in synonymizing *auricapilla* with *eoa.* I disagree with Buden (1979) who synonymized *eoa* with *albicollis.*

Dendroica petechia gundlachi Baird

Dendroica gundlachi Baird, 1865:197 (Cuba). (USNM)

Subspecific characters.—Both sexes near *flaviceps* but duller and greener above; rump greenish (not yellowish); less brilliant yellow (more greenish) below; chestnut crown usually more extensive. Compared with *eoa,* both sexes duller and greener above; duller yellow below; males with chestnut crown usually less extensive. Compared with *solaris* and *albicollis,* males greener above.

Distribution.—Cuba, Isle of Pines, and mangroves of southern Florida from Florida Bay Island, Virginia Key near Miami, and Florida Keys (Stevenson & Anderson 1993).

Specimens examined.—Cuba (99); Isle of Pines (21); Florida (2).

Remarks.—This subspecies was first reported as breeding in southern Florida by Greene (1942) who collected two specimens (USNM) near Key West in mid-July. The two specimens have tarsi of 20.3 and 21.8 mm, and are more similar to *gundlachi* than to *flaviceps* in dorsal color.

Dendroica petechia flaviceps Chapman

Dendroica petechia flaviceps Chapman, 1892: 310 (Rum Cay, Bahamas). (AMNH)

Subspecific characters.—Both sexes near *gundlachi* but more yellow above; rump yellowish; more yellowish (less greenish) below. Topotypical *flaviceps* are brighter (lacking a greenish cast) below than *gundlachi*; specimens from elsewhere in the Bahamas are more similar to *gundlachi.* Compared with *solaris* and *albicollis,* males duller yellow below. Fall and spring plumages definitely more yellowish (less greenish) above than *gundlachi*; most yellowish females from Cuba are still greener above than *flaviceps.*

Distribution.—Bahama Islands.

Specimens examined.—Various Bahama Islands (103).

Remarks.—Peters (1927) characterized *flaviceps* as similar to *gundlachi,* but with the chestnut of the crown less extensive and the tarsi longer. Hellmayr (1935) commented that specimens of *flaviceps* are generally brighter in color and the wings are more rounded than in *gundlachi.* Bond (1942) synonymized *flaviceps* with *gundlachi* stating that the characters "such as more rounded wing, longer tarsus and brighter coloration did not hold." Others (e.g., Lowery & Monroe 1968, Buden 1979) followed Bond (1942).

Wiedenfeld (1991) stated that birds with the longest tarsi are from the northern Bahamas. Measurements of tarsi of *flaviceps* (n = 17) in this study range from 20.2 to 23.6, with a mean of 21.6, and of *gundlachi* from Cuba (n = 14) range from 19.5 to 21.1, with a mean of 20.3. Individual measurements of *flaviceps* overlap 30% of those of *gundlachi*; individuals of *gundlachi* overlap 50% of those of *flaviceps.*

Dendroica petechia albicollis (Gmelin)

Motacilla albicollis Gmelin, 1789:983 (in insula S. Dominici [= Santo Domingo]).

Subspecific characters.—Both sexes with more yellowish (less dull and greenish) backs and more yellow crowns than *eoa* and duller and more greenish (less yellowish) above than *solaris.* Males brighter yellow below than *flaviceps* and more yellowish above than *gundlachi.* Females with some pale chestnut on foreheads and grayer above than *eoa* and *solaris.*

Distribution.—Hispaniola, Vache, and Tortue islands.

Specimens.—Hispaniola (27).

Remarks.—Buden (1979) synonymized *eoa* with *albicollis.*

Dendroica petechia chlora, new subspecies

Holotype.—USNM 280265, adult male, Tororu Island, Siete Hermanos islands, Domican Republic, collected 31 January 1929 by A. J. Poole and W. M. Perrygo (original no. 165).

Subspecific characters.—Males nearest *albicollis* but back and crown distinctly darker green; edges of secondaries and primaries greener (less yellow); chestnut on crown darker. Compared with *solaris*, males much darker above and less yellow below than *solaris*. Compared with *gundlachi*, males slightly greener above and usually paler yellow below. One of two females darker and less grayish above than *albicollis* (the other specimen cannot be distinguished from *albicollis*).

Distribution.—Siete Hermanos islands, off Hispaniola.

Specimens examined.—Siete Hermanos islands (8).

Etymology.—Greek, *chloros*, for the greener color of the plumage.

Remarks.—A male from Fort Liberty, mainland Haiti, a locality about 10 miles SSW of the type locality of *chlora*, resembles *albicollis* in color.

Dendroica petechia solaris Wetmore

Dendroica petechia solaris Wetmore, 1929:1 (Z'Etriotes, Île de la Gonave [in Gulf of Gonaïves], Republic of Haiti, Hispaniola). (USNM)

Subspecific characters.—Males nearest *albicollis* but brighter and more yellowish above, and on edges of primaries and secondaries. Compared with *chlora*, males paler (less dark green) than those of *chlora*. Females average paler and more yellowish above than *albicollis*.

Distribution.—Resident on Gonave and Petite Gonave islands off Haiti.

Specimens examined.—Gonave (27); Petite Gonave (4).

Remarks.—Although *solaris* was listed as a distinct subspecies by Bond (1930) and by Hellmayr (1935), Lowery & Monroe (1968) synonymized the name with *albicollis*.

Dendroica petechia bartholemica Sundevall

Dendroeca petechia bartholemica Sundevall, 1870:607 (St. Bartholemew). Royal Natural History Museum, Stockholm (fide Gydlenstolpe 1926)

Dendroeca petechia cruciana Sundevall, 1870:608 (St. Croix). Cambridge Univ. (fide Hellmayr 1935)

Subspecific characters.—Near *albicollis*, but both sexes average brighter yellow below; males with chestnut on the head and breast more extensive. Compared with *melanoptera*, males with crown less distinctly capped with chestnut.

Distribution.—Puerto Rico, islands east of Puerto Rico, Virgin Islands, northern Lesser Antilles from Anguilla to St. Martin, St. Bartholomew, Barbuda, St. Eustatius, Nevis, St. Kitts, Antigua, and Montserrat.

Specimens examined.—Puerto Rico (97); Virgin Islands (17); St. Martin (2); Barbuda (4); St. Kitts and Nevis (8); Antigua (17); Montserrat (2).

Remarks.—According to Peters (1927), specimens that he identified as *cruciana* from St. Croix were "quite distinctive" from those he identified as *bartholemica* from St. Thomas. However, Wetmore (1927:105) concluded that the range of *cruciana* extends east to Antigua, and that *cruciana* and *bartholemica* "are closely similar" in color. I found that overlap in color between populations is extensive, with some specimens from the northern Lesser Antilles ("*bartholemica*") being brighter below and having more chestnut on the crown than specimens from Puerto Rico ("*cruciana*"). The only female from Montserrat examined has a yellowish rump. Use of the name *bartholemica* for this subspecies follows Ridgway (1903) who acted as the first revisor.

Dendroica petechia melanoptera Lawrence

Dendroeca petechia melanoptera Lawrence, 1879:453 (Guadeloupe). (USNM)

Subspecific characters.—Males nearest *bartholemica* but with chestnut crown more distinct. Females average slightly more yellowish on rump than *bartholemica.*

Distribution.—Central Lesser Antilles: Guadeloupe, Désirade, Marie Galante, Îles des Saintes, and Dominica.

Specimens examined.—Guadeloupe (9); Dominica (7); Marie Galante (2).

Dendroica petechia ruficapilla (Gmelin)

Motacilla ruficapilla Gmelin, 1789:490 (in Martinica = Martinique).

Dendroica rufigula Baird, 1865:204. (Martinique). ANSP

Dendroeca granadensis Sharpe, 1885:284 (Colombia = Martinique). (BM)

Subspecific characters.—Differs from Antillean subspecies by having a chestnut hood, thus resembling subspecies in the *erithachorides* group. Birds from Martinique are similar in size to subspecies in the *petechia* group (Wiedenfeld 1991).

Distribution.—Martinique, Lesser Antilles.

Specimens examined.—Martinique (10).

Remarks.—According to Peters (1927), the name *ruficapilla* was based on females from Guadeloupe that were originally characterized as having a yellow throat, whereas birds from Martinique (= "*rufigula*" in Peters, footnote) have throats that are "generally clouded with rufous." Hellmayr (1935) concluded that there are no valid grounds for Peters' treatment and most subsequent authors have followed Hellmayr.

Sharpe (1885) referred to three specimens listed by Sclater (1862:32) in his indeterminable description of *granadensis.* Hellmayr (1935), who examined one of the specimens, believed that the name *granadensis* was probably a synonym of *ruficapilla.* Apparently on the recommendation of A. Wetmore (notes on file, USNM), Warren & Harrison (1971) listed one of the three specimens as a syntype of *granadensis.* Based on measurements and description of plumage (P. R. Colston, in litt.), the specimen listed by Warren & Harrison (1971) is identifiable as *ruficapilla.* The characters of a second specimen (BM), examined by Browning and S. L. Olson, agree with Colston's characterizations of the specimen listed by Warren & Harrison (1971). A third specimen (BM) is similar in size and color to *erithachorides.* Because the three syntypes of *granadensis* represent more than one subspecies, I designate BM 1884.5.5.15.356, the same specimen listed by Warren & Harrison (1971), as the lectotype of *Dendroeca granadensis* Sharpe.

Dendroica petechia babad Bond

Dendroica petechia babad Bond, 1927:571 (St. Lucia, British West Indies). (ANSP)

Subspecific characters.—Males nearest *melanoptera* but slightly more yellowish (less greenish) below; slightly darker chestnut cap. Chestnut areas more extensive than *alsiosa* and much paler than nominate *petechia.*

Distribution.—St. Lucia, Lesser Antilles.

Specimens examined.—St. Lucia (4).

Remarks.—I agree with Bond (1936) who stated that *babad* is "barely distinguishable" from birds from Dominica (*melanoptera*). The purported differences in crown color (Bond 1927; Hellmayr 1935) between the adjacent subspecies *alsiosa* and *melanoptera* are exaggerated.

Dendroica petechia petechia (Linnaeus)

Motacilla petechia Linnaeus, 1766:234 (in America septentrionali = Barbados, Lesser Antilles).

Dendroica capitalis Lawrence, 1868:359 (Barbados, Lesser Antilles). (AMNH)

Dendroeca petechia c. *barbadensis* Sundevall:608 (Barbados). (USNM)

Subspecific characters.—Males nearest *rufopileata* but greener (less yellowish) below; chestnut cap slightly darker; darker above than either *rufopileata* or *obscura*. Chestnut areas much darker than *alsiosa*. Females paler (less blackish) below than *rufopileata;* more yellowish (less greenish) above than *babad*, and greener above than *alsiosa*.

Distribution.—Barbados, Lesser Antilles.

Specimens examined.—Barbados (12).

Remarks.—The name *petechia* was used for the Jamaican populations until Peters (1927) determined that Edwards' plate is of a bird from the Barbados population.

Dendroica petechia alsiosa Peters

Dendroica petechia alsiosa Peters, 1926:41 (Prune Island, east of Union Island, Grenadines). (MCZ)

Subspecific characters.—Males near *melanoptera*, but more yellow (less greenish) above; yellow (not greenish) immediately above the bill and cheeks. Compared with *babad* and nominate *petechia*, males with slightly paler ventral chestnut streaks. Crown color paler than in nominate *petechia*. Females more yellowish (less greenish) above than *babad*.

Distribution.—Grenadine islands, Lesser Antilles.

Specimens examined.—Prune Island (5); Union and Mayero islands (2).

Remarks.—Males from Prune Island have slightly darker crowns than the two males from Union and Mayero islands.

Dendroica petechia rufopileata Ridgway

Dendroica rufopileata Ridgway, 1884:173 (Curaçao). (USNM)

Subspecific characters.—Males near *obscura* but yellowish-green (not dark green) above; chestnut areas paler, especially ventral streaks. Chestnut crown darker than all previously listed subspecies of *petechia* group, except nominate *petechia*. Compared with *aurifrons*, males darker above; chestnut streaks slightly darker and wider.

Distribution.—Aruba, Curaçao, and Bonaire; Blanquilla, Margarita, and Islas Los Testigos, off northern Venezuela.

Specimens examined.—Aruba (13); Curaçao (31); Bonaire (13); Blanquilla (16); Islas Los Testigos (11).

Remarks.—Birds in the eastern and western parts of the range of *rufopileata* are separated by a darker subspecies, *obscura* (see below), and the taxonomy of the complex has varied historically. When Ridgway (1884) named *rufopileata*, birds from the islands off Venezuela were known only from Curaçao. Hartert (1893) discovered similar birds on Aruba and Bonaire, and Lowe (1907) extended the range of *rufopileata* to include Isla Blanquilla. Cory (1909) named *obscura* from Isla Los Roques and, although he noted differences between the now disjunct eastern and western parts of the range of *rufopileata*, he considered these too minor for recognition of a third subspecies. Peters (1927) essentially followed Cory (1909) and included specimens from Isla Las Aves in *obscura*. Although Hellmayr (1935) synonymized *obscura* with *rufopileata*, he characterized birds from the range of *obscura* as dark, and birds from Blanquilla, Testigos, and Tortuga as brighter yellow above, with wider yellow margins on the wings, than in birds from western islands. Phelps & Phelps (1950) followed Hellmayr (1935), but they (Phelps & Phelps 1951) later recognized *obscura*, adding that specimens from Tortuga are intermediate between *rufopileata* and *aurifrons* from islands to the south (see below) but closer to the latter. Voous (1957), who recognized both *rufopileata* and *obscura*, reported that 2 of 8 specimens from Aruba have faint streaks on the throat as in *cienagae* (see below). Voous (1957) also, followed by Phelps & Phelps (1959) and Lowery & Monroe (1968), included specimens from Isla La Orchila (formerly in *rufopileata*) in *obscura*.

The two populations of *rufopileata* are generally similar, but males from the western islands of Isla Blanquilla and Isla Los Testigos have slightly darker ventral chestnut streaks than 66% of the specimens from Bonaire, Curaçao, and Aruba. The chestnut on the crown of the western population is darker than about 50% of the eastern birds, and about 25% of the eastern birds are more yellow on the rump than in western birds. I do not view these differences as sufficient for taxonomic recognition.

Dendroica petechia obscura Cory

Dendroica ruficapilla obscura Cory, 1909: 217 (Isla Los Roques, Leeward Islands). (FM)

Subspecific characters.—Near *rufopileata* but dark greenish (less yellowish) above, with chestnut area darker, especially ventral streaks.

Distribution.—Islas Los Roques, Islas Las Aves, and Isla La Orchila, off northern Venezuela.

Specimens examined.—Isla Las Aves (7); Islas Los Roques (19); Isla La Orchila (1).

Remarks.—See under *rufopileata.*

Dendroica petechia aurifrons Phelps & Phelps, Jr.

Dendroica petechia aurifrons Phelps & Phelps, Jr., 1950:21 (Puerto de La Cruz, Anzoátegui, Venezuela). AMNH

Subspecific characters.—Males more yellowish (less greenish) above and more yellow (not chestnut) on the crown than *cienagae* and *paraguanae;* slightly paler below than *cienagae.* Compared with *rufopileata,* males slightly paler above; chestnut streaks narrower.

Distribution.—Coast of Anzoátegui and extreme western Sucre (at Cumaná), north-central Venezuela, and islands immediately offshore, including Isla La Tortuga, Islas Las Tortuguillas, and Isla de Pirítu.

Specimens examined.—Isla La Tortuga (3); Venezuela mainland (2).

Summary of *D. p. petechia* group

Generally, the ventral chestnut streaks are more prominent in males from the western Caribbean islands than those from other populations. The chestnut cap ranges from pale in males from the Greater Antilles to dark in birds from the southern Lesser Antilles and parts of islands off Venezuela.

More specifically, the ventral chestnut streaks of birds from Isla Providencia (*armouri*) are darker than those from Cozumel (*rufivertex*), and are more extensive than birds from Isla Andrés (*flavida*). Populations from the northeastern Caribbean islands are generally greener above, with less extensive chestnut caps than birds from the southern islands. Birds from Cuba and southern Florida (*gundlachi*) are duller and greener above than those from the Bahama Islands (*flaviceps*) and are still greener above than birds from the main island of Hispaniola (*albicollis*). Populations of the islands off Hispaniola from Gonave and Petite Gonave islands (*solaris*) are more yellow above than *albicollis* and birds from the Siete Hermanos islands (*chlora*) are darker above than *albicollis* and *gundlachi.* Birds from Puerto Rico and the northern Lesser Antilles (*bartholemica*) are brighter yellow above and below, with more prominent chestnut caps, than *albicollis.* The chestnut cap is still more prominent in males from the central Lesser Antilles (*melanoptera*). The populations of Martinique (*ruficapilla*) have a chestnut hood similar to that of the *erithachorides* group. Birds from St. Lucia (*babad*) are more yellow above, with darker chestnut caps, than *melanoptera.* Males from Barbados (*petechia*) are still more yellow above, with still darker caps. The chestnut streaks and caps of birds from the Grenadine islands (*alsiosa*) are paler than *petechia.* The caps of birds from the islands off northern Venezuela (*rufopileata* and *obscura*) are darker than *petechia.* Back color of *rufopileata* is paler than *obscura.* Males of the populations from western coastal Venezuela and adjacent islands (*aurifrons*) are paler above, with narrower chestnut streaks than *rufopileata.*

Dendroica p. erithachorides group

Subspecies in the *erithachorides* group differ from those in the *aestiva* and *petechia* groups by having chestnut heads. Birds also differ from the *aestiva* group by having rounded wings. Members of the *erithachorides* group are usually found in mangroves.

Dendroica petechia oraria Parkes & Dickerman

Dendroica petechia oraria Parkes & Dickerman, 1967:87 (two miles south of Buena Vista (= about nine miles north of Tlacotalpán), Veracruz, Mexico). (CM)

Subspecific characters.—Males nearest *bryanti* but more greenish (less yellowish) above; averaging paler yellow below; averaging less heavily streaked with chestnut below, especially flanks. The only female examined, from Veracruz, is paler and more yellow above and below than females of *bryanti.*

Distribution.—Coastal southern Tamaulipas to Tabasco, Mexico. Intergrades with *bryanti* in eastern Tabasco and western Campeche.

Specimens examined.—Tamaulipas (5); Veracruz (19); Tabasco (4); Campeche (4).

Dendroica petechia bryanti Ridgway

Dendroica vieillotii var. *Bryanti* Ridgway, 1873:605 (Belize, British Honduras = Belize, Belize) fide Parkes & Dickerman (1967). (USNM)

Subspecific characters.—Males near *oraria* but more yellowish (less greenish) above; brighter yellow below; chestnut streaks averaging narrower. Compared with *erithachorides,* both sexes greener above; males with narrower less prominent chestnut streaks below.

Distribution.—Caribbean coast from Yucatan Peninsula, Mexico to Campeche and Nicaragua. Possibly breeds on Isla Mujeres, Quintana Roo (Parkes & Dickerman 1967). Intergrades with *oraria* in eastern Tabasco and western Campeche.

Specimens examined.—Quintana Roo (8); Yucatan (19); Belize (7); Honduras (3); Nicaragua (9).

Dendroica petechia erithachorides Baird

Dendroica erihtachorides [sic] Baird, *in* Baird, Cassin, & Lawrence, 1858:283 (South America = Cartegena, Colombia, fide Hellmayr [1935]). (USNM)

Dendroica Vieilloti Cassin, 1860:192 (Cartagena, Colombia). (USNM)

[*Dendroeca petechia*] i) *panamensis* ? Sundevall, 1870:609 (Cartagena, Department of Bolívar, Colombia). (USNM)

Subspecific characters.—Males near *bryanti* but darker above; darker chestnut head; more conspicuous chestnut streaks. Compared with *chrysendeta,* males less yellowish below; chestnut bib more defined; less heavily streaked below. Females greener on back and rump (less yellow) than *bryanti* and *chrysendeta.*

Distribution.—Caribbean coast from Costa Rica, locally, to Panama (Bocas del Toro and islands), and Caribbean coast of Colombia.

Specimens examined.—Costa Rica (5); Panama (29); Colombia (7).

Remarks.—Cherrie (1891:524) remarked that specimens from Limón, Costa Rica, have broader chestnut streaks than do northern examples of *bryanti,* and that the throat of the Limón birds is closer to that in specimens from Panama. I found that males from elsewhere along the coast of Costa Rica also have broader chestnut streaks and are slightly darker above than northern examples of *bryanti.* I agree with Stiles & Skutch (1989) in extending the northern range of *erithachorides* to Costa Rica. The populations from Limón, Costa Rica, and Bocas del Toro, Panama, are apparently disjunct; there are no mangroves between the two localities. Specimens of both sexes from Escudo de Varaguas, Bocas del Toro, Panama, are duller above than specimens of *erithachorides* from the mainland and islands off Almirante, Panama, but I provisionally assign them to this subspecies.

Dendroica petechia chrysendeta Wetmore

Dendroica petechia chrysendeta Wetmore, 1946:52 (Laguna de Tucacas, Puerto López, Guajira, Colombia). (USNM)

Subspecific characters.—Males near *erithachorides* but yellow areas brighter; chestnut of head and upper breast darker, more extensive on the head. Compared with *paraguanae,* back more yellowish (less green); chestnut less extensive on the breast.

Distribution.—Coastal Guajira Peninsula, northeastern Colombia and Bahía Portete, Puerto López, Castilletes, and Paraguipa in western Venezuela.

Specimens examined.—Guajira Peninsula (6).

Remarks.—Specimens from Bahía Portete are intermediate in color between *erithachorides* and *chrysendeta* (Wetmore 1946b). Variation in the dorsal yellow of *chrysendeta* and some populations of *paraguanae* are similar (N. K. Klein, pers. comm.).

Dendroica petechia paraguanae Phelps & Gilliard

Dendroica petechia paraguanae Phelps & Gilliard, 1941:10 (La Boca, Adícora, Paraguaná Peninsula, Falcón, Venezuela).

Subspecific characters.—Both sexes darker and greener above than *chrysendeta.*

Distribution.—Paraguaná Peninsula, Falcón, northwestern Venezuela.

Specimens examined.—Paraguaná Peninsula (8).

Dendroica petechia cienagae Zimmer & Phelps

Dendroica petechia cienagae Zimmer & Phelps, 1944:14 (La Cienaga, sea level, between Ocumare de la Costa and Turiamo, Aragua, Venezuela). (AMNH)

Subspecific characters.—Compared with *aurifrons,* males brighter yellow below; throat and forehead more chestnut; chestnut streaks wider. Compared with *chrysendeta,* males darker and greener above; chestnut regions paler.

Distribution.—Coast of Carabobo and Aragua, north-central Venezuela, and small islands off Falcón.

Specimens examined.—Aragua (2).

Dendroica petechia castaneiceps Ridgway

Dendroica bryanti castaneiceps Ridgway, 1885:350 (La Paz, Lower California). (USNM)

Dendroica erithachorides hueyi van Rossem, 1947:50 (San Ignacio Lagoon, Pacific coast of Baja California). SDMNH

Subspecific characters.—Both sexes nearest *rhizophorae* but average slightly greener above; males with chestnut streaks less dense and narrower. Males with slightly longer tails (51.9–58.1, mean 55.9, $n = 13$) than *rhizophorae* (48.7–54.3, mean 51.0, $n = 9$).

Distribution.—Both coasts of Baja California from San Ignacio and Pond lagoons (Pacific coast) south to lat. 27°N.

Specimens examined.—Baja California (63).

Remarks.—Specimens from San Ignacio Lagoon ("*hueyi*") are fairly consistently dull and green above and pale below, but are within the range of variation of *castaneiceps* from elsewhere.

Dendroica petechia rhizophorae van Rossem

Dendroica erithachorides rhizophorae van

Rossem, 1935:67 (Tobari Bay, Sonora, Mexico). (SDNHM)

Subspecific characters. — Both sexes nearest *castaneiceps* but average slightly more yellow below (less greenish); males with chestnut streaks usually wider; males with slightly shorter tails (see above) than *castaneiceps.* Both sexes more yellow on the back and rump than the subspecies from Sinaloa to Honduras (below). Compared with *xanthotera,* males with slightly narrower chestnut streaks below; chestnut bib more sharpely defined.

Distribution. — Coastal Sonora from Tepopa Bay to Mazatlán, Sinaloa, Mexico. Intergrades with the next subspecies apparently at Mazatlán, Sinaloa.

Specimens examined. — Sonora (8).

Remarks. — Van Rossem (1935) stated that the "tail has more yellow than in *xanthotera*; more than in *castaneiceps.*" I found that the amount of yellow on the tail is too variable individually for identifying *castaneiceps* from *rhizophorae.* There is nearly complete overlap in measurements of exposed culmen of *rhizophorae* and *castaneiceps* (contra van Rossem 1935).

Dendroica petechia phillipsi, new subspecies

Holotype. — DMNH 36348, adult male, La Piñita de Jaltemba, El Islote, southwestern Nayarit, Mexico, 16 April 1955, collected by A. R. Phillips (original number 3903).

Subspecific characters. — Compared with *rhizophorae* and *xanthotera,* both sexes with greener back and rump; yellow below with slight greenish cast; edges of terials, wing coverts, and outer edges of rectrices greener. Chestnut streaks resemble *rhizophorae.*

Distribution. — Pacific coast from Sinaloa to Honduras. Intergrades with *rhizophorae* apparently at Mazatlán, Sinaloa; intergrades with *xanthotera* at San Lorenzo, Honduras.

Specimens examined. — Mexico: Sinaloa (7); Nayarit (16); Oaxaca (1); Chiapas (2); Honduras (4).

Etymology. — For Allan R. Phillips in recognition of his contributions to the taxonomy of birds.

Remarks. — Lowery & Monroe (1968) did not list breeding localities of *D. petechia* from the Pacific Coast of Mexico south of Nayarit. The species probably breeds along the shore of Colima (Schaldach 1963), is possibly a permanent resident of coastal Oaxaca (Binford 1989), and is a resident of coastal Chiapas (Alvarez 1964). The breeding status of the two males from Chiapas is unknown. One of seven old specimens from Mazatlán has a yellowish rump similar to *rhizophorae.* A male from San Lorenzo, Honduras, is green above but otherwise it is similar to specimens of *xanthotera.*

Dendroica petechia xanthotera Todd

Dendroica bryanti xanthotera Todd, 1924: 123 (Puntarenas, Costa Rica). (CM)

Subspecific characters. — Compared with *phillipsi,* both sexes more yellow on the back and rump; males with chestnut more extensive on head; ventral chestnut streaks wider; chestnut bib not sharpely defined. Compared with *aithocorys,* males with chestnut hood restricted and darker; ventral chestnut streaks narrower. Females with less chestnut below than *aithocorys.*

Distribution. — Pacific coast of Nicaragua and Costa Rica. Intergrades with *phillipsi* at San Lorenzo, Honduras.

Specimens examined. — Costa Rica (25).

Dendroica petechia aithocorys Olson

Dendroica petechia aithocorys Olson, 1980: 474 (5 miles east of La Honda, near Los Santos, Los Santos Providence, Panama). (USNM)

Subspecific characters. — Males nearest *xanthotera* but slightly more yellow above;

chestnut hood paler and extends into upper breast; chestnut streaks wider and less sparse. Compared with *iguanae,* males greener above; chestnut hood paler. Compared with *aequatorialis,* males with darker chestnut hood; upper breast not streaked with yellow. Females more yellow (less greenish) below and more heavily streaked with chestnut than *aequatorialis* and *xanthotera.*

Distribution.—Pacific coast of Panama from Chiriquí to Coclé including Isla Coiba and Azuero Peninsula. Intergrades with *aequatorialis* at Puerto Aguadulce.

Specimens examined.—(77); same specimens compared by Olson (1980).

Remarks.—Wetmore (1957) regarded birds from the above range as "intermediates between *aequatorialis* and *xanthotera,*" and he and Lowery & Monroe (1968) referred them to the former name. Specimens from Isla Coiba are slightly less streaked below than other specimens of *aithocorys.* More specimens from Isla Coiba have dorsal chestnut streaks than do other specimens of *aithocorys* but these differences are minor and inconsistent. Three adult males, three adult females, and one subadult male (all USNM) from Isla Brincanco are slightly duller green above and paler yellow below, and the females are slightly less marked with chestnut than other specimens of *aithocorys* from elsewhere.

Dendroica petechia iguanae Olson

Dendroica petechia iguanae Olson, 1980:475 (Isla Iguana, Los Santos Province, Panama). (USNM)

Subspecific characters.—Males nearest *aithocorys* but darker, greener (less yellow) above and below; darker chestnut hood; chestnut streaks more dense. Chestnut hood darker than *aequatorialis.* Females near *aithocorys* but more greenish (less yellow) below; average more heavily streaked below.

Distribution.—Isla Iguana, Los Santos Province, Panama.

Specimens examined.—(13); same specimens compared by Olson (1980).

Dendroica petechia aequatorialis Sundevall

Dendroeca petechia aequatorialis Sundevall, 1870:609 (Guayaquil, Ecuador [= Panama City, Panama]). Royal Natural History Museum, Stockholm (fide Gyldenstolpe 1926)

Subspecific characters.—Males nearest *aithocorys* but chestnut of the head region paler; upper breast streaked with yellow. Compared with *jubaris,* males duller yellow below; chestnut region of head forms a definite but suffused hood vs. a cap. Females nearest *jubaris* but less yellow below; more heavily streaked with chestnut below than *aithocorys.*

Distribution.—Pacific coast of the Province of Panamá and the Pearl Islands. Intergrades with *jubaris* at Río Majé.

Specimens examined.—(95); same specimens compared by Olson (1980); 20 others from Pearl Islands.

Remarks.—Thayer & Bangs (1905) and Wetmore (1946a) reported that many of the specimens from Isla San Jose, Pearl Islands, were golden-orange where the yellow plumage normally occurs. I found individual specimens of other subspecies, including examples in the *aestiva* group, with traces of orange feathers. The large number of entirely golden-orange birds from Isla San Jose cannot be explained.

Olson (1980) reported that males collected at the mouth of Río Majé show traces of yellow in the cheeks and that this may indicate intergradation between *aequatorialis* and *jubaris.* More noticeable in the Río Majé males is that the crown and cheeks are intermediate between these two subspecies in the hue of chestnut. Ventrally, the Majé specimens are more similar to *jubaris* than to *aequatorialis* in the hue and amount of chestnut streaks. The amount of yellow in the throats of the Majé series is also similar to that of *jubaris* but the yellow of the lower ventral regions is duller and thus similar to that of *aequatorialis.*

Dendroica petechia jubaris Olson

Dendroica petechia jubaris Olson, 1980:478 (Nuquí, [lat.] 5°40'N, Dept. Chocó, Colombia). (USNM)

Subspecific characters.—Compared to *aequatorialis,* males with dark chestnut crowns with remaining chestnut areas paler (tawny) and more suffused with yellow; chestnut hood absent; chestnut streaks wide and suffused on bright yellow ventral surface; distinct chestnut cap; throat yellowish. Females nearest *aequatorialis* but more heavily streaked with chestnut below; chestnut on head paler than other Pacific coast subspecies from Panama; more heavily streaked with chestnut below than *peruviana.*

Distribution.—Darién, Panama, south along the Pacific coast of Chocó, at least to Buenaventura, Valle del Cauca, Colombia.

Specimens examined.—(26); same specimens compared by Olson (1980).

Dendroica petechia peruviana Sundevall

Dendroeca petechia peruviana Sundevall, 1870:609 (Callao, Peru, and Guayaquil, Ecuador; type from Callao [?], fide Gyldenstolpe [1926]). RNHM (fide Gyldenstolpe 1926).

Subspecific characters.—Males nearest *jubaris* but crown less suffused with pale chestnut; cheeks, lores, and chin more yellow. Females with little to no ventral chestnut streaking.

Distribution.—Nariño, extreme southwestern coastal Colombia to northern coastal Peru, and possibly as far south as Lima.

Specimens examined.—Colombia: Nariño (4); Esmeraldas (2); El Oro (8); Ecuador (6).

Remarks.—The cheeks of a specimen from Nariño have some pale chestnut feathers; chestnut on the checks of two specimens from Esmeraldas is even paler.

Dendroica petechia aureola (Gould)

Sylvicola aureola Gould, in Darwin, 1839: 86 (Galápagos Islands)

Subspecific characters.—Nearest *peruviana* but males less heavily streaked and both sexes usually less bright yellow below.

Distribution.—Cocos Island and Galápagos Archipelago.

Specimens examined.—Cocos Islands (27); Galápagos Islands (90).

Remarks.—Plumage patterns in *aureola* resemble subspecies in the *petechia* group. However, specimens of *aureola* are more similar in size to birds of the *erithachorides* group (Wiedenfeld 1991).

Summary of *D. p. erithachorides* group

Generally, the chestnut streaks are narrower in northern males from the Pacific and Caribbean populations and are wider in most other populations. The chestnut on the hood and neck of males ranges from dark and forming (more or less) a hood in northern birds to paler and no distinct hood in southern populations from the Pacific coast and islands off western South America.

More specifically, northern populations of the Caribbean coast from Tamaulipas and Tabasco, Mexico (*oraria*), Yucatan to Nicaragua (*bryanti*), and from the Pacific coast from Baja California (*castaneiceps*), Sonora (*rhizophorae*), Sinaloa to Honduras (*phillipsi*), and Nicaragua to Costa Rica (*xanthotera*) have relatively narrower ventral chestnut streaks than other populations of the *erithachorides* group. Back color of the northernmost populations of Pacific coast (*castaneiceps*) is greener than *rhizophorae,* but it is more yellow than in *phillipsi,* the next subspecies to the south. Males from along the Pacific coast of western Panama (*aithocorys*) have more extensive chestnut hoods than *xanthotera,* the chestnut is darker in birds from Isla Iguana (*iguanae*), the chestnut is paler, with the upper breast being more yellow, in birds from the Provice of Panama (*aequatorialis*), and the chestnut is even paler, with more yellow in the upper breast, in birds from eastern Pamama to Buenaventura, Colombia (*jubaris*). Males from coastal southwestern Colombia to northern Peru (*peruviana*) have less chestnut and more yellow on the head than the other mainland populations of the Pacific coast. The populations of the Cocos and Galápagos islands (*aureola*) have still less chestnut on the head and neck, thus *aureola* is superficially similar to subspecies in the *petechia* group. Males from the Caribbean coasts of Costa Rica, Panama, and western Colombia (*erithachorides*) have darker chestnut heads than *bryanti,* but they are paler than birds from the Guajira Peninsula, Colombia (*chrysendeta*). Males from the Parajuaná Peninsula, Venezuela (*paraguanae*), are darker and greener above than *chrysendeta.*

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A NEW SPECIES OF *OCADIA* (TESTUDINES: BATAGURINAE) FROM SOUTHWESTERN CHINA

William P. McCord and John B. Iverson

Abstract.—A new species of batagurine turtle, *Ocadia glyphistoma,* purportedly from southwestern Guangxi Province, China, differs from *Ocadia sinensis* by having fewer broad neck stripes, bold dark markings on the ventral surfaces of the hind limbs, a distinctive medial notch in the tomium of the upper jaw, a broader carapace and plastron, a longer plastral forelobe, relatively shorter interpectoral, interabdominal, and interanal seams, and a relatively longer interhumeral seam. It differs from *Ocadia philippeni* by having bold dark markings on ventral surfaces of the hind limbs, no obvious wash of ventral pink to orange pigment, a distinctive medial notch in the tomium of the upper jaw, a broader shell, a relatively shorter plastron and bridge, and relatively shorter interpectoral, interabdominal, and interanal seams.

McCord & Iverson (1992) recently described a distinctive species of batagurine turtle (*Ocadia philippeni*) from Hainan Island, China, and compared that form with its only recognized congener, *Ocadia sinensis.* But during 1990 and 1991, Mr. Oscar Shiu of Hong Kong sent McCord a series of another distinct stripe-necked batagurine turtle from southwestern China with clear affinities to both *O. sinensis* and *O. philippeni* (Fig. 1). Univariate analysis of variance (Table 1) and discriminant function analysis (Fig. 2) demonstrated that these new turtles were similar, but morphometrically distinct from the latter two species, and so they are described herein as the third species of the genus *Ocadia* even though skeletal material is not yet available for definitive generic placement (e.g., McDowell 1964, Hirayama 1984, Gaffney & Meylan 1988). A study of the mitochondrial genome of all Asian batagurines is underway by J. W. Bickham, Iverson, and McCord to test this allocation.

Materials and Methods

Preserved material was borrowed from the American Museum of Natural History (AMNH), the British Museum of Natural History (BMNH), the California Academy of Sciences (CAS), the Field Museum of Natural History (FMNH), the Museum of Comparative Zoology at Harvard (MCZ), the Museum of Vertebrate Zoology at Berkeley (MVZ), the Florida Museum of Natural History at the University of Florida (UF), and the United States National Museum (USNM), and living material was available in McCord's private collection (WPM). Methods of measurement and analysis follow McCord and Iverson (1991). Character abbreviations are in Table 1. All measurements are in mm.

Specimens examined included: *Ocadia philippeni*: China, Hainan Island (UF 80765–66 [holotye and paratype]; WPM 1–7, alive). *Ocadia sinensis*: "Laos" (UF 80817–19 [3 specs]; WPM 1, alive), Vietnam (BMNH 1903.7.2.1; MCZ 21051), Taiwan (FMNH 121230–32, 127172–73, 127175–78, 127180, 195492, 199750–51), China, Hainan Island (AMNH 30173, 30176–78, 30183–84, 30186–91, 30193, 30195–96; FMNH 6613 [formerly AMNH 30194]; MCZ 20687; MVZ 23940; UF 80816 [1 skeleton]), China, mainland (BMNH 1947.3.5.26 [holotype]; MVZ 23943; WPM 1–2, alive), and No Data (BMNH 1947.3.4.24, cotype of *Emys Bennettii*). *Ocadia glyphistoma*: China (UF 84818 [holotype]; WPM 1–9, alive).

Results and Discussion

Ocadia glyphistoma, new species
Guangxi stripe-necked turtle
Fig. 1

Holotype.—UF #84818, an adult male, preserved in alcohol; reported to have been collected near the Vietnam border southwest of Nanning, Guangxi Province, China, but purchased from local people near Nanning by Mr. Oscar Shiu, in the spring of 1991.

Diagnosis.—A medium-sized species of *Ocadia* (Table 2) most similar to *O. philippeni,* with a wide, basically tricarinate carapace having a prominent middorsal keel and weak lateral keels; an unhinged plastron; a medial notch in the tomium of the upper jaw (unnotched in other *Ocadia*); usually four yellow, black-bordered lateral head and neck stripes separated by narrow brown stripes (at least eight black-bordered, narrow, cream to yellow stripes in *O. sinensis*); the ventral surfaces of shell and skin not washed with pink, orange, or salmon (so colored in *O. philippeni*); the ventral surfaces of thighs boldly marked with dark pigment (no such dark markings in O. *sinensis* or O. *philippeni*); a relatively long plastral forelobe (maximum length averages 41% of carapace length [CL] in female and 37% in male *O. glyphistoma,* 42% and 39% in *O. philippeni,* and 38% and 36% in *O. sinensis*); a relatively long interhumeral seam (seam length averages 8.8% of CL in female and 8.5% in male *O. glyphistoma,* 8.6% and 6.2% in *O. philippeni,* and 5.6% and 5.3% in *O. sinensis*); a relatively short interpectoral seam (length averages 18% of CL in female and 17.5% in male *O. glyphistoma,* 21% and 20% in *O. philippeni,* and 21% and 20% in *O. sinensis*); a relatively short interabdominal seam (length averages 21% of CL in female and 22% in male *O. glyphistoma,* 25% and 23% in *O. philippeni,* and 26% and 23.5% in *O. sinensis*); and a relatively short interanal seam (length averages 9.6% of CL in female and 8.5% in male *O. glyphistoma,* 11.2% and 12.4% in *O. philippeni,* and 10.6% and 10.1% in *O. sinensis*) [see also Table 2 and Fig. 3].

Description (based on two adult females, five adult males, one subadult female and two subadult males, including the holotype).—Carapace length to at least 199 mm in males and at least 180 mm in females, elliptical, moderately tricarinate with a prominent medial keel and weak lateral keels, moderately domed (maximum shell height/CL = 0.338 to 0.435; mean = 0.41 for females, 0.38 for males), widest at marginal M7 or M8 (maximum carapace width/CL = 0.74 to 0.80 for females and 0.68 to 0.75 for males; means = 0.77 and 0.72, respectively), with a slightly serrated posterior margin, and with moderately obvious growth annuli (least obvious in old individuals). M1, 7, 8, and 9 largest (along carapace margin), approximately coequal in length; M11 smallest; M9 tallest; M9–11 distinctly flared. Cervical scute small, usually longer than wide, wider posteriorly than anteriorly, and indented medially along the posterior margin. Vertebrals V2–5 wider than long; V1 usually wider than long, but not contacting seam between M1 and M2; V5 usually not even close to contacting M10. Prominent medial keel most pronounced on V3 and V4; lateral keels weak (usually) to absent, but if present, most pronounced on costal C3. Carapace dark brown to nearly black, with seams more darkly marked; ca-

Fig. 1. (color). Head and plastral patterns of *Ocadia glyphistoma* (compare with color figures of *O. sinensis* and *O. philippeni* in McCord and Iverson, 1992). Carapace length of male in upper left is 118 mm; that of male in lower left is 180 mm; and that of female on right is 180 mm.

Table 1.—Results of univariate analysis of variance of residuals of 16 characters versus carapace length for three species of *Ocadia* (sexes analyzed separately). Differences are coded by first letter of species name; i.e., "s-g" indicates a significant difference between *sinensis* and *glyphistoma* for that character for the indicated sex. Methods of character measurement are in McCord and Iverson (1991).

Character	Males		Females	
	F	Differences	*F*	Differences
Maximum carapace width (CW)	3.72*	s-g; p-s	2.64	—
Maximum carapace height (CH)	1.46	—	0.01	—
Maximum plastron length (PL)	0.90	—	2.95	—
Maximum forelobe length (FL)	4.82*	p-g; p-s	9.03**	p-s
Maximum hindlobe length (HL)	0.82	—	4.01*	s-g; p-s
Plastral width (PW1)	2.30	—	1.62	—
Plastral width (PW3)	9.38***	p-g; p-s	4.24*	p-s
Plastral width (PW4)	10.34***	p-g; p-s	2.03	—
Bridge length (BL)	1.90	—	3.30*	p-g
Gular width (GW)	0.69	—	0.22	—
Gular length (GL)	4.44*	p-g; p-s	0.60	—
Interhumeral seam length (IH)	8.19**	p-g; s-g	4.95*	p-s
Interpectoral seam length (IP)	5.67**	p-g; s-g	2.77	s-g
Interabdominal seam length (IAB)	1.49	—	8.41**	p-g; s-g
Interfemoral seam length (IF)	11.31***	p-g; p-s	1.16	—
Interanal seam length (IAN)	17.08***	all	1.44	—

* $0.01 < P < 0.05$.
** $0.001 < P < 0.01$.
*** $P < 0.001$.

rinae usually not distinctly colored. A black notch on ventral posterolateral portion of each marginal, sometimes covering more than one-half of some marginals.

Maximum plastron length shorter than carapace length (PL/CL = 0.95–0.98 in females; 0.87 to 0.95 in males). Plastron slightly upturned anteriorly, with no hinge present. Plastral forelobe width (PW1) at level of junction of humeropectoral seam and lateral plastral margin relatively wide (PW1/CL = 0.38 to 0.44 in females and 0.36 to 0.42 in males; means = 0.42 and 0.38, respectively). Anterior width of plastral hindlobe (PW3: at lateral junction of abdominofemoral seam) relatively wide (PW3/CL = 0.45 to 0.47 in females and 0.40 to 0.43 in males; means = 0.46 and 0.42, respectively). Plastral hindlobe with relatively deep anal notch. Bridge moderately long (BL/CL = 0.37 to 0.39 in females and 0.33 to 0.37 in males; means = 0.38 and 0.35, respectively); single large axillary and inguinal scutes on each bridge. Average plastral formula (see also Table 2 and Fig. 1 for diagnostic ratios): interabdominal seam (IAB) > interpectoral seam (IF) ≥ interfemoral seam (IP) ≫ gular length (GL) ≫ interanal seam (IH) ≥ interhumeral seam (IAN). Plastron dark yellow-cream (Fig. 1), with a large (covering up to half of scute), black blotch on each scute (primarily on older portion of scute). A smaller black blotch also occurring on bridge area of pectoral and abdominal scutes, and on axillary (usually) and inguinal scutes.

Head narrow; upper jaw unhooked, but with medial notch; triturating surfaces of medium width. Very small tubercles evident between angle of jaw and tympanum. Dorsum of head uniform dark olive-brown. Four (or sometimes five) narrow longitudinal black-bordered yellow stripes on side of head, separated by narrow brown or olive stripes; all four originating at orbit, upper two passing above tympanum, third from

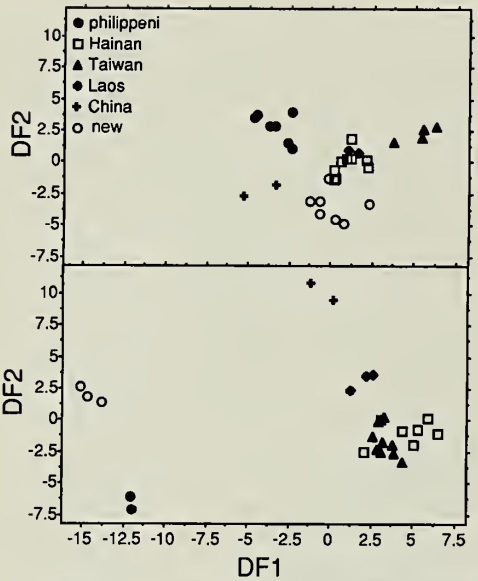

Fig. 2. Plot of first two canonical axes for specimens of *Ocadia* based on discriminant function analysis of the residuals of 16 characters (listed in Table 1; method as in McCord and Iverson, 1991) for males (top) and females. First and second axes account for 42.7% and 30.5% of variation, respectively, for males, and 66.0% and 20.2% for females. Geographic locations represent populations of *O. sinensis.*

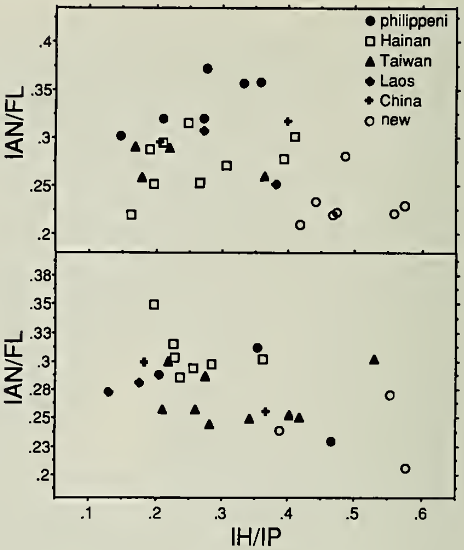

Fig. 3. Bivariate plot of relationships among males (top) and females of species of the genus *Ocadia* based on the characters IH/IP (interhumeral seam length/interpectoral seam length) and IAN/FL (interanal seam length/maximum plastral forelobe length). Geographic locations represent populations of *O. sinensis.*

top passing through tympanum and sometimes broken anteriorly, and lower stripe passing below tympanum. All stripes extending posteriorly to base of neck. Anterior continuations of stripes from orbit to nares variably obvious. Chin yellow, with variable vague black mottling (sometimes forming circles), but with seven black-bordered yellow longitudinal stripes (often discontinuous) extending from level of tympanum to base of neck. Tomia yellow with variable thin black markings. Black horizontal line across eye (through pupil); iris yellow-green.

Anterior surface of antebrachium covered with large, imbricate scales, the largest of which are sickle to spade-shaped; largest scales on hindlimb at heel, but much smaller than largest forelimb scales. Upper parts of limbs and tail covered with fine scales. Exposed parts of forelimbs dark olive-gray to nearly black, with faded yellow or orange or cream stripes (often discontinuous) extending outward from base of limbs variable distances onto limb; stripes barely visible on dorsal surface of antebrachium, but very obvious on ventral aspect of limbs. Stripes on posterolateral margins of each limb always obvious and extending at least to heel. Recessed areas of axillary region and between neck and forelimbs boldly marked with alternating dark gray and yellow to faded orange stripes. Recessed areas of inguinal region mostly yellow, but with some vague faded, dark gray blotching. Tail moderately long, gray-black dorsally, with a pair of vague longitudinal dorsolateral dark brown stripes extending along full length of tail; gray-black ventrally, but flecked with yellow or cream, and with a pair of longitudinal ventrolateral cream to light brown stripes extending the full length of the tail.

Males with a slightly concave plastron; females with a flat plastron. Males with a longer tail than females; vent at level of pos-

Table 2.—Morphometric characters useful in discriminating among species of the genus *Ocadia*. Character abbreviations are interhumeral seam length (IH), interpectoral seam length (IP), interanal seam length (IAN), interabdominal seam length (IAB), and maximum plastral forelobe length (FL). Values are means followed by range in parentheses. Common alphabetic superscripts following ranges indicate species means for that character that are significantly different ($P < 0.05$) by Fisher's (protected) least significant difference test.

Sample	Sex	*n*	Carapace length (mm)	IH/IP	IAN/FL	FL/IP	FL/IAB
O. philippeni							
Hainan	M	7	169.0 (113–199)	0.31 (0.15–0.60)^{a}	0.32 (0.22–0.37)^{d}	1.92 (1.77–2.36)^{f}	1.73 (1.39–1.94)^{k}
	F	2	216.7 (214–219)	0.41 (0.35–0.46)	0.27 (0.23–0.31)	1.99 (1.99–1.99)^{h}	1.66 (1.55–1.81)^{l}
O. sinensis							
Hainan	M	9	125.3 (107–155)	0.27 (0.16–0.41)	0.27 (0.22–0.32)	1.81 (1.66–1.97)	1.51 (1.30–1.65)
	F	7	146.8 (114–220)	0.26 (0.20–0.36)	0.31 (0.29–0.35)	1.82 (1.68–2.04)	1.45 (1.29–1.63)
Taiwan	M	4	177.7 (155–200)	0.23 (0.17–0.37)	0.27 (0.26–0.29)	1.86 (1.74–1.94)	1.53 (1.43–1.70)
	F	9	201.0 (176–235)	0.33 (0.21–0.53)	0.27 (0.25–0.30)	1.88 (1.76–2.10)	1.45 (1.37–1.59)
China	M	2	133.5 (117–150)	0.30 (0.21–0.40)	0.31 (0.30–0.32)	1.82 (1.74–1.91)	1.56 (1.52–1.59)
	F	2	261.0 (251–271)	0.28 (0.18–0.37)	0.28 (0.26–0.30)	1.82 (1.73–1.91)	1.43 (1.30–1.57)
"Laos"	M	2	141.4 (136–147)	0.33 (0.27–0.38)	0.28 (0.25–0.31)	1.81 (1.74–1.88)	1.74 (1.53–1.95)
	F	3	223.1 (195–258)	0.17 (0.13–0.20)	0.28 (0.27–0.29)	1.74 (1.67–1.81)	1.45 (1.37–1.53)
Total	M	17	140.5 (107–200)	0.27 (0.16–0.41)^{b}	0.28 (0.22–0.32)^{d}	1.82 (1.66–1.97)^{g}	1.54 (1.30–1.95)^{jk}
	F	21	191.8 (114–271)	0.28 (0.13–0.53)^{c}	0.28 (0.25–0.35)^{e}	1.84 (1.67–2.10)^{i}	1.45 (1.29–1.63)^{l}
O. glyphistoma							
China	M	7	169.9 (102–245)	0.49 (0.42–0.57)^{ab}	0.23 (0.21–0.28)^{d}	2.11 (1.89–2.25)^{fg}	1.71 (1.52–1.90)^{j}
	F	3	152.9 (121–180)	0.51 (0.39–0.58)^{c}	0.24 (0.21–0.27)^{e}	2.36 (2.03–2.85)^{hi}	1.95 (1.83–2.04)^{l}

terior carapace margin in males; anterior to it in females.

Etymology.—From the Greek *glyphis* (carved or notched) and *stoma* (mouth), in reference to the species' distinctively notched upper jaw.

Other material.—Two adult females, four adult males, one subadult female, and two subadult males (all from type locality, but not designated as paratypes); specimens all alive in the collection of William P. McCord (WPM 1-9), and to be deposited on their death in the UF collection.

Distribution.—Known only from the region of the type locality. The precise locality could not be determined since the turtles were collected by local people.

Remarks.—Our studies of the genus *Ocadia* have clarified the provenance of the type material of *O. sinensis* and *O. bennettii,* as well as their taxonomic relationship. Based on the original description and illustrations of *Emys bennettii* Gray (1844, 1855) and on Iverson's examination of one of the cotypes (BMNH 1947.3.4.24), we concur with Günther (1864:27) that *Emys bennettii* is synonymous with *Ocadia sinensis.* In addition, discriminant function analysis performed with that cotype as an unknown suggested that it originated on Taiwan and not on Hainan Island or the Chinese mainland (see range map in Iverson 1992). Measurements from the holotype of *O. sinensis* (BMNH 1947.3.5.26) were also analyzed and the specimen was confirmed to have originated on the Chinese mainland.

We can also clarify somewhat the distribution of the genus *Ocadia* in Vietnam and adjacent China. Based on the descriptions of Siebenrock (1903), Bourret (1941; with illustrations), and Petzold (1963), *O. sinensis* is known from at least as far west as the Red River basin in Vietnam. Although we have not examined the specimens on which those descriptions were apparently based (e.g., Rijksmuseum van Natuurlijke Histoire of Leiden 4750, and Zoologisches Institut und Museum of Hamburg R00414 and R00416), the illustrations in Bourret (1941) are clearly of *O. sinensis.* In addition, MCZ 21051 from Phuc Son, Vietnam, and BMNH 1903.7.2.1 from "Annam" are also *O. sinensis.* Furthermore, given that Bourret (1941) called this species the most common emydid in the Tonkin (Red) delta region, and that Felix (1965) also found it to be common in the area west of Hanoi, its occurrence in at least the Red River basin in Vietnam seems unquestionable. However, this suggests that the range of *O. glyphistoma* in southwestern Guangxi Province, China, lies wholly within the range of *O. sinensis,* and that the two species may be broadly sympatric. Indeed, *O. sinensis* has been reported to occur only 40 km north of Nanning, Guangxi (at Wuming) by Lin (1984, in Buskirk, 1989). Unfortunately, until more museum material for this genus from southwestern China and adjacent Vietnam is available, the precise distributions of the individual species will remain uncertain.

Acknowledgments

This species was collected through the efforts of Oscar Shiu of Hong Kong. Curators and collection managers of the institutions listed in the text (especially D. L. Auth of UF) facilitated specimen loans. L. Carbone conscientiously typed early drafts of the manuscript. Support for Iverson was provided by Earlham College, the Joseph Moore Museum of Natural History, The National Science Foundation (RFO 9021844 and DUE 9351508), and his family.

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A NEW SPECIES OF MONTANE PITVIPER (SERPENTES: VIPERIDAE: *BOTHROPS*) FROM COCHABAMBA, BOLIVIA

Michael B. Harvey

Abstract.—*Bothrops jonathani* is a new species described from the Bolivian altiplano and adjacent xeric mountain sides, an area previously unknown to be inhabited by any species of pitviper. The new taxon is distantly allopatric from its most phenotypically similar congener *B. alternatus.* The new species is distinguished from other *Bothrops* by higher scale counts, relatively short hemipenial spines, a unique color pattern, and distinct prelacunal and second supralabial.

Many of the forty-one (Campbell & Lamar 1989, 1992) currently recognized species of South American crotalines are rarely collected and remain poorly known despite recent advances in their study. South American species formerly referred to *Bothrops* (sensu lato) were placed in five genera (Burger 1971, Pérez-Higareda et al. 1985, Campbell & Lamar 1989). Evidence that three of these genera are monophyletic has recently come from biochemical and anatomical characters (Werman 1992), while the same analysis showed that *Bothrops* (sensu Burger 1971) is polyphyletic if *Bothriopsis* is recognized. Within *Bothrops* (sensu stricto), evidence in support of two monophyletic lineages referred to loosely as the "*neuwiedi*" and "*atrox*" groups was provided (Werman 1992). However, these groups have yet to be formally defined or diagnosed.

Although several crotalines occur at high elevations in the Andes, most species inhabit cloud forest or wet, upper montane forest. Only two species, *Bothrops lojanus* and *B. ammodytoides* occur in relatively xeric habitats above 2000 m and no pitvipers are known from the altiplano of Peru, Bolivia, and Argentina. Incidental to research (Harvey & Smith 1993, 1994) in the cis-Andean cloud forests of Santa Cruz and Cochabamba, Bolivia, a small herpetological collection was made in the altiplano and adjacent intermontane valleys of Cochabamba. Among material collected were two pitvipers herein described as a new species.

Methods

A string and meter stick were used to measure snout-vent length (SVL), tail length (TL), and tail circumference (TC) at the level of the sixth subcaudal. With a dial caliper, distances were measured to the nearest 0.1 mm from the antero-ventral corner of the skin surrounding the eye to the caudal border of the pit (EP), the antero-dorsal border of the skin surrounding the eye to the center of the nostril (EN), the caudo-dorsal to antero-ventral edges of the skin surrounding the eye (ED), and from the tip of the snout to the skin covering the caudalmost tip of the articular (HL). Nomenclature for the hemipenis is that of Dowling & Savage (1960). Scale counts of the new taxon were compared with ranges of other species reported by Campbell & Lamar (1989) and specimens examined in this study (Appendix).

Fig. 1. *Bothrops jonathani,* female paratype. UTA R-34564, SVL 540 mm. Photo by Eric N. Smith.

Bothrops jonathani, new species
Figs. 1–2

Holotype.—Museo de Historia Natural "Noel Kempff Mercado" (MNK) R-1000, adult male collected on Highway 4 on 17 Jan 1992 by M. B. Harvey, approximately 35 km N (by road) of El Empalme, Provincia Carrasco, Departamento de Cochabamba, approximately 2800 m (17°45′S, 65°00′W).

Paratype.—The University of Texas at Arlington (UTA) R-34564, adult female collected on 30 Dec 1991 by M. B. Harvey and E. N. Smith on Highway 4, 97 km S (by road) of Cochabamba, 3220 m.

Diagnosis.—*Bothrops jonathani* is distinguished from all other species of *Bothrops* by the following combination of characteristics: (1) prelacunal and second supralabial distinct; (2) high numbers of supralabials, intersupraoculars, and mid-body scale rows; (3) hemipenial spines two-thirds length of adjacent subcaudals; (4) anterior supralabials with distinctive pattern; (5) paraventral spots diffuse; (6) gular stripes short.

Description of holotype.—Rostral subtriangular, about as wide as tall, about as wide as mental; nasal distinctly divided both above and below the naris; loreal single, bound dorsally by canthal; prefoveals 6/6; subfoveals in single row, increasing posteriorly to four rows of interoculabials; postfoveals 2/2; lacunal not contacting supralabials; preoculars 2/2; upper preocular elongate and contributing anteriorly to canthus; lower preocular squarish; suboculars 2/2, the first teardrop-shaped, the second elongate and crescent-shaped; postoculars 2/2; supralabials 11/12; infralabials 14 (right side incomplete, see remarks), first pair contacting medially; mental much broader than long; chin shields elongate, contacting first three infralabials; gulars in five rows between chin shields and first ventral; seven rows of gulars separating first ventral from infralabials; two internasals; canthals 1/1,

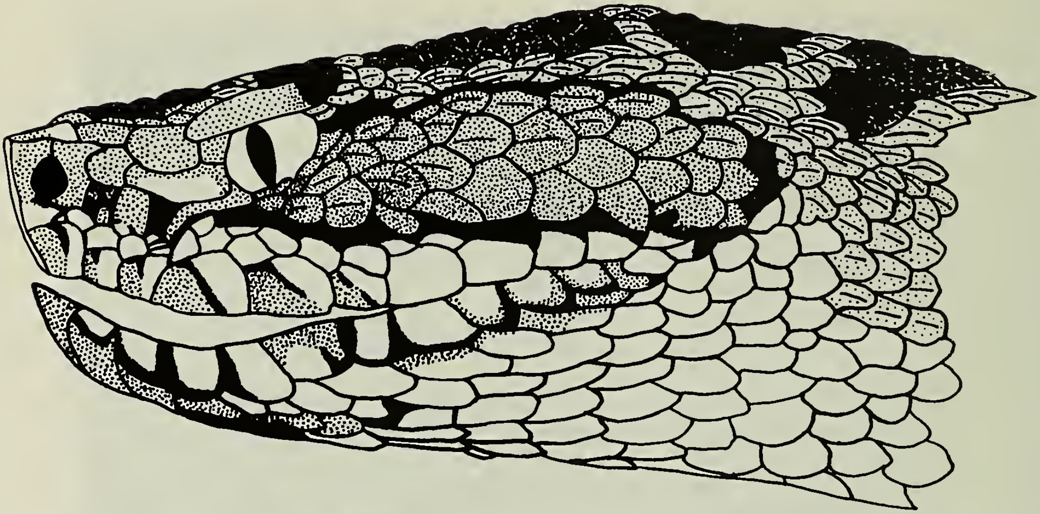

Fig. 2. Facial pattern of female paratype of *Bothrops jonathani.* UTA R-34564, Head Length 30.7 mm.

separated posteriorly by seven intercanthals; supraoculars about twice as long as wide, separated caudally by 10 intersupraoculars; dorsals 31–33–23; ventrals 166; anal entire; subcaudals 39, all divided; supra-anals seven; tail spine as long as adjacent five subcaudals; dorsals covering anterior 25% of tail spine.

Dorsal scales three times as long as wide anteriorly becoming wider posteriorly, only about 1.5 times as long as wide on tail; dorsal scales strongly keeled; paraventral row of scales smooth to very weakly keeled posteriorly, noticeably keeled on tail posterior to subcaudal 16; paraventrals about twice as wide as adjacent dorsal scales; most dorsal head and temporal scales strongly keeled; internasals, canthals, and supraoculars smooth; scale row dorsal to supralabials smooth.

Hemipenis (left): subcylindrical and bilobed; bifurcation of sulcus spermaticus at level of third subcaudal; bifurcation of lobes at sixth subcaudal; distribution of large to small keratinized spines asymmetrical on sulcate aspect of hemipenis, extending from level of first subcaudal along lateral surface, from level of third subcaudal on medial surface; largest spines on medial and lateral surfaces 2 mm or ⅔ length of adjacent subcaudals; spines grading to finely papillate calyces at level of eighth subcaudal; papillae on calyces present only where ridges join; ridges of calyces extending medially to become lips of sulcus; lips of sulcus spinulate and papillate; asulcate surface of hemipenis covered in small and inconspicuous spines below bifurcation of lobes.

Color in preservative (ethanol after buffered formalin): Facial color pattern complex; broad, dark brown postocular band edged in black and extending from ventral and caudal borders of eye to enclose posterior border of supralabial 9, most of supralabials 10–12, and two scale rows caudal to the rictus, extending across the adjacent infralabials and four rows of gulars; white stripe anterior to postocular band and extending from ventral edge of supralabial 10 to subfoveal region and including part or all of supralabials 4–11; dorsocaudal corners of supralabials 1–6 white to grey; remainder of these scales dark tan; ventral border of prenasal white, edged in black; preocular, foveal, and nasal regions dark tan; ventral surface of head white with black and smoke-grey markings; smoke-grey stripes on gulars between chin shields and infralabials extending from level of infralabial 9 to include first 3 infralabials and mental; infralabials

Table 1.—Comparison of selected diagnostic characteristics of certain Bolivian and Argentinian *Bothrops*.

Characteristic	*B. jonathani*	*B. alternatus*	*B. neuwiedi*	*B. ammodytoides*
Supralabials	9–12	8–10	7–10	8–11
Intersupraoculars	10–12	8–13	6–9	7–11
Mid-body scale rows	30–33	24–37	21–29	23–25
Subfoveal row of scales	present	present	absent	absent
Rostral	normal	normal	normal	elongate
Lengths of hemipenial spines	⅔ subcaudals	⅔ subcaudals	>1 subcaudal	not examined
Gular stripes	short	long	short or absent	short
Anterior supralabials	patterned	without pattern	without pattern	without pattern
Paraventral spots	diffuse, not on ventrals	defined, overlapping ventrals	diffuse to somewhat defined, overlapping ventrals	very diffuse, overlapping ventrals

10–12 grey; other infralabials white and edged in black; most white gulars edged in black posteriorly, rarely immaculate.

Ground coloration of ventrals white; a smoke-grey ventral pattern beginning anteriorly as a medial stripe on first 20–30 ventrals but becoming many, staggered bands posteriorly; ventrals mostly smoke-grey caudally; subcaudals mostly smoke-grey becoming uniformly smoke-grey by subcaudal 27; tail spine smoke-grey.

Dorsal ground coloration dark tan; 34 pairs of large, dark brown blotches edged in cream meeting or staggered mid-dorsally; mid-dorsal blotches mostly rectangular, but C-shaped caudally; 49 small, dark brown blotches on flanks and sides of tail; most anterior blotches occupying dorsals 6–9 and 12–22; about 80 diffuse black blotches covering paraventrals and dorsals 1–2, but paraventrals and dorsals 1–2 never completely black; large medial blotch occupying most of frontorostrals; parallel dark stripes beginning on posterior ⅓ of supraoculars and extending caudally onto neck.

Variations.—The female paratype is similar to the holotype with some noteworthy differences. The nasals are not completely separated dorsal to the nares. A large preocular is divided into two scales, and the smaller preocular is fused to the supralacunal. There are 5/5 prefoveals, no postfoveals, 5/3 suboculars owing to fragmentation of the crescent-shaped subocular, 3/3 postoculars, 9/11 supralabials, 13/14 infralabials, 8 intercanthals, 12 intersupraoculars, 28-30-21 dorsals, 175 ventrals, 37 subcaudals, and 26 dentary teeth. (Palatine and pterygoid teeth were not counted.) The tail spine is laterally compressed but bluntly rounded rather than pointed and 1.5 times as wide as the tail spine of the holotype.

Dorsal and ventral colors of the paratype are similar to those of the holotype although some differences in pattern exist. A broad postocular stripe reaches the rictus, but does not extend onto the infralabials and gulars as in the holotype. Parallel stripes on the top of the head are broken into four blotches, a pair covering the caudal one-third of the supraoculars and 6/5 intersupraoculars, two pairs in the parietal and occipital regions, and two crescent shaped blotches on the neck. There are 30 mid-dorsal blotches and 49 lateral blotches, with the first blotches occupying dorsals 5–9 and 11–21.

Measurements: (Measurements of holotype followed by those of paratype in parentheses) SVL 540 (540), TL 80 (60), TC 41 (28), HL 32.7 (30.7), EP 2.5–1.8 (1.8–1.9), EN 6.6–6.6 (6.3–6.4), ED 3.5–4.0 (3.8–4.0).

Remarks.—The holotype had been run over by an automobile damaging the head so that measurements from the eye to the pit and the eye diameter are approximate. The caudalmost supralabials have been lost

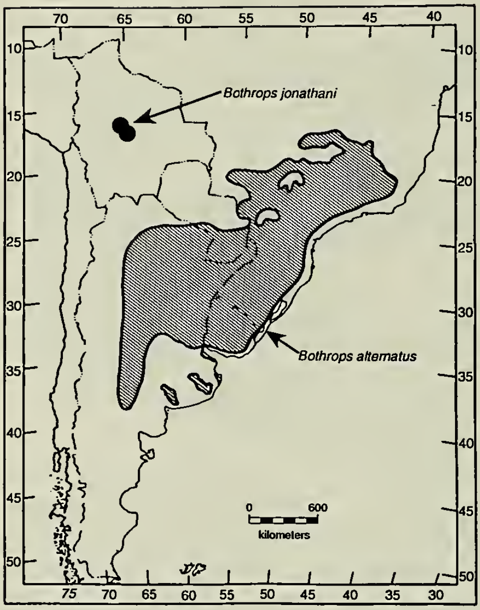

Fig. 3. Distribution of *Bothrops jonathani* and its presumed closest relative, *B. alternatus.* (Distribution of latter species after Campbell & Lamar 1989.)

on the right side; only twelve remain. Some teeth may be missing, but 4 palatine, 12 pterygoid, and 16 dentary teeth remain.

Distribution.—Bothrops jonathani is known from two localities at 2800 and 3220 m in Cochabamba (Fig. 3). Low, xeric-adapted shrubs cover the rocky hillsides where the holotype was found dead on the road. The paratype came from an area typical of the Bolivian altiplano: a dry, rocky grassland, largely devoid of bushes except around dry stream beds. Both specimens were found on sunny days in the afternoon. Air temperature was 27°C when the paratype was collected.

Etymology.—The specific epithet is a patronym for Jonathan A. Campbell in recognition of his considerable contributions to the biology of neotropical pitvipers.

Comparisons.—Bothrops jonathani is most similar to *B. alternatus.* In addition to having fewer supralabials, *B. alternatus* exhibits a distinctive color pattern that readily distinguishes it from *B. jonathani.* In *B. alternatus,* stripes extending from the mental reach the level of the ventrals or, more often, to the angle of the jaw. These stripes extend only about two-thirds as far in *B. jonathani.* The first six supralabials of the new species are dark brown, but edged dorsocaudally in white to pale grey (Fig. 2); whereas, the same scales in *B. alternatus* are either uniformly pale or diffusely pigmented but always lack a definite pattern. In *B. alternatus,* the postocular stripe is edged dorsally in cream. However, the postocular stripe grades abruptly to the dark tan ground coloration of the dorsum in *B. jonathani.* Finally, *B. alternatus* has a row of well defined spots on the lateral edges of the ventrals, the paraventrals, and one to two rows of dorsals above the paraventrals. In *B. jonathani,* these ventrolateral spots are diffuse and do not extend onto the ventrals.

Most scale counts are higher in *B. jonathani* than in either *B. neuwiedi* or *B. ammodytoides* (Table 1). Additionally, *B. ammodytoides,* and *B. neuwiedi* lack a row of subfoveals. In *B. ammodytoides* the rostral is vertically elongated so that the snout is upturned; a normal rostral occurs in the other species. Finally, in *B. neuwiedi* the largest hemipenial spines are two to three times as long as those of *B. jonathani.*

Five additional species of *Bothrops* occur in Bolivia, but are unlikely to be confused with *Bothrops jonathani.* The wet forest inhabitant *B. microphthalmus* differs from the former by having transverse cross-bands and by usually lacking a dorsal head pattern. Numbers of intersupraoculars, supralabials, infralabials, and mid-body scale rows are lower in *B. microphthalmus* than in *B. jonathani. Bothrops atrox, B. brazili, B. jararacussu,* and *B. sanctaecrucis* possess lacunalabial scales, whereas *B. jonathani* posses a distinct lacunal and second supralabial. As for *B. microphthalmus,* these species generally posses fewer numbers of intersupraoculars, supralabials, infralabials, and mid-body scale rows.

Within Bolivia, *Bothrops jonathani* is likely only to be confused with *B. neuwiedi.* However, the considerably more similar species *B. alternatus* reaches northern Argentina and may eventually be found in Bolivia (Fig. 3). Neither *B. alternatus* nor *B. neuwiedi* have been reported above 700 m and are almost certainly not sympatric with *B. jonathani*. *Bothrops neuwiedi* often occurs in dry areas, similar in this respect to the rain-shadow valleys and dry altiplano where *B. jonathani* occurs; but *B. alternatus* is found in deciduous forests and often associated with swampy areas, riparian situations, and generally more mesic habitats (Campbell & Lamar 1989) than the dry grasslands and desert scrub where *B. jonathani* was collected. Finally, a third similarly patterned species could eventually prove to be sympatric with *B. jonathani*. *Bothrops ammodytoides* also occurs in areas of montane desert scrub and reaches elevations of 2000 m in the Andes of Argentina (Campbell & Lamar 1989).

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Appendix

Specimens Examined

Specimens examined are followed by collection locality in parentheses. Abbreviations refer to American Museum of Natural History (AMNH), Chicago Field Museum of Natural History (FMNH), Harvard Museum of Comparative Zoology (MCZ), National Museum of Natural History (USNM), the Museo de Historia Natural "Noel Kempff Mercado," Santa Cruz, Bolivia (MNK), the University of Texas at Arlington Collection of Vertebrates (UTA).

Bothrops alternatus (25): BRAZIL: Rio Grande do Sul; UTA R-32427. São Paulo; FMNH R-2620, 171265, 171272, 171281–82, 171289, 171298. SE Brazil; MCZ R-17734, 17748–51. PARAGUAY: Central; UTA R-2848, 5602, 7484–85, 7573, 9721. URUGUAY: Cerro Largo; FMNH R-12344. Treinta y Tres; FMNH R-10595. UNKNOWN (reportedly from Argentina): UTA R-4999, 6306, 6789. UNKNOWN: UTA R-32420.

Bothrops ammodytoides (10): ARGENTINA: Buenos Aires; FMNH 10830, 10832. ARGENTINA: Chubut; MCZ 150292. La Roja; USNM 73421. ARGENTINA: Mendoza; FMNH 9994, MCZ 58104–07. San Luís; UTA R-16334.

Bothrops microphthalmus (1): ECUADOR: Zamorra; UTA R-23530.

Bothrops neuwiedi (19): ARGENTINA: Tucumán; FMNH 229950. BOLIVIA: Santa Cruz; AMNH 36008–09, MNK 124, 168, 178, 189, 197, 475. BRAZIL: Goiás; UTA 28232. Minas Gerais; FMNH 171255. Paraná; MCZ 112528. São Paulo; FMNH 171277, MCZ 112526. PARAGUAY: UTA R-2849, 5603, 9834–35. URUGUAY: Lavelleja; 7601.

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A NEW SPECIES OF *PLECTROHYLA* (ANURA: HYLIDAE) FROM A PREMONTANE RAINFOREST IN NORTHERN HONDURAS

Larry David Wilson, James R. McCranie, and Gustavo A. Cruz

Abstract.—A new species of *Plectrohyla, P. chrysopleura,* from moderate elevations in the Cordillera Nombre de Dios of northern Honduras is described and illustrated, as is its tadpole. Its combination of prominent golden yellow flashmarks, blunt prepollex, moderate size, vocal slits present in males, spatulate teeth, and weakly to moderately tuberculate dorsal surfaces easily distinguishes it from the other species of *Plectrohyla.* Several problems with a recent phylogenetic analysis of the genus *Plectrohyla* are noted and a phylogenetic reanalysis indicates that the new species is the one closest to the ancestral stock of the genus.

Field work in the Quebrada de Oro region of northern Honduras continues to uncover herpetological novelties. The first trip was in June, 1980, and since that time, we have described a new genus and five new species of anurans from this area in the central portion of the department of Atlántida (McCranie & Wilson 1986; McCranie, Savage, & Wilson 1989; McCranie, Wilson, & Williams 1989; Savage et al. 1988). Recently, a sixth new anuran described below was collected. Quebrada de Oro is a tributary of the Río Viejo, in turn a tributary of the Río Cangrejal, which flows into the Caribbean at La Ceiba, Honduras (see McCranie, Wilson, & Williams 1989, for a description of the area).

In May 1988, we collected specimens of a distinctive new species of the montane genus *Plectrohyla* at the Quebrada de Oro locality. Adults were found at elevations ranging from 930 to 990 m. McCranie and Eric Hedl, then a member of the United States Peace Corps stationed in Trujillo, Honduras, returned in 1989 and collected one adult at 990 m and two tadpoles at 1010 m.

Although this species probably occurs in suitable localities at higher elevations in the Río Viejo drainage, the known elevational range is near the lower limit for this genus. Duellman & Campbell (1992) indicated that the known elevational range for the other fifteen species of *Plectrohyla* is 615 to 3500 meters. Most species of *Plectrohyla* occur at intermediate elevations (1500–2700 m; sensu Stuart 1963), but a few, including the one described herein, range downward into moderate elevations (600–1500 m; sensu Stuart 1963). *Plectrohyla teuchestes* ranges downward to ca. 1000 m, *P. guatemalensis* and *P. hartwegi* to slightly less than 1000 m (we have collected *P. guatemalensis* as low as 990 m in the Sierra de Agalta above Catacamas in Honduras), and *P. matudai* and *P. quecchi* occur as low as 615–700 m.

The region of the "golden stream" (Quebrada de Oro) has been surprisingly productive of new taxa (others remain to be described). It is a figurative "gold mine" and once again has produced something "golden," the "golden-sided tree frog."

Methods

All measurements are in millimeters, made to the nearest tenth with dial calipers with the aid of a dissecting microscope. The

Fig. 1. *Plectrohyla chrysopleura*, new species, male holotype (USNM 316547), SVL 63.8 mm.

dorsal ground colors were compared to the color swatches in Smithe (1975). Color numbers used below refer to that publication. Webbing formulas follow Savage & Heyer (1967) as modified by Myers & Duellman (1982). Subjective evaluations of tadpole jaw sheath configurations are patterned after Altig & Johnston (1986). The phylogenetic analysis was conducted using Swofford's (1991) software package PAUP (Phylogenetic Analysis Using Parsimony, version 3.0s) on a Macintosh Plus.

Plectrohyla chrysopleura, new species
Fig. 1

Holotype.—National Museum of Natural History (USNM) 316547, an adult male from along the Quebrada de Oro (15°38′N, 86°47′W), 970 m elev., tributary of the Río Viejo, south slope of Cerro Búfalo, Cordillera Nombre de Dios, Departamento de Atlántida, Honduras, collected 23 May 1988 by James R. McCranie and Larry David Wilson. Original number LDW 8907.

Paratypes.—USNM 316548, adult male, same data as for holotype, except elevation 930 m; USNM 316549–50, both adult males, same data as for holotype, except elevations unrecorded and collected 3 May, 1988 by Gustavo A. Cruz; USNM 316551, adult male, same data as for holotype, except elevation 990 m and collected 1 August 1989 by Eric Hedl and James R. McCranie.

Diagnosis.—A species of *Plectrohyla* distinguished from its congeners by the following combination of characteristics: moderate size (56.6–65.6 mm snout-vent length); dorsum weakly to moderately tuberculate; vocal slits present; maxillary-premaxillary teeth spatulate; no vertical rostral keel; prepollex flat, elongate, terminally blunt; dorsum Smoke Gray (color 45) with a bronze sheen or Cinnamon (color 123A); prominent golden yellow flashmarks present on front and hind limbs, side of body, axilla, and groin (all flashmarks hidden when frog is at rest).

Description of holotype.—Adult male with snout-vent length (SVL) of 63.8; tibia length 37.7, 59.1 percent of SVL; foot length 31.0, 48.6 percent of SVL; head length 21.4, 33.5 percent of SVL; head width 23.0, 36.1 percent of SVL. Snout of moderate length, distance from anterior edge of orbit to tip of snout 8.6, 134.3 percent diameter of eye; snout truncate in dorsal aspect and in profile, lacking a vertical rostral keel; canthal ridge slightly thickened; loreal region slightly concave; lips moderately thickened, slightly flared. Nostrils protuberant, directed dorsolaterally, situated near tip of snout; internarial distance 4.9; internarial area slightly depressed near point of convergence of canthal ridges; top of head flat; interorbital distance 6.3, 27.4 percent of head width; diameter of eye 6.4; width of eyelid 4.9, 21.3 percent of head width. Moderately heavy dermal fold extending posteriorly from posterior edge of orbit, merging with body contour above point of insertion of arm, barely covering upper edge of tympanum, remainder of tympanum distinct; diameter of tympanum 3.3 mm, 51.6 percent of eye diameter.

Arms moderately robust, forearm slightly heavier than upper arm; distinct transverse fold on wrist. No axillary membrane. Fingers long, slender; length of fingers from shortest to longest, 1-2-4-3, fourth toe nearly as long as second; disc on third finger subequal in size to tympanum; webbing vestigial between first and second fingers, webbing formula II 2-3 III 2 1/2-2^+ IV; subarticular tubercles large, subconical; distal tubercle on fourth finger normal; supernumerary tubercles in single rows on proximal segments of fingers; pollex flat, elongate, terminally blunt, spine not protruding through skin, lacking nuptial excrescences. Heels slightly overlapping when hindlimbs extended to right angles of body; no transverse dermal fold on heel; inner tarsal fold extending full length of tarsus; no outer tarsal fold; inner metatarsal tubercle ovoid, barely visible from above; no outer metatarsal tubercle. Toes long, slender; length of toes from shortest to longest, 1-2-5-3-4, fifth toe nearly as long as third; discs moderately large; subarticular tubercles moderately large, subconical; supernumerary tubercles small, low, in single row on proximal segment of each digit; toes about three-fourths webbed, webbing formula I 1^+-1 1/2 II 1^+-2 III 1^+-2 IV 2-1^+ V.

Vent opening directed posteroventrally at level of mid-thigh; anal sheath short, broad. Skin on dorsal surface, throat, and chest weakly tuberculate; skin on ventral surfaces of forearms moderately tuberculate; skin on belly, ventral surfaces of thighs, and below vent granular; skin on ventral surface of shanks smooth. Tongue nearly round; upper jaw shallowly notched medially; maxillary-premaxillary teeth spatulate; vomerine teeth 6-5, situated on small elliptical elevations between ovoid choanae; vocal slits present, extending from midlateral edge of tongue to angle of jaw; vocal sac single, median, subgular.

Color in life: dorsum of head, body, and limbs Smoke Gray (color 45) with a slight bronze sheen; tympanum pale coppery bronze; lips slightly paler than remainder of head; iris gold with black reticulations; prominent golden yellow flashmarks at axilla, side of chest, and underside of arm (all contiguous), similar but slightly darker flashmarks at groin, on anterior surface of thigh, underside of shank, upper surface of tarsus, and upper surface of foot (all flashmarks hidden when frog at rest); chin and chest gray with a golden sheen; belly gray

Table 1.—Variation in measurements (in millimeters) and proportions (percentages) in five male *Plectrohyla chrysopleura.* Character abbreviations are in brackets. Means are in parentheses following ranges.

Character	Measurements and proportions	
Snout–vent length [SVL]	56.6–65.6	(62.1)
Tibia length [TL]	29.3–37.7	(34.1)
(TL/SVL)	46.6–59.2	(54.9)
Foot length [FL]	26.5–31.6	(29.3)
(FL/SVL)	45.5–48.6	(47.1)
Head length [HL]	20.0–21.7	(20.7)
(HL/SVL)	32.4–35.5	(35.1)
Head width [HW]	20.8–23.0	(21.8)
(HW/SVL)	33.5–37.1	(35.1)
Snout length [SL]	7.6–9.2	(8.3)
(SL/ED)	121.2–146.0	(133.1)
Eye diameter [ED]	5.8–6.6	(6.3)
Internarial distance	4.3–5.2	(4.8)
Interorbital distance [IOD]	5.9–7.2	(6.3)
(IOD/HW)	27.4–31.4	(28.8)
Eyelid width [EW]	4.9–5.4	(5.2)
(EW/HW)	21.3–25.7	(23.8)
Tympanum diameter [TD]	3.0–3.8	(3.4)
(TD/ED)	47.0–58.7	(53.1)

with yellowish cast, as is undersurface of thigh; posterior thigh surface golden yellow with dense olive green smudging; palms pale gray; soles gray.

Color in alcohol: dorsal surfaces grayish-brown; ventral surfaces pale gray; flash-marks dirty white.

Variation.—Measurements and proportions of all specimens are given in Table 1. Color and pattern of the paratypes are in essential agreement with that of the holotype, except that the dorsal surfaces of USNM 316551 were Cinnamon (color 123A) in life. Most paratypes are somewhat more tuberculate on the dorsal surfaces than is the holotype.

Description of tadpole.—One lot of two *Plectrohyla* tadpoles (USNM 316552) presumed to be of this species (no other *Plectrohyla* is known from the type locality nor is expected to occur there) is available. A tadpole (Fig. 2A) in stage 36 (Gosner 1960) may be described as follows: body length 16.8; tail length 27.8; total length 44.6; body slightly depressed, a little wider than high; snout semicircular in dorsal aspect, rounded in profile; eyes moderately small, widely separated, directed laterally; nostrils situated at a point slightly closer to eyes than tip of snout, directed anterolaterally; spiracle sinistral, directed posterodorsally, situated near midline, at a point about two-thirds distance from tip of snout to posterior end of body; vent tube moderately long, dextral; caudal musculature robust, extending nearly to tip of rounded tail; height of caudal musculature at midlength of tail greater than height of either dorsal or ventral fins; dorsal fin extending very narrowly onto posterior end of body.

Oral disc (Fig. 2B) large, ventral, completely bordered by two rows of moderately large marginal papillae (ca. 10/mm); single row of submarginal papillae surrounding A-1 and P-3 tooth rows, larger (ca. 7/mm) than marginal papillae; submarginal papillary row expanding to two-three rows lateral to jaw sheaths; oral disc not emarginated; keratinized jaw sheaths medium-sized, bearing short, pointed serrations; upper jaw sheath widely arched, with well-developed lateral processes; lower jaw sheath widely V-shaped; labial tooth rows ⅔ with second anterior row narrowly interrupted medially; anterior tooth rows subequal, long, extending to lateral portion of oral disc; posterior tooth rows subequal, noticeably shorter than anterior rows.

The second tadpole is in stage 26 and has a body length of 13.4, a tail length of 20.9, and a total length of 34.3. This specimen is very similar in morphological features to the larger tadpole described above.

Color in life of the larger tadpole was as follows: body brown; caudal musculature creamy-tan, boldly spotted with brown; caudal fins clear with brown spots. The smaller tadpole was similar, except that it lacked the bold markings on the caudal musculature and tail fins.

Natural history notes.—All adults, for

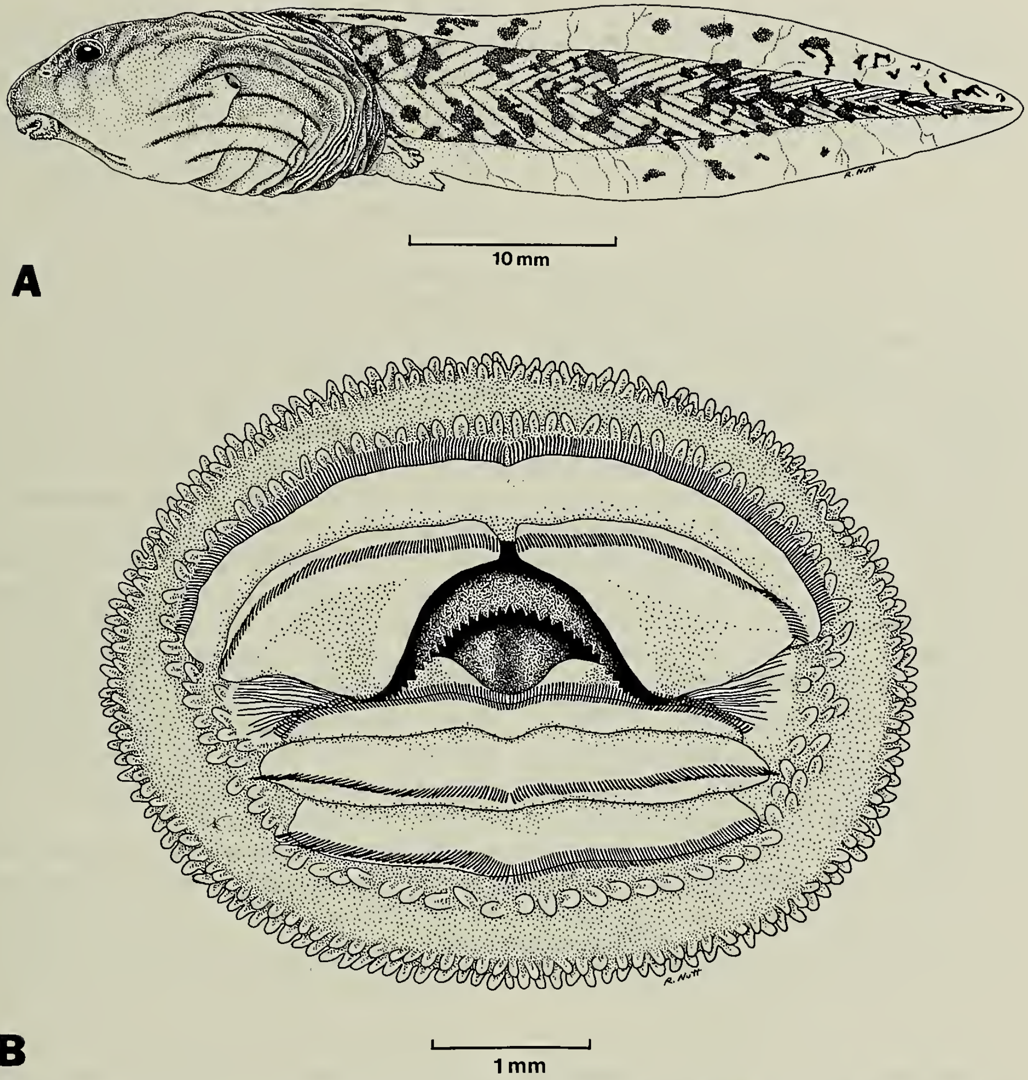

Fig. 2. Tadpole of *Plectrohyla chrysopleura* (USNM 316552) in Gosner stage 36: (A) lateral view; (B) oral disc.

which information is available, were collected at night on boulders in splash zones near waterfalls in the Quebrada de Oro. The tadpoles were collected in a plunge pool in a small tributary of the Quebrada de Oro with tadpoles of *Ptychohyla spinipollex* and *Rana maculata.*

The vegetation of the Quebrada de Oro area lies in the Premontane Wet Forest formation of Holdridge (1967), and was described by McCranie, Wilson, & Williams (1989). The section of Quebrada de Oro in which we have worked since 1980 was decimated by a huge landslide in November of 1988, precipitated by deforestation on the steep hills above the stream. The impact on the populations of the numerous species of amphibians resident in the environs of the stream is unknown, but is thought to be substantial.

Etymology.—The name *chrysopleura* is derived from the Greek words *chrysos* and *pleura,* meaning "gold" and "side," respectively, in reference to the yellow flash markings on the frog.

Discussion

With the description of *Plectrohyla chrysopleura,* the genus now comprises sixteen described species. The recent reappraisal of the genus by Duellman & Campbell (1992) perforce leaves a number of questions unanswered.

Duellman & Campbell (1992) described two new species of *Plectrohyla* (*P. acanthodes* and *P. teuchestes*), segregating them from the formerly composite *P. guatemalensis.* In addition, they conducted "two levels of phylogenetic analysis" of the fifteen known species. The first analysis involved an attempt to identify suitable out-groups and to establish the monophyly of *Plectrohyla.* The second was an effort to create a cladogram for the in-group, *Plectrohyla.*

As Duellman & Campbell (1992:25) acknowledged, ". . . the morphological data set that [was used] is not sufficent to resolve the phylogenetic relationships among the species of *Plectrohyla.*" Questions also exist concerning their out-group analysis. We discuss our concern with the latter first.

Duellman & Campbell (1992) identified four synapomorphies uniting *Plectrohyla* and the *Hyla bistincta* group as sister-taxa. Unfortunately, they do not unequivocally indicate their concept of the latter group. They make reference to the work of Duellman (1970), who recognized the *Hyla bistincta* group as comprising nine species. They (1992:21) further stated that two of the species included by Duellman (1970) in the group, *H. charadricola* and *H. chryses,* ". . . lack the thick, glandular dorsal skin characteristic of the other, larger species in the group." As a consequence, they did not include these species in the first out-group. No mention was made, however, of the species described and placed subsequently in the *bistincta* group or related groups by Adler & Dennis (1972) and Caldwell (1974). The latter work is especially important, inasmuch as Caldwell reorganized the members of Duellman's (1970) *bistincta* group (plus the species described subsequently, including her own, as well as *H. arborescandens*) into four species groups (*bistincta, arborescandens, charadricola,* and *crassa*), leaving the *bistincta* group with only two members (*bistincta* and *pentheter*). Perhaps, Duellman & Campbell (1992:21) had Caldwell's study in mind when they penned the quizzical statement, "The monophyly of the *Hyla bistincta* group seems to be assured, but the limits of the group remain to be ascertained." This statement appears to constitute a reverse non sequitur, i.e., the second clause of the sentence is supposed to follow from the first. Group limits (i.e., content) have to be established before a case for monophyly can be made. If this had been done, making a case for the *bistincta* group as the first out-group and sister-taxon of *Plectrohyla* would rest upon a secure base instead of being equivocal.

The choice of the second out-group, the species *Hyla miotympanum,* by Duellman & Campbell (1992:21), was acknowledged to be ". . . frought [sic] with uncertainty." They appear to have selected this taxon by a process of elimination, excluding from consideration various groups of stream-breeding hylines with highly-specialized tadpoles. They doubtless had little choice, inasmuch as their decision was hampered by ". . . the absence of phylogenetic analyses of the diverse groups of hylids" (p. 21). In light of the questions concerning the choice of out-groups, we wonder what weight can be given to the determination of features as apomorphies or plesiomorphies. Pursuing the work to clarify such matters is outside of the scope of the present work and thus we tentatively accept Duellman & Campbell's (1992) out-group analysis in attempting to determine the phylogenetic position of *Plectrohyla chrysopleura.* We also accept the hypothesis that the genus *Plectrohyla* is

Table 2.—Morphological characters and coded character states used in phylogenetic analysis of *Plectrohyla*. Number in parentheses following a character refers to the respective character number in Duellman & Campbell (1992). State 0 is the primitive condition. Character transformation is 0 → 1 in all characters except character 3, which is 0 → 1 → 2 → 3.

Character	Character states
1. Squamosal (11)	0: otic ramus of squamosal articulating with the crista parotica 1: otic ramus of squamosal not articulating with the crista parotica
2. Humerus (12)	0: humerus round in section 1: humerus having well-developed flanges
3. Prepollex (13)	0: prepollex slightly enlarged, cartilaginous or ossified, rounded or elliptical 1: prepollex enlarged, elongated, ossified, flat, terminally blunt 2: prepollex enlarged, elongated, ossified, terminally curved with a single spine 3: prepollex enlarged, elongated, ossified, with two curved spines
4. Rostrum (14)	0: rostrum plain 1: rostrum with vertical keel
5. Linea masculinea (15)	0: linea masculinea absent 1: linea masculinea present
6. Vocal slits (16)	0: vocal slits present 1: vocal slits absent
7. Expansion of oral disc (18)	0: oral disc not expanded and suctorial 1: oral disc expanded and suctorial
8. Serrations on upper jaw sheath (19)	0: serrations subequal in size 1: two or more serrations enlarged, fanglike
9. Length of posterior tooth rows (21)	0: posterior tooth rows shorter than anterior rows 1: posterior tooth rows equal in length to anterior rows
10. Lateral processes on upper jaw sheath (20)	0: lateral processes well-developed 1: lateral processes weak or absent
11. Maxillary teeth	0: maxillary teeth spatulate 1: maxillary teeth pointed

monophyletic, although we feel that such an opinion would stand on much firmer footing were the phylogenetic relationships within the presumed sister-taxon, the *Hyla bistincta* group, and those of Middle American stream-breeding hylids in general, better understood.

The in-group analysis of *Plectrohyla* carried out by Duellman & Campbell (1992), however, is particularly frustrating, in part due to the uncooperative nature of the members of the genus. Sufficient-sized series of some of the species of *Plectrohyla* are notoriously difficult to assemble. Nonetheless, rendering a strict consensus tree possessing a polytomy of 11 clades for 15 species is close to having no in-group analysis at all. For Duellman and Campbell to imply in the title that their paper somehow resolves the "phylogenetic relationships" of the species of *Plectrohyla* is certainly misleading.

The characters and states used by Duellman & Campbell (1992) in the in-group analysis contain several mistakes and/or potential ambiguities. We thought that a more effective analysis would modify their hypothesis about the group relationships. As a result, we undertook a phylogenetic reanalysis of the genus *Plectrohyla*; discussion of our treatment of characters follows.

A major oversight of Duellman & Campbell was the fashion in which the states associated with the prepollex were coded in the out-group (their character 8) and in-group (their character 13) analyses. The enlarged, ossified nature of the prepollex in species of *Plectrohyla* was cited as evidence for the monophyly of the genus. In the in-group analysis, however, three states were identified for this character, viz., (1) blunt, (2) pointed, simple, and (3) pointed, bifid. The polarization and transformation serialization was identified as 0 → 1 → 2 in the same order. The "0" condition, however, was stated by Duellman & Campbell (1992:23) to be "The primitive condition (that found in both the first and second out-groups) . . . ." Thus, a blunt, enlarged, and ossified prepollex is indicated as occurring in *Hyla miotympanum* and members of the *H. bistincta* group. Such is patently not the case, so the character states and their polarity were recoded (Table 2).

A second concern is with Duellman & Campbell's character 17 (rows of accessory papillae). Two states were given for this character as follows (0 → 1):

0 = one row of accessory papillae on each labium.
1 = one row of accessory papillae on anterior labium and two rows on posterior labium.

Five species of *Plectrohyla* (*hartwegi, ixil, matudai, pokomchi,* and *teuchestes*) were said to have the derived state. However, Duellman & Campbell (1984:396) stated that there is a "single row of larger papillae medial to fringing papillae" in *pokomchi.* Their illustration (fig. 6) of the *pokomchi* tadpole also shows one row of large accessory papillae (= submarginal papillae) on the posterior labium in this species. Duellman & Campbell (1992:16) also stated that there are "four or five large submarginal papillae between posterior labial tooth row and posterior margin of lip" in *teuchestes* and (p. 10) that there are "6–8 large papillae medially between third posterior tooth row and posterior edge of disc" in *hartwegi.* Thus, the situation in *hartwegi* and *teuchestes* is radically different from the condition where there are two rows of submarginal papillae on the posterior labium as found in *ixil* and *matudai* tadpoles (compare illustrations of latter two species in Duellman (1970), with those of *hartwegi* and *teuchestes* in Duellman & Campbell 1992). We have deleted this character from our analysis because of the erroneous scoring of this character by Duellman & Campbell and the fact that an examination of the tadpoles of each species of *Plectrohyla* would be necessary before we could confidently recode this feature. Such an analysis is outside the limits of our study, but we would urge future workers studying the phylogeny of *Plectrohyla* to investigate the potential utility of this character.

A third problem is Duellman & Campbell's character 20 (lateral processes on upper jaw sheath). Three states were given for this character as follows (0 → 1 → 2):

0 = lateral processes long.
1 = lateral processes short.
2 = lateral processes weak or absent.

Two species (*acanthodes* and *guatemalensis*) were said to have the state 0, two (*avia* and *pokomchi*) state 1, and the remaining species (where known) state 2. Campbell & Kubin (1990:table 1) defined the lateral processes of *acanthodes* (as *guatemalensis*: Campbell & Kubin's source of information for this taxon was Duellman (1970), who actually described and illustrated the *acanthodes* tadpole under the name *guatemalensis*), *avia, pokomchi,* and *sagorum* as "short, narrow." These four species, all with "short" lateral processes, are coded three different ways in Duellman & Campbell's data matrix. Also, numerous contradicting statements can be found in Duellman & Campbell (1992) by comparing the species diagnosis for *acanthodes, dasypus, glandulosa, guatemalensis, pokomchi, quecchi, sagorum,* and *tecunumani* with their data matrix (table 8). Additionally, Honduran *P. glandulosa* tadpoles (*glandulosa* coded state

Table 3.—Character matrix for the species of *Plectrohyla* in the phylogenetic analysis. Missing characters coded 9. Character numbers refer to Table 2.

Taxon	Character										
	1	2	3	4	5	6	7	8	9	10	11
Ancestor	0	0	0	0	0	0	0	0	0	0	0
P. acanthodes	0	1	3	0	0	1	0	0	0	0	0
P. avia	0	1	2	0	0	1	0	0	0	1	1
P. chrysopleura	0	1	1	0	0	0	0	0	0	0	0
P. dasypus	0	1	1	0	0	0	0	0	0	1	0
P. glandulosa A	0	1	1	0	0	1	0	0	0	1	1
P. glandulosa B	0	1	1	0	0	1	0	0	0	0	1
P. guatemalensis	0	1	3	0	0	1	0	0	0	0	0
P. hartwegi	0	1	3	0	0	1	1	0	1	1	0
P. ixil	1	0	2	0	1	0	0	1	0	1	0
P. lacertosa	0	1	1	0	0	1	9	9	9	9	1
P. matudai	1	0	2	0	1	0	0	1	0	1	0
P. pokomchi	0	1	3	0	0	0	0	0	0	1	0
P. pycnochila	0	1	1	0	0	1	9	9	9	9	0
P. quecchi	0	1	2	1	0	0	0	0	0	1	0
P. sagorum	0	1	2	1	0	0	0	0	0	1	1
P. tecunumani	0	1	1	0	0	1	0	0	0	1	1
P. teuchestes	0	1	3	0	0	1	1	0	1	1	0

2 by Duellman & Campbell) have lateral processes similar in length to those of *P. guatemalensis* (*guatemalensis* coded state 0 by Duellman & Campbell). Because of the contradictory evidence, we have recoded this character as either well-developed, or weak or absent (Table 2). This action necessitates distinguishing Guatemalan *P. glandulosa,* with weak or absent lateral processes, from Honduran *P. glandulosa.* These taxa are labeled *glandulosa* A and *glandulosa* B, respectively, in our data matrix (Table 3). The nine species coded in Duellman & Campbell's (1992) data matrix as having "weak or absent" lateral processes were similarily coded in our data matrix, whereas the remaining species (where the tadpoles are known) were coded as well-developed (Table 3).

A final matter relates to the lack of use of a character discussed by Duellman (1970), viz., the nature of the maxillary teeth (spatulate vs. pointed). Maxillary teeth of the *H. bistincta* group (sensu Duellman 1970) are spatulate, as are those of most species of Middle American hylids (Duellman 1970). Thus, we hypothesize that spatulate teeth represent the ancestral state and pointed teeth the derived one. If such were the case (again, what exactly are the limits of the *bistincta* group?), then the character would be polarized and is added to our analysis (Tables 2, 3). Duellman & Campbell (1992) did not indicate condition of the maxillary teeth in *P. acanthodes,* but as specimens of this species were included within the composite *P. guatemalensis* by Duellman (1970), which has spatulate teeth, then those of *acanthodes* probably are spatulate and we have so coded them. The characteristics for all species in the analysis are given in Table 3.

We confined our searches for the most parsimonious phylogenetic hypothesis as closely as possible to the methods used by Duellman & Campbell (1992) in their PAUP analysis. However, our PAUP program (3.0) is a later version than that (2.4) used by Duellman & Campbell. The global branch-swapping option used by Duellman & Campbell is not available on version 3.0; instead a subtree pruning-regrafting (SPR) option is available that is ". . . approximately, but not exactly, equivalent to the

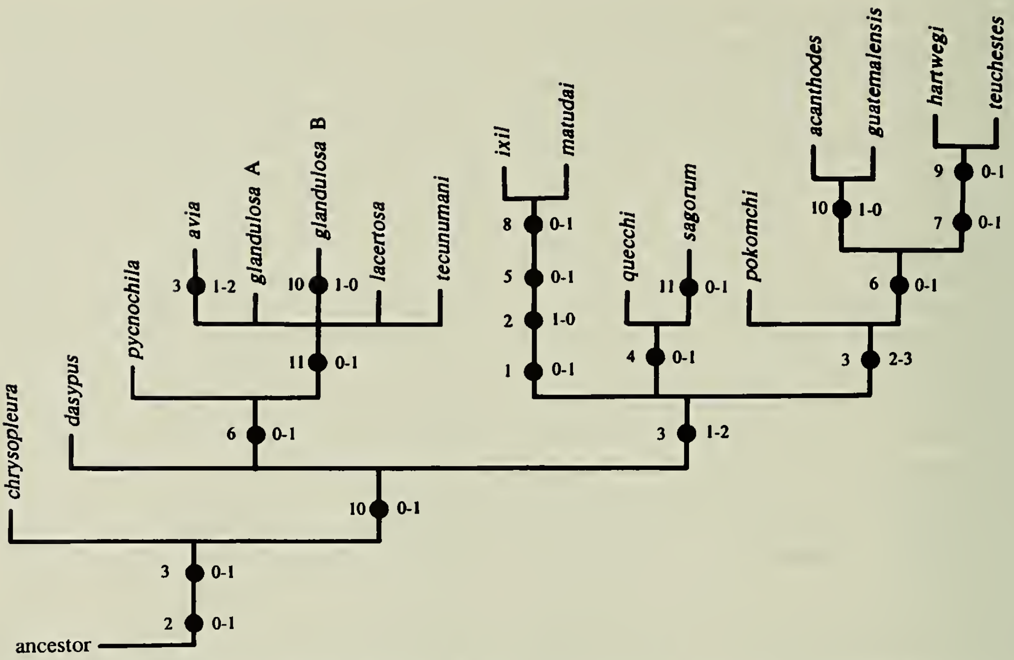

Fig. 3. Strict and Adams consensus cladogram for the members of the genus *Plectrohyla*. Character numbers (to the left of the circles) and changes in character states (to the right of the circles) refer to numbers in Table 2.

'global' procedure used in earlier versions of PAUP" (Swofford, 1991:31 in user's manual). Also available is a new procedure, the tree bisection-reconnection (TBR) option. Also new to PAUP 3.0 is the ability to yield polytomies by collapsing branches having a maximum length of zero. Using the data matrix in Table 3, we made searches using both the SPR and TBR branch-swapping options. Each branch-swapping option was executed first with the zero-length branches collapsed, then executed with the zero-length branches not collapsed. Each search was conducted with the MULPARS option in effect, the stepwise addition option closest, and the tree rooted using the outgroup method. Strict consensus and Adams consensus trees were generated for each of the four searches. All eight consensus trees generated were identical, regardless of the search options used. When the zero-length branches were not collapsed, 300 equally parsimonious trees were retained in both the SPR and TBR searches (matrix set at 300, the exact number that can be found is unknown), whereas, when the zero-length branches were collapsed, only two equally parsimonious trees were found under both the SPR and TBR searches. Each of these two trees was identical to its counterpart under the other branch-swapping option. Tree 2 differs from tree 1 (Fig. 3) only by *glandulosa* B + *lacertosa* forming a clade by assigning a reversal to character 10, which is missing datum for *lacertosa*. All trees have 19 steps and a consistency index of 0.684. Thus, even though our data matrix contains an equal number of characters, plus two more taxa than Duellman & Campbell's matrix, our trees are one step shorter and have a slightly higher consistency index (0.650 in Duellman & Campbell's trees). More importantly, the unresolved polytomy of 11 clades for 15 taxa in Duellman & Campbell's strict consensus tree (their fig. 19) is almost fully resolved (Fig. 3). Whereas our cladogram can undoubtably be improved upon by a more thorough analysis of the genus, it is a substantial improvement over that offered by Duellman & Campbell. *Plectrohyla chrysopleura,* the species herein described, is the species closest to the ancestral stock of the genus, based upon our phylogenetic analysis.

A more minor concern, but nonetheless irritating, with the Duellman & Campbell (1992) revision are contradictions between some tadpole descriptions and their identifying characteristics in the tadpole key or one of the tadpole illustrations. Duellman & Campbell (1992:4) stated that the posterior tooth rows of *acanthodes* tadpoles are ". . . slightly shorter than upper [= anterior] rows, third shortest," whereas, in the key we are told in couplet 7, leading to *acanthodes* in couplet 9, that the posterior tooth rows are subequal in length. The other part of couplet 7, "Third lower [= posterior] labial tooth row shorter than others," leads to couplet 10 and past *acanthodes. Plectrohyla teuchestes* tadpoles supposedly have a "Distinct smooth, sharply raised fold between fringing papillae and anterior tooth row" (Table 3; also see couplet 2 in tadpole key), whereas Duellman & Campbell's drawing of the *teuchestes* tadpole (their fig. 15) indicates that the "fold" is papillate or scalloped throughout. Also, Duellman & Campbell (1992:fig. 8) illustrate the *P. guatemalensis* tadpole with the caudal musculature extending dorsally onto the body nearly to the eyes, quite a remarkable feature. Other statements also are confusing: i.e., *acanthodes* tadpoles with "two rows of small labial papillae fringing disc, except only one row midventrally" (p. 4) or "Lips having a single row of small fringing papillae" (couplet 5 leading to *acanthodes*); and *guatemalensis* tadpoles reported to have "one row of small labial papillae anteriorly and laterally, two rows midventrally" (p. 8) but "Lips having two rows of small fringing papillae" (couplet 5 leading to *guatemalensis*). Considering the extent of the Duellman & Campbell inconsistencies, we suggest that anyone trying to use their tadpole key do so with caution. Finally, the specific name *pycnochila* is misspelled throughout Duellman & Campbell's paper as *pychnochila* and the number in the second section of tadpole couplet 3 leading to couplet 5 is misprinted 6.

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IDENTIFICATION OF THE TAXA XENOCEPHALIDAE, *XENOCEPHALUS,* AND *X. ARMATUS* (OSTEICHTHYES: URANOSCOPIDAE)

Victor G. Springer and Marie-Louise Bauchot

Abstract.—Xenocephalinae Kaup, 1858 (currently recognized as a valid family), is a junior synonym of Uranoscopidae (dating from at least 1832; no subfamilies recognized). *Xenocephalus* Kaup, 1858, is a senior synonym of the currently recognized genus *Gnathagnus* Gill, 1861. *Xenocephalus armatus* Kaup, 1858, is a senior synonym of the currently recognized species *Gnathagnus innotabilis* Waite, 1904. A neotype is designated for *Xenocephalus armatus,* which was erroneously described from New Ireland, but in fact was based on a specimen from New Zealand.

Kaup (1858) described a new subfamily, genus, and species of fish (Xenocephalinae, *Xenocephalus armatus*), which he included in the family Gadidae. Kaup's taxa have been carried along in the systematic ichthyological literature ever since, but their identities and affinities have remained enigmatic. It is the purpose of our study to clarify and fix the systematic status of Kaup's three taxa.

Taxonomic History of Kaup's Taxa

Kaup (1858) stated that *Xenocephalus armatus* was distantly related to the Macrurinae, one of the four subfamilies he recognized in the Gadidae (the others, Gadinae, Brotulinae). Subsequent mention of Kaup's taxa followed soon after their original descriptions, but most authors had nothing substantive to add to his description. We include here, with minimal comment, all references we have encountered in an intensive search of the scientific literature for mention of Xenocephalinae (or a family-group based on it), *Xenocephalus,* or *X. armatus.* Our purpose in doing so is to demonstrate that Kaup's taxa cannot be considered as nomina oblita, and the genus and species, at least (and the family group, usually) have always, been considered as senior synonyms, albeit of questionable affinities (authors listed chronologically by earliest publication):

Bleeker (1859) essentially followed Kaup by listing *Xenocephalus* in a subfamily Xenocephaliformes of a family Gadoidei. Günther (1862) included *Xenocephalus armatus,* with no mention of Xenocephalinae, as an "Appendix to the Anacanthini gadoidei," and (1880) stated that *Xenocephalus* was "a gadoid anacanth," but (1909) presciently opined that it appeared to be a larval form of a fish that is unrelated to the anacanthin gadoids; Gill (1872, 1884, family listed essentially according to Günther, 1862); Gill (1888, family "approximated to Ophidioidea"; 1893, family listed under Ophidioidea); Scudder (1882, genus listed); Perrier (1903, genus in Macruridae); Jordan (1905, 1907, 1925, genus included in Zoarcidae under "the great family Blenniidae"; 1919, genus listed; 1923, family included in Blenniiformes); Fowler (1928, family, genus, species recognized); Berg (1940, 1947, 1955, family and genus listed in Blennioidei); Neave (1940, genus listed); Schultz (1948, family listed in Blennioidea); Munro (1956, family, genus, species listed; 1967, family, genus, species questionably included in Blennioidei); Golvan (1962, genus included in Macrouridae; 1965, genus listed in Macrouridae, and family and genus listed in Blennioidei); Greenwood et al. (1966, family listed in Blennioidei); Norman (1966), genus and species doubtfully referred to Blennioidea; this long-delayed posthumous publication was essentially complete by 1938 and contains no references more recent than 1944; Norman included the statement, erroneous even in 1938, that *Xenocephalus* had not been recognized since its original description); Romer (1966, family listed in Blennioidei); Gosline (1968, family listed, affinities questionable); McAllister (1968, family listed in Blennioidei); Lindberg (1971, 1974, family included in Blennioidei); Wheeler (1975, 1979, remarks on family, genus, species, "There is every possibility that the only known specimen was a damaged or aberrant specimen of some other fish . . . Validity of family doubtful."); Nelson (1976, family, genus, species, questionably included in Blennioidea; 1984, family, genus, species listed; quotes V. G. Springer's opinion that species is possibly larval form of dactylopterid, chaetodontid, or scatophagid); Bond (1979, family listed in Blennioidea); Matarese et al. (1984, family listed in Blennioidea); Kailola (1987, family, genus, species incertae sedis); Eschmeyer (1990: 425, family, genus, species, species, "family placement uncertain, based on young"; page 484, family, genus listed under Suborder Trachinoidei); Springer (1993, family, genus, species probably a dactylopterid).

During the course of our literature search, we encountered the descriptions of *Xenocephalus* Wasmann (1887), based on a beetle, and *Xenocephalus* Leakey (1965), based on a partial skull of a fossil mammal. Both are clearly junior homonyms of *Xenocephalus* Kaup, and have been provided with replacement names (see Gentry & Gentry 1978:359). Except for Wasmann (1887), Leakey (1965), Romer (1966), and Gentry & Gentry (1978), we excluded consideration of literature bearing on the junior homonyms of *Xenocephalus* Kaup.

Disposition of the Holotype of *Xenocephalus armatus*

Prior to the 1990s, there is no indication that anyone made an attempt to locate the holotype of *Xenocephalus armatus* or an illustration of it, which Kaup (1858) indicated he had published elsewhere. Kaup stated that the specimen was in the Paris Museum and had been sent there by [J.-R.-C.] Quoy and [P.] Gaimard, who had obtained it during the d'Urville Expedition [= Astrolabe expedition of 1826–1829 under the command of J. S. C. Dumont d'Urville]. Springer (1993) reported that, at his request, M.-L. Bauchot and M. Desoutter of the Muséum National d'Histoire Naturelle (MNHN) had searched [during January, 1991] the MNHN collection unsuccessfully for the holotype and for information about it among the unpublished plates and records of the Astrolabe expedition [not all of which were known to them in 1991]. A second search of the MNHN collection in January, 1993, also was unsuccessful, although many other specimens referred to in an unpublished Quoy manuscript have been located. As we will discuss, information on the specimen was found in the Bibliothèque Centrale, MNHN, among the unpublished descriptions (file MS 104), drawings (MS 840), and plates (MS 106) of the Astrolabe fishes.

Even though Kaup (1858) stated that the holotype was in the Paris Museum, and he had spent three months working in the fish collection at the museum on two visits during 1855 and 1856 (Heldmann 1955), he may have actually studied the specimen in London. In J. E. Gray's preface to Kaup (1856), it is noted that Kaup had specimens from the French, Leyden, Vienna, Frankfurt, Berlin, and Stuttgart museums sent to the British Museum, which Kaup visited several times between 1846 and 1854, so that he could compare them directly with

British Museum specimens. If the specimen was sent to the British Museum, it apparently is not there now (search made of several parts of the collection by D. Siebert at our request).

Under the circumstances we consider the holotype lost. A fortuitous circumstance, discussed later in our study, allows us to replace it with a neotype that conforms in many ways with Kaup's holotype.

Historical Background of Kaup's Description

Kaup (1858) wrote, in German, "This strange form, of which I give a twice-size illustration in my large work, was transmitted by Messrs. Quoy & Gaimard, Expedition d'Urville, to the Paris Museum, where it is found under the name of Grenadier from New Ireland."

Kaup's memory must have deceived him. He had never published an illustration of the New Ireland grenadier. The large work, to which he referred, was undoubtedly his extensive Das Tierreich (Kaup 1835–1837). In it, he mentioned, but did not illustrate, a species of macrourid to which he gave "grenadiere" as part of its common name. It is also possible that Kaup was thinking about the extensive unpublished portion of the manuscript and plates of the Astrolabe expedition. Quoy & Gaimard (1834) published a study of the fishes obtained by that expedition, but their report, for reasons unknown, includes the descriptions of only 49 species, accompanied by only 12 colored plates, of the large number actually prepared: almost 300 species descriptions and at least 120 plates. Although the unpublished portions were apparently known to Kaup and other of his contemporaries, their existence has been generally unrecognized for more than 100 years, until recently, when one of us (Bauchot) located them among the archives of the MNHN central library. There is, perhaps, evidence that Kaup derived part of his description from the unpublished Quoy & Gaimard manuscript. In addition to the unpublished finished plates, there are numerous preliminary colored drawings, presumably prepared in the field, upon which the finished illustrations for the plates are based.

Identity of *Xenocephalus armatus*

It is important for the determination of the identity of *Xenocephalus armatus* to demonstrate that Kaup's description referred to a specimen that was also described and figured earlier by Quoy & Gaimard in their unpublished manuscript. We believe we have located such a description and here present a translation of it followed by a translation of Kaup's (1858) description.

Translation of Quoy & Gaimard [MS 104 (3$^{\text{éme}}$ mémoir:412–413)]; new scientific name here disclaimed and not to be considered available for permanent scientific record or taxonomic purposes [see ICZN Article 8(b)]:

Spotted Grenadier
Lepidolepous punctatus N.
Plate 223, figures 2–3

[Both the preliminary sketches and final figures for Plate 223, figures 2–3 are in color. We present herein, as our Fig. 1, black-and-white reproductions of the preliminary sketches, which we believe are more accurate than the final figures.]

> This fish has an excessively large, bony, boxlike head, quite truncate in front; the mouth is quite large, almost vertical, situated but little on the ventral part of the head; the teeth large and like a card [= fine and set closely in rows]; the large eye of gold color, with a very prominent [bony] orbit dorsally, which has a notch anteriorly. The opercle consists of a movable triangular piece. The preopercle has a very prominent posteriorly directed spine, below the opercle, and two other smaller spines more ventrally. One sees four ridges on top of the head. The belly

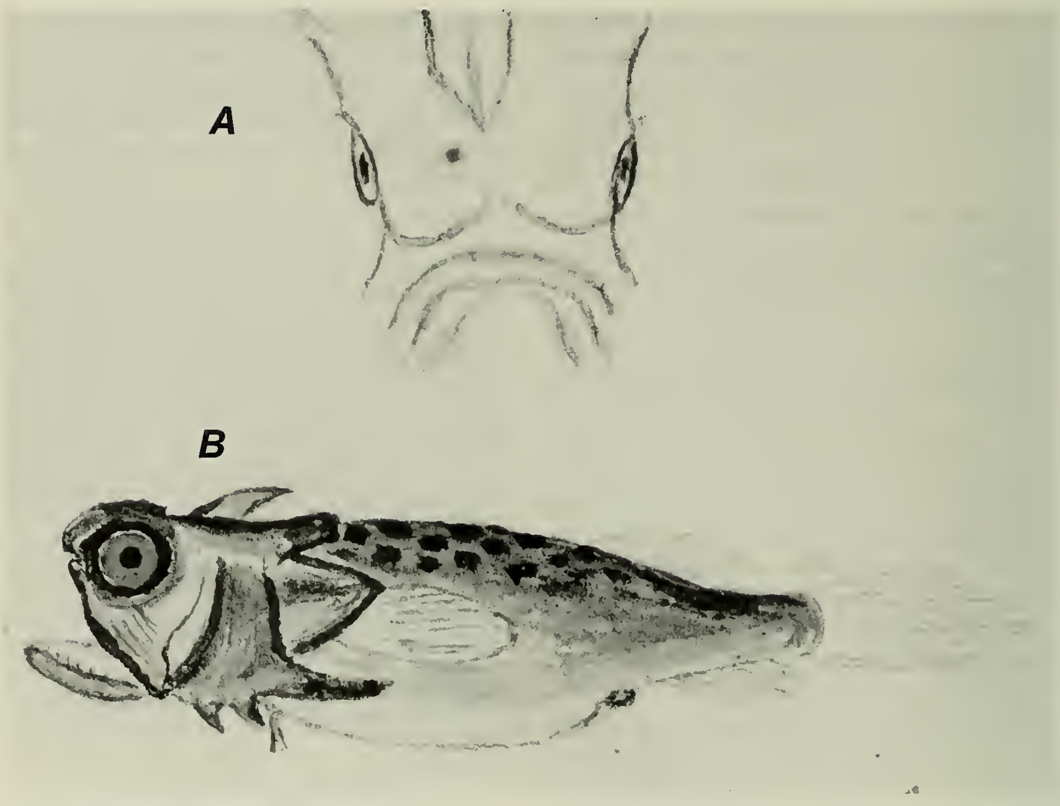

Fig. 1. Original preliminary manuscript illustrations of holotype of *Xenocephalus armatus*: A, dorsal view of head, mouth at bottom of figure; B, lateral view (original is in color).

is prominent, round and soft. The rest of the body ends as a point while becoming compressed. A single dorsal fin placed posteriorly, reaches the origin of the caudal. The anal fin has the same placement [opposite to the dorsal fin]. The pectoral fins are large and round, as [is] the caudal, which appears, however, pointed when it is collapsed [not displayed]. The lateral line is slightly curved. The ventral fins are exceptionally small, placed very anteriorly, and almost covered by the gill membrane covers, which are exceptionally broad.

The general color is deep blue dorsally with some spots of the same color, but slightly darker. The cheeks are a very clear blue, just as the sides. The belly is silver and the fins are whitish.

This fish, 14 lines long [= 31.6 mm; according to Grand Dictionnaire Encyclopédique Larousse, 1984, Tome 6, p. 6295, 1 ligne = 2.2558 mm; American dictionaries indicate that a line is one-twelfth of an inch, or 2.117 mm], was collected 18 Feb 1827, near the island of Mayor in the bay of Abundance [Bay of Plenty] on the coast of New Zealand [emphasis ours].

Translation of Kaup.—First Subfamily Xenocephalinae Kp.

The abnormally large head is armed with shields and spines. First dorsal fin missing. Second dorsal fin and anal fin slightly separated from caudal. One genus.

I. *Xenocephalus* Kaup. With truncated head to which the body is joined as an

> appendage; head and operculum armed. Pectoral and caudal developed. Anus on the posterior half of the body. Tiny teeth in both jaws, none on vomer and palatines. Tongue free, thick, almost filling the entire mouth, blunt in front with short tip. Lateral line on the dorsal half of the body and slightly arched [just] following the head.
>
> 1) *Xenocephalus armatus* Kp. The moderately large eye golden yellow, dark spotted below the eyelid [?]. Head shields yellowish brown; the naked skin between them blackish. Body blackish brown with black spots on the dorsum. Belly gold yellow with gloss. Fins yellowish white. 2nd D. 7, A. 10, P. 21, V. 5, C. 20.
>
> This strange form, of which I give a twice-size illustration in my larger work, was transmitted by Messrs. Quoy & Gaimard, Exped. d'Urville to the Paris Museum, where it is found under the name Grenadier from New Ireland [emphasis ours]. This subfamily is so far very poor in species and other than the one above I know of no species that belongs to this animal group. It is distantly related to the Macrurinae. [Length of specimen not provided.]

Aside from certain differences, which we will discuss, we believe that the similarities between the Quoy & Gaimard and Kaup descriptions, and Kaup's indication that his specimen was received from Quoy & Gaimard, are sufficient evidence to conclude that the descriptions were based on the same specimen.

We believe that the most important difference between the two descriptions is in the designation of the type localities. Kaup either made a mistake in reporting the type locality as New Ireland (one of the islands in the Bismarck Archipelago northeast of eastern New Guinea) or he was misinformed about the locality by whoever was responsible for providing him with the information.

Other differences between the two descriptions are mainly additional characters given by Kaup: the fin-ray counts, lack of vomerine and palatine dentition, shape of the tongue, and position of anus (the last is in agreement with its indication on Quoy & Gaimard's illustration). Except for the fin-ray counts and putative lack of vomerine and palatine teeth, these characters indicate that Kaup did examine the holotype of *Xenocephalus armatus*.

After concluding that the holotype of *Xenocephalus armatus* is the species described and figured by Quoy & Gaimard from New Zealand, we searched among the species of fishes known from New Zealand for clues to the identity of *X. armatus*. Considering the general gestalt of Quoy & Gaimard's illustration, and particularly the armored head and lack of a spinous dorsal fin, we quickly narrowed the possibilities to the Uranoscopidae. No other family of New Zealand fishes contains species that approach the appearance or description of *X. armatus*.

There are five genera and seven species of uranoscopids reported from New Zealand (Paulin et al. 1989, Kishimoto 1990, Okamura & Kishimoto 1993): 1—*Pleuroscopus pseudodorsalis* Barnard, a deep-dwelling species that also occurs around southern Australia, the southwestern Indian Ocean, and the southeastern Atlantic (Kishimoto et al. 1988); 2—*Genyagnus monopterygius* (Schneider *in* Bloch & Schneider 1801 [Forster MS]), which is endemic to New Zealand (although originally and undoubtedly erroneously, also reported to occur in Tahiti; see Fowler 1928: 428, as *Anema monopterygium,* for comment); 3—*Gnathagnus innotabilis* (Waite), which also occurs in Australia (Kishimoto 1989); 4—*Kathetostoma giganteum* Haast, which is endemic to New Zealand; 5—*Kathetostoma laeve* (Schneider *in* Bloch & Schneider), a deep-water species that is known from the Norfolk Ridge to southern New Zealand, and southern Australia (Kishimoto 1990);

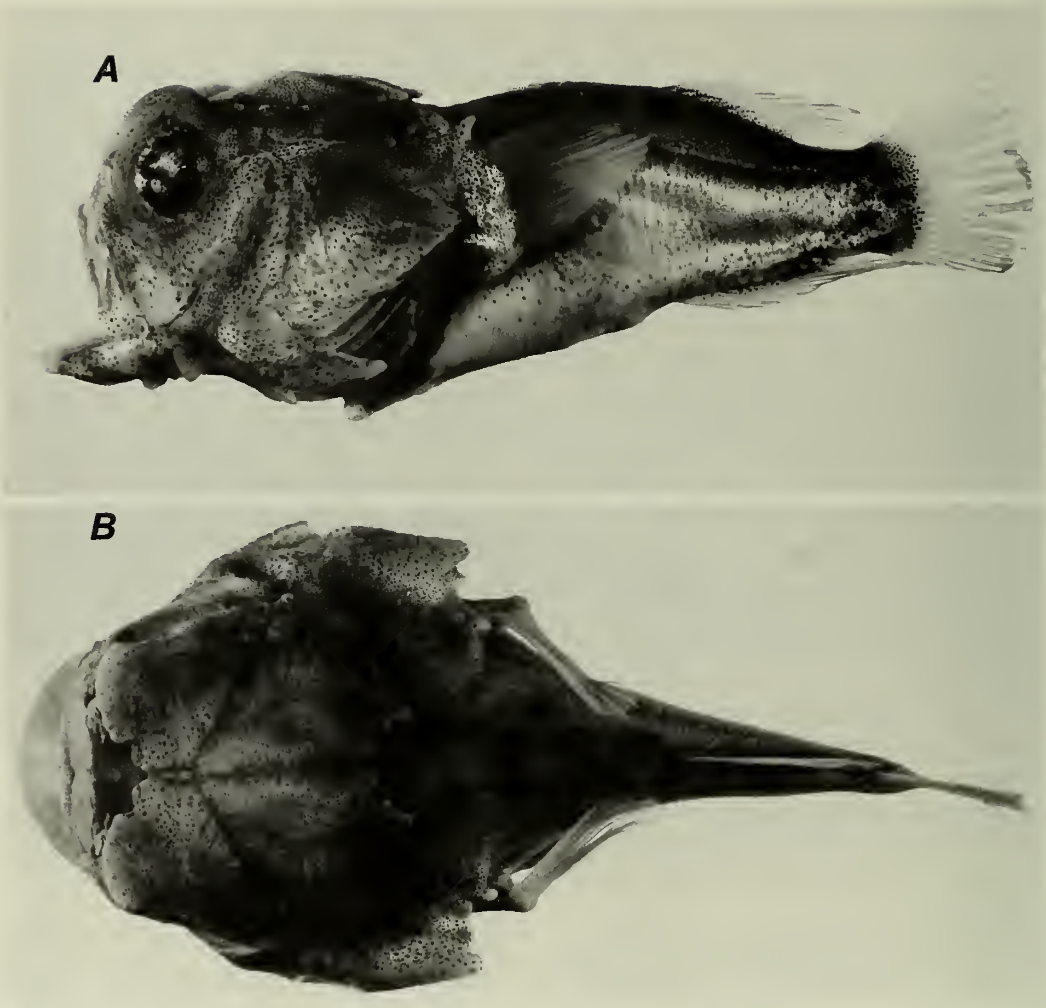

Fig. 2. Neotype of *Xenocephalus armatus*, NMNZ P.30131, 26.6 mm Sl: A, lateral view; B, dorsal view.

6—an unnamed deep-water species of *Kathetostoma* (Paulin et al. 1989, who reported two unnamed *Kathetostoma* species, one of which we assume is *K. laeve*, which they did not report), extra New Zealand distribution unknown; 7—*Selenoscopus turbisquamatus* Okamura & Kishimoto, which is known from off the Kii Peninsula, Pacific coast of central Japan, the Kyushu-Palau Ridge, and the Norfolk Ridge, at depths from 100–510 m (Okamura & Kishimoto 1993).

A detailed descriptive account of all New Zealand uranoscopids, including at least fin-ray counts, has not appeared, but we believe that we can narrow our search among those present to the single species identifiable with *Xenocephalus armatus*.

Among all uranoscopids, the deep-dwelling genus *Pleuroscopus* has segmented dorsal- and anal-fin ray counts closest to those reported by Kaup for *Xenocephalus armatus* (as few as 9 and 10, respectively, in *Pleuroscopus*, Kishimoto et al. 1988). Even so, *Pleuroscopus* can be excluded from consideration because it has a series of 8 to 11 tubercule-like spines preceding the segmented-ray portion of the dorsal fin. It is also notable that very small specimens of *Pleuroscopus* are unknown. Kishimoto et al. (1988) reported that specimens smaller than 242 mm SL are "currently unobtainable." In view of the absence of small specimens, and the apparently restricted deep-water habitat of the species, it seems unlikely that the Astrolabe would have acquired a juvenile 31 mm TL.

Genyagnus monopterygius, although commonly available at small sizes, can be excluded from consideration for several reasons: it has an obvious mental barbel and lingual lure (both noticeable in specimens at least as small as 27 mm TL); the head is not noticeably enlarged nor heavily armored in specimens within the size range of the holotype of *Xenocephalus* (no large preopercular spines as in *Xenocephalus*); its eyes are located on top of the head (on side of head dorsally in *Xenocephalus*); the color pattern dorsally on the body of small juveniles consists of a dark stripe-like marking (no large dark spots, but numerous pale spots in adults); the pectoral-fin rays number only 16–18 (21 reported by Kaup for *Xenocephalus*); and the dorsal fin rays, 18 or 19, appear to be too numerous even if mistakes in the counts were made by Kaup.

Kathetostoma (generically), of which small specimens are often collected, can be excluded from consideration because even at small sizes it has a conspicuous, elongate humeral spine and all spines on the ventral border of the preopercle are relatively fine and ventrally directed; furthermore, the color pattern dorsally on the body does not consist of large dark spots in any specimens we have seen. No humeral spine is indicated in Quoy & Gaimard's figure of *Xenocephalus armatus,* and the posteriormost preopercular spine is greatly enlarged and posteriorly directed.

We believe that *Xenocephalus armatus* is conspecific with *Gnathagnus innotabilis* Waite (1904), described from New South Wales, but currently recognized as also occurring in New Zealand waters (Paulin et al. 1989). We are fortunate to have an approximately 31.0 mm TL specimen (small terminal portion of caudal fin now broken off) of *G. innotabilis* from New Zealand (Fig. 2a, b) to serve as a basis for comparison. The large and heavily armored head of the specimen, including the long posteriorly directed preopercular spine with two smaller spines ventrally on the preopercle, and large dark spots dorsally on the body strongly corroborate the conspecificity of the two species.

There are differences between the description of *X. armatus* and characters exhibited by *G. innotabilis,* particularly in the dentition and dorsal- and anal fin-ray counts given by Kaup (1858). We believe these differences are due to the inadequacy of the optical equipment available during the 1850s. Small specimens of *G. innotabilis* that we have examined have a few tiny, inconspicuous teeth on the vomer and palatines (we even overlooked these in our initial examination of our 31 mm specimen). The species has 11 or 12 dorsal-fin rays and 16 anal-fin rays, 4 and 6 rays more than reported for *Xenocephalus* (additionally, the last dorsal-fin ray may be simple or split to the base in *G. innotabilis*; we counted either condition as one ray). We can discern 11 dorsal-fin rays and 8 anal-fin rays, however, from Quoy & Gaimard's illustration, as opposed to the 7 and 10, respectively, of Kaup's description. Using a Leitz widefield stereo microscope RS (ES model has same optics), which affords the finest resolution of any dissecting scope we know, it was only with difficulty that we were able to make accurate counts of dorsal- and anal-fin rays on our 31 mm specimen. We verified these counts with counts made from radiographs of the specimen. It is because of this difficulty that we believe Kaup's dorsal- and anal-fin ray counts were in error.

All adult uranoscopids have essentially

the same number of branched caudal-fin rays (10), but branching is not evident in small specimens we examined. The number of segmented nonbranched rays appears to increase with growth, but probably not the total number of caudal-fin elements (also includes procurrent rays and spines). The dorsal- and ventralmost of the procurrent elements decrease considerably in size serially as one progresses anteriorly, and are difficult to count accurately in small specimens, unless, as we presume, the specimens are cleared and stained. We were unable to make an accurate count of the total number of caudal-fin elements in our 31 mm specimen, but a total count of 20, as given by Kaup for *Xenocephalus,* for all caudal-fin elements is probably slightly less than the number in *G. innotabilis.*

In order to eliminate the possibility that the New Ireland type locality might actually be correct, we attempted to identify *Xenocephalus armatus* with a species from that area, given the additional information provided by the Quoy & Gaimard manuscript. In that, we were unsuccessful in identifying *Xenocephalus armatus* with any fish species known from the New Guinea area, particularly political Papua New Guinea, which includes New Ireland. Additionally, only two genera of uranoscopids are known from New Guinea: *Uranoscopus* Linnaeus and *Ichthyoscopus* Swainson (Kailola 1987). *Uranoscopus* has a conspicuous spinous dorsal fin and *Ichthyoscopus* lacks spinous processes on the ventral margin of the preopercle (Pietsch 1989), characters that exclude both genera as possibly being congeneric with *Xenocephalus.*

Designation of Neotype for *Xenocephalus armatus*

In order to fix Kaup's species, we here designate our 31 mm specimen (26.6 mm SL from midtip of upper lip to caudal-fin base), NMNZ P.30131 (formerly USNM 325034) as neotype of *Xenocephalus armatus* Kaup. Dorsal-fin rays 11, last ray split to base; anal-fin rays 15, last ray split to base; pectoral-fin rays (r/l) 20/21; vertebrae 27; 7 nonelement-bearing pterygiophores (predorsals) anterior to pterygiophore supporting first dorsal-fin ray. Tiny, widely spaced teeth present on vomer and palatines.

The posteriorly projecting preopercle spine on each side of the head is broken, but the ends are still attached.

The neotype was obtained from the collection of the Fisheries Laboratory in Wellington, New Zealand, by G. D. Johnson, who brought the specimen to our attention and informed us that there was no other data associated with the specimen.

Taxonomic Consequences of the Identity of *Xenocephalus armatus*

The identification of *Xenocephalus armatus* Kaup, 1858, has the following consequences: Xenocephalinae Kaup, 1858, becomes a junior synonym of Uranoscopidae (dating at least as early as Bonaparte 1832—as Uranoscopini—and Richardson 1848:iv—as Uranoscopidae); *Xenocephalus* Kaup, 1858, is a valid senior synonym for a genus of Uranoscopidae, taking priority over *Gnathagnus* Gill, 1861, and its junior synonyms (see Pietsch 1989:294); and *X. armatus* Kaup, 1858, is a valid senior synonym for a species of *Xenocephalus,* taking priority over *Gnathagnus innotabilis* Waite, 1904.

Comparative Material

(Institutional abbreviations follow those in Leviton et al., 1985.)

Astroscopus y-graecum.—Louisiana: Four Bayou Pass, USNM 185647 (1 specimen: ca. 41 mm SL); Barataria Bay, USNM 187947 (2: 30.9–35.2); off coast, USNM 156863 (1: 38.4).

Genyagnus monopterygius.—New Zealand: Nukumaru Reef, Wanganui, NMNZ

P.10463 (3 specimens: ca. 40–48 mm SL); Mangakino Channel, Pourerere, NMNZ P.26278 (2: 22.2–28.2); Hauraki Gulf, NMNZ P.21876 (2: 34.8–59.1); Castlepoint, NMNZ P.17311 (1: 22.1); Manakau Harbour, NMNZ P.2457 (1: 16.6); Tokomaru Bay, NMNZ P.2038 (2: 24.3–24.7); Old Wharf, Kaikoura, NMNZ P.25700 (1: 29.6); Port Hardy, D'Urville Island, NMNZ P.5332 (1: 21.4).

Ichthyoscopus lebeck?.—Indonesia: Ambon, USNM 325474 (1 specimens: 117 mm SL).

Kathetostoma giganteum.—New Zealand: off Cape Farewell, NMNZ P.16605 (1 specimen: 54.8 mm SL); Oamaru, NMNZ P.10684 (1: 78.5); Dunedin, USNM 318371 (1: 84.9)

Kathetostoma sp.—Off Caribbean Panama: 9°18′N, 80°35′W, USNM 187907 (2 specimens: 41.0–64.4 mm SL).

Pleuroscopus pseudodorsalis.—New Zealand: NMNZ P.19668 (1 specimen: ca. 325 mm SL), P.20151 (2: ca. 335, 350), P.22102 (1: ca. 295), P.27963 (1: ca. 270).

Uranoscopus spp.—Australia: New South Wales: off Clarence River Country, AMS I.32120005 (1 specimen: 54.7 mm SL); Collaroy Beach, Sydney, AMS IB.4119 (1: 17.5); off Newcastle, AMS I.33445004 (1: 53.1); Tweeds Head Country, AMS I.23687009 (1: ca. 29). Queensland: N of Townsville, AMS I.25837002 (3:52.3–52.5).

Xenocephalus armatus (as *Gnathagnus innotabilis*).—Australia: New South Wales, Montague Island, AMS IB.1298 (4 specimens: 12.8–16.0 mm SL). New Zealand: NMNZ P.23224 (1: 57.8 mm SL); Bay of Plenty, NMNZ P.11115 (1:48.2); off Tauraga Harbor, NMNZ 16118 (1: 104). Stomach of bluefin tuna, AMS I.B1297 (1: 30.3).

Xenocephalus elongatus.—Japan: Suruga Bay, USNM 296634 (1: 105 mm SL). Philippines: Romblon Island, USNM 122528 (1: 75.9).

Xenocephalus egregius.—Texas: Gulf of Mexico off Padre Island, USNM 268445 (1 specimen: 72.0 mm SL).

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CREAGRUTUS MELASMA, A NEW SPECIES OF CHARACID FISH (TELEOSTEI: CHARACIFORMES) FROM UPLAND STREAMS OF NORTHERN VENEZUELA

Richard P. Vari, Antony S. Harold, and Donald C. Taphorn

Abstract.—*Creagrutus melasma,* new species, occurs in a band across the northern headwaters of the Río Orinoco from Táchira state in the west to Monagas in the east. The species is also known from several Caribbean versant drainages, including the Ríos Tuy and Neverí. This small-bodied species, which barely exceeds 40 mm SL, is distinguished from congeners by its dorsal-fin and humeral pigmentation as well as a combination of meristic characters.

Resumen.—Se describe una nueva especie de *Creagrutus* que habita una franja en el piedmonte norte de las cuencas altas afluentes del Río Orinoco desde el estado Táchira en el oeste hasta Monagas en el este. La especie es también conocida desde varias cuencas del Mar Caribe, incluyendo los ríos Tuy y Neverí. Esta especie tiene un cuerpo pequeño que raramente excede los 40 mm de longitud estándar. Se distingue de sus congéneres por la pigmentación en la aleta dorsal, la forma de la mancha humeral, y la combinación de varias caracteres merísticas.

The presence of *Creagrutus* Günther in Lago de Valencia and adjoining drainages of northern Venezuela was first noted by Eigenmann (1920:12). Eigenmann, followed by Pearse (1920:11), identified these populations as *C. beni,* a species described by Eigenmann (1911:172) from the Río Beni, northeastern Bolivia. Although Eigenmann (1920:12) noted the darkly pigmented dorsal fin in material from Lago de Valencia and the Río Bue, a feature absent in *C. beni,* he considered the pigmentation a juvenile condition. The absence of such pigmentation in juveniles from elsewhere in the range of *C. beni* (see Eigenmann 1927:421–423) was not discussed.

The Lago de Valencia *Creagrutus* populations with dark dorsal-fin pigmentation, described herein as *C. melasma,* were independently recognized as distinct from all congeners by two of the authors (RPV & ASH) during their revisionary study of the genus and by the third author (DCT) in the course of research on fishes of the Río Apure basin (Taphorn 1992:173–175). The ongoing review of *Creagrutus* by the first two authors indicates that the new species has distinctive derived pigmentation patterns of the dorsal fin and humeral mark and is further separable from congeners on the basis of a combination of various meristic and morphometric characters. It is broadly distributed in northern headwaters of the Río Orinoco and several Caribbean drainage basins, being particularly common in the Lago de Valencia basin and northern headwaters of the Río Apure. It is described herein to make its name available for an ongoing phylogenetic study (RPV & ASH) of *Creagrutus* and putatively related taxa.

Materials and methods.—Specimens are deposited in the following collections: Academy of Natural Sciences of Philadelphia (ANSP); California Academy of Sciences (CAS), including former Indiana University collections (IU); Illinois Natural

Fig. 1. *Creagrutus melasma,* new species, holotype, MBUCV V-22198, 32.4 mm; Venezuela, Estado Guarico, Parque Nacional Guatopo, Río Orituco, first bridge along road from Santa Teresa to Altagracia.

History Survey, Champaign (INHS); Museo de Biología, Universidad Central de Venezuela, Caracas (MBUCV); Museo de Ciencias Naturales, Universidad Nacional Experimental de los Llanos Occidentales Ezequiel Zamora, Guanare, Venezuela (MCNG); Museo de Historia Natural La Salle, Caracas (MHNLS), and National Museum of Natural History, Smithsonian Institution (USNM). Counts and measurements were taken following methods outlined in Harold & Vari (1994). Range of standard lengths (in mm) of specimens measured for meristic and morphometric data are cited, followed by the number of specimens measured.

Creagrutus melasma, new species
Fig. 1

Creagrutus beni (not of Eigenmann 1911).—Eigenmann 1920:12 (Venezuela, Lago de Valencia and adjoining rivers; specimens from Maracay, IU 15133, and Isla del Buro (=Isla El Burro), IU 15134).—Pearse 1920:12, 24, 25, 43 (Venezuela, Lago de Valencia; food items and parasites; specimens served as basis for Eigenmann 1920 and 1927 citations).—Eigenmann 1927: 422 (in part; specimens from Venezuela, Maracay, IU 15133, and Isla del Buro (=Isla El Burro), IU 15134).

Holotype.—MBUCV V-22198, 32.4 mm, Venezuela, Estado Guarico, Parque Nacional Guatopo, Río Orituco, first bridge along road from Santa Teresa to Altagracia; collected by H. Moreno and A. Machado-Allison, 20 May 1992.

Paratypes.—All collected in Venezuela:

Estado Aragua: MBUCV-V21257, 56 specimens; 34.2–40.7 mm (3), CAS 79622, 10 specimens; Río Tuy basin, mouth of Río Cagua, ~10 km from Guayes, collected by R. Royero et al., 6 Apr 1991.

Estado Carabobo: ANSP 134171, 48 specimens; 33.5–34.2 mm (3), Río Guacara basin, Río Vigirima, ~10 km NNW of Guacara (~10°24′N, 67°55′W), collected by N. R. Foster et al., 30 Nov 1966. INHS 60021, 10 specimens; 33.2–36.0 mm (3), Lago de Valencia basin, Vigirima, Río Las Penitas (~10°20′N, 67°52′W), collected by D. C. Taphorn et al., 29 Nov 1990. MHNLS 503, 6 specimens; Lago de Valencia, at Guataparo dike, W of Valencia. MCNG 15354, 56 specimens; Río Manuare, collected by D. C. Taphorn, 19 Oct 1985. MCNG 15354, 56 specimens; Río Manuare, about 16 km along river from Manuare (09°59′N, 67°45′10″W), collected by C. Olds et al., 19 Oct 1985. MCNG 24622, 34 specimens; Caño La Camarca, N of San Diego, collected by D. C. Taphorn, 29 Dec 1990.

Estado Guarico: MBUCV V-24020, 2 specimens; 32.0–33.9 mm (2), collected with holotype.

Estado Yaracuy: USNM 219615, 3 specimens; 22.8–36.3 mm (3), USNM 219616, 1 specimen; 31.8 mm, Río Cojedas basin, Quebrada Grande, between Nirqua and Chivacoa, collected by F. Mago-Leccia, 19 May 1978.

Non-type specimens examined.—(all collected in Venezuela):

Estado Anzoátegui: MBUCV V-15444, 1 specimen; Quebrada Las Minas, tributary of Río Querecual.

Estado Apure: MCNG 10302, 19 specimens; Caño Naporal, tributary of Río Portuguesa. ANSP 165139, 1 specimen; Río Capanaparo, ~5.0 km downstream from crossing of highway between San Fernando de Apure and Puerto Paez (7°02′N, 67°25′W).

Estado Aragua: CAS 69297 (formerly IU 15133), 75 specimens; Río Bue at Maracay. MBUCV V-3045, Lago de Valencia basin, Río Limon, east of I.N.A. (Agricultural Research Institute). MCNG 14201, 3 specimens; Río Pao, near La Candelaria.

Estado Barinas: MCNG 5271, 402 specimens; MCNG 5401, 9 specimens; caño at entrance to Boconó dam. MCNG 8877, 8 specimens; Río Boconó at dam site. MCNG 5648, 12 specimens; Río Tucupido at Las Cañoas. MCNG 6347, 2 specimens; Caño Musao. MCNG 11944, 4 specimens; Caño Las Maravillas. MCNG 6546, 2 specimens; caño at Estero Chiguira.

Estado Bolivar: MHNLS 7240, 2 specimens; Caicara.

Estado Carabobo: CAS 69294 (formerly IU 15134), 266 specimens; Lago de Valencia, Isla El Burro. MHNLS 5882, 1 specimen; Lago de Valencia, Muelle Nuevo, opposite Isla El Burro. INHS 60446, 35 specimens; 32.2–35.0 mm (5), Lago de Valencia basin, Caño la Cumara, 3 km N of San Diego (10°16.55′N, 67°56.21′W). MBUCV uncat., 6 specimens; Lago de Valencia. MBUCV V-9919, 1 specimen; Río Onoto, Puente Onoto, about 40 km from San Carlos. MCNG 15281, 5 specimens; Río Chirigu, tributary of Río Pao. MCNG 15295, 7 specimens; caño near Belen. MCNG 15342, 60 specimens; Caño Guamita. MCNG 24647, Río Las Penitas at Vigirima.

Estado Cojedas: MCNG 6786, 2 specimens; Quebrada Camoruco. MCNG 13780, 6 specimens; Río Chorreron, 10 km from Apartaderos. MHNLS 2502, 1 specimen; Quebrada Guabinas, at highway from San Carlos to Acarigua. MHNLS 499, 6 specimens; Río Portuguesa basin, Río Manrique, 2 km upstream of Manrique. MHNLS 520, 10 specimens; Río Portuguesa basin, Quebrada Tierra Caliente, 5 km W of Manrique.

Estado Miranda: MCNG 14296, 3 specimens; at bridge near Araguita.

Estado Monagas: MBUCV V-9753, 1 specimen; Río Caripe, Sector Salle, on the Las Parcelas Road, 6 km from Carripito. MCNG 16977, 3 specimens; Río Cocoyal. MHNLS 517, 2 specimens; quebrada N of San Francisco de Maturin. MHNLS 527, 9 specimens; Río Colorado at San Antonio de Maturin. MHNLS 8064, 1 specimen; Río Aragua, at road from Maturin to Quiriquire, about 10 km from Maturin (63°25′W). MHNLS 8879, 1 specimen; Río Aragua, 10 km from Aragua de Maturin, at road from Maturin to Quiriquire. MHNLS 9437, 16 specimens; Distrito Acosta, Río Caripe basin, Embalse El Guamo.

Estado Portuguesa: MCNG 122, 1 specimen; Caño La Lora, tributary of Río Tucupido. MCNG 2443, 9 specimens; tributary of Río Tucupido. MCNG 8835, 3 specimens; Río Tucupido at dam site. MCNG 9215, 2 specimens; Río Tucupido, Los Hierros. MHNLS 6361, 2 specimens; Río Tucupido, Los Hierros, 7 km N of Tucupido. MHNLS 2678, 6 specimens; caño N of Tucupido, 6 km along road to Los Hierros. MCNG 19303, 3 specimens; MCNG 19638, 1 specimen; MCNG 19798, 6 specimens; Embalse Tucupido. MCNG 10666, 6 specimens; caño tributary of Río Boconó, near dam. MCNG 703, 8 specimens; tributary of Río Boconó, upstream from Puerto Paez. MCNG 124, 1 specimen; caño at road from Chabasquen to Barquismeto, tributary of upper Río Guanare. MCNG 10858, 5 specimens; Caño Buchi, between Acarigua and Guanare. MCNG 11261, 1 specimen; Río Las Marias, bridge on Highway 5. MCNG 13314, 1 specimen; MCNG 19769, 1 specimen; Río Las Marias. MCNG 11616, 5 specimens; Río Are, at bridge on Highway 5 between km 227 and 228. MCNG 11842, 1 specimen; Caño Bombicito, near Aparición. MCNG 15380, 14 specimens; Caño Volcan. MCNG 16727, 1 specimen; Caño San Rafael, at km 247 on Highway 5. MCNG 18737, 5 specimens; Río Saguas.

Estado Sucre: MBUCV V-15419, 2 specimens; Río Neverí, at road to Turimiquire, near Cambural. MBUCV V-15423, 3 specimens; Río Neverí, at road to Turimiquire, near Paraparo. MBUCV V-15428, 4 specimens; Río Neverí, near Paraparo. MBUCV V-15405, 2 specimens; Río Neverí, Quebrada Carrasposo. MBUCV V-15451, 3 specimens; Caño Cruz de Agua. MCNG 17051, 1 specimen; Caño Juan Antonio.

Estado Táchira: MCNG 6484, 4 specimens; tributary of Río Quinimari. MCNG 6626, 3 specimens; caño tributary to Río Chururu. MCNG 11661, 21 specimens; Caño Toronduy, at bridge on San Cristobal road. MCNG 11790, 1 specimen; Río San Agaton.

Diagnosis.—*Creagrutus melasma* has the unique jaw structure and premaxillary dentition typical of *Creagrutus.* Form of the humeral mark in this species is unique within *Creagrutus* (see "Remarks" below), darkest immediately dorsal to lateral line, vertically elongate, and oriented vertically to obliquely from anteroventral to posterodorsal. Distinctive large, dark spot on anterior portion of dorsal fin. Other characters which, in combination, serve to distinguish the species are small body size; short, stout gill-rakers, those of ceratobranchial and epibranchial about equal in length; and 5 teeth in main premaxillary row, with anterior tooth slightly displaced anteriorly and medially.

Table 1.—Morphometric and meristic features of holotype and ranges of values for 20 paratypes of *Creagrutus melasma,* new species. Standard length is expressed in mm; measurements 1 to 14 are percentages of standard length; 15 to 17 are percentages of head length.

	Holotype	Paratypes
Morphometrics		
Standard length	32.4	22.8–40.7
1. Snout to anal-fin origin	61.4	61.9–66.7
2. Snout to pelvic-fin origin	47.7	46.8–51.2
3. Snout to pectoral-fin origin	26.5	24.3–27.2
4. Snout to dorsal-fin origin	49.8	48.4–53.8
5. Dorsal-fin origin to hypural joint	56.9	53.3–57.7
6. Dorsal-fin origin to anal-fin origin	31.3	30.7–36.8
7. Dorsal-fin origin to pelvic-fin origin	30.2	29.0–35.2
8. Dorsal-fin origin to pectoral-fin origin	34.5	32.5–39.0
9. Caudal peduncle depth	11.9	11.5–13.1
10. Pectoral-fin length	21.3	18.7–21.5
11. Pelvic-fin length	15.9	14.8–16.7
12. Dorsal-fin length	25.7	21.4–28.5
13. Anal-fin length	21.3	18.6–21.6
14. Head length	26.4	24.5–26.9
15. Postorbital head length	43.8	42.4–47.8
16. Snout length	28.3	24.0–29.0
17. Bony orbital diameter	32.8	30.9–36.2
18. Interorbital width	31.9	29.3–34.7
Meristics		
Lateral line scales	35	34–36
Scale rows between dorsal-fin origin and lateral line	5	5–6
Scale rows between anal-fin origin and lateral line	4	4–5
Predorsal median scales	10	10–11
Branched dorsal-fin rays	8	7–8
Branched anal-fin rays	11	10–12
Branched pelvic-fin rays	7	7
Pectoral-fin rays	10	10–12
Vertebrae	35	34–36

Description.—Morphometric and meristic data for holotype and paratypes presented in Table 1. Body size relatively small, maximum observed standard length about 41 mm. Maximum body depth at pelvic-fin origin. Anterior profile of snout and dorsal profile of head meeting in rounded obtuse angle near vertical line immediately anterior to nares. Dorsal profile of head posterior to that line inclined and slightly convex. Predorsal profile of body slightly arched between supraoccipital and dorsal-fin origin. Dorsal profile of body straight to slightly concave between dorsal-fin origin and adipose fin. Dorsal profile from adipose fin to caudal-fin base straight. Ventral profile of head and body smoothly convex from margin of lower lip to pelvic-fin origin or with indistinct rounded obtuse angle delimiting anteroventral angle of dentary.

Upper jaw longer than, and overhanging, lower jaw. Anterior surface of snout fleshy, as in other *Creagrutus,* with minute papillae over surface. Greatest concentration of papillae on upper lip, margin of upper jaw, and in mouth on fleshy, plicate flaps between premaxillary teeth. Lower jaw with thick, fleshy anterior region and numerous papillae on lip. Infraorbitals poorly developed compared to many *Creagrutus* species, covering less than one half of cheek, with ventral and posterior margins of series broadly separated from preopercle. Posteroventral margins of infraorbitals three and four rounded, with indentation or concavity at their juncture. Curvature of posteroventral margin of third infraorbital approximately concentric with margin of orbit.

Premaxillary dentition with three major components: 1) undulating main row of five, rounded unicuspid to tricuspid teeth; anterior tooth slightly displaced anteromedially; 2) triangular cluster of three larger tricuspidate teeth, crowded together on medial portion of premaxilla; and 3) single tooth, similar in morphology to those of main premaxillary row, occurring lateral to third or fourth tooth of that row. Maxilla with two or three, rarely four, unicuspid to tricuspid teeth. Dentary teeth six, anterior three largest and tricuspid followed by three unicuspid teeth becoming successively shorter posteriorly.

Unpaired fins relatively large compared with most *Creagrutus*; similar to that of *C. lepidus* Vari et al. (1993). Dorsal-fin origin slightly posterior to vertical through pelvic-fin origin. Dorsal fin ii,8, rarely ii,7; distal margin nearly straight, with slight elongation of anterior rays. Anal fin ii or iii,10-12; distal margin slightly concave with anterior rays more elongate. Single, paired hooks present on 3 to 6 anterior branched anal-fin rays in males; hooks restricted to posterolateral surface of main shaft and posterior, secondary branch of each ray. Pectoral fin i,10-12; fin reaching posteriorly almost to pelvic-fin base. Pelvic fin i,7; approaching or, especially in sexually mature males, reaching anal-fin origin; with distal portion turned medially in some individuals giving fin slightly cupped appearance. Pelvic-fin hooks, when present, on all but smallest, distal branches of all branched rays.

Gill-rakers short and stout, those of ceratobranchial and epibranchial about equal in length; $3–6+8–10 = 11–16$ ($n = 21$).

Color in alcohol.—Dorsal surface of head with dark, shallow and deep chromatophores. Large, stellate deep-lying chromatophores lining interior surface of frontal, except in region of anterior fontanel. Shallow chromatophores punctate, present over most dorsal surfaces; most concentrated on snout and on ventral of upper lip, with small crescent of dark pigmentation immediately anterior of nares. Three patches of chromatophores extending posteriorly from portion of main field immediately dorsal to anterior margin of orbit; one over each orbit and one along midline over fontanel. Band of scattered dark chromatophores extending from pigmentation on snout posteriorly to anteroventral margin of orbit and then around ventral and posterior margin of orbit. Scattered stellate dark chromatophores overlying dorsal portions of infraorbitals and opercle. Dorsal portion of body with small dark chromatophores concentrated on and below posterior portion of scales; overall pattern reticulate. Anterior one-half of predorsal surface with longitudinal concentration of large stellate chromatophores. Small dark chromatophores along dorsal-fin base. Humeral mark darkest immediately dorsal to lateral line, vertically elongate with orientation ranging from vertical to somewhat posterodorsally oblique. Dark midlateral stripe extending from pectoral girdle to caudal-fin base (Fig. 1). Stripe diffuse anteriorly; most sharply defined ventrally and posteriorly; expanded into diffuse triangle extending slightly ventral to lateral line on caudal peduncle. Region of body between midlateral stripe and anal-fin base unpigmented or with very small dark chromatophores delineating myosepta. Dorsally tapered concentrations of dark pigment located between bundles of fin-ray musculature at base of anal fin.

Small dark chromatophores on caudal-fin membranes; greatest concentrations along central and outer branched rays and dorsal and ventral procurrent rays. Small dark chromatophores on anal-fin membranes mainly restricted to narrow bands along anterior and posterior margins of fin rays. Slightly larger, darker chromatophores forming diffuse longitudinal band on distal one-third of anal fin; some specimens with greatly enlarged chromatophores, giving appearance of dark spot on fin anteriorly. Small dark chromatophores present across dorsal-fin membranes; large, very dark chromatophores concentrated in central portion of anterior one-half of fin, giving appearance of large dark spot (spot well developed across observed size range; present in 14.8 mm SL juvenile, MBUCV V-21257). Pectoral fins with series of dark chromatophores associated with most rays, most numerous laterally. Pelvic fins unpigmented.

Color in life.—Dorsal and anal fins with bright red anteriorly, and black centrally (see color plate in Roman 1992:169). Dorsal lobe of caudal fin red. Dorsal surface of eye with red patch overlying reflective guanine.

Distribution.—Northern Venezuela east of the Andes from Estado Táchira in the west to Sucre in the east. Occurs in many upland tributaries of the Río Orinoco basin and the Ríos Tuy and Neverí of the Caribbean versant.

Ecology.—This species inhabits small, shallow, shady streams of the Andean piedmont where the water is usually clear and substrate ranges from sand to gravel (Taphorn 1992:174). The diet of adults consists of small seeds, ostracods, gastropods, and aquatic insects, especially chironomid larvae (Pearse 1920:24, 25; Winemiller, pers. comm. in Taphorn 1992:174). Spawning occurs throughout the wet season, with individuals probably spawning more than once a season (Taphorn 1992:174).

Etymology.—A noun in apposition from the Greek melasma, meaning a black spot, in reference to the distinctive pigmentation of the dorsal fin.

Remarks.—Material herein referred to *Creagrutus melasma* was identified as *C. beni* by Eigenmann (1920:12; 1927:422). This is puzzling, given the distinctiveness of the new species and the fact that Eigenmann described *C. beni.* We have examined the holotype of *C. beni* and other material from near the type locality. *Creagrutus melasma* and *C. beni* are readily distinguished by number of vertebrae (34 or 35, 1 specimen out of 60 had 36, in *C. melasma* versus 38 in the holotype of *C. beni*), and relative size of the infraorbital bones (poorly developed, with posteroventral margin of the series distinctly separated from the preopercle in *C. melasma* compared to well developed, with the posteroventral margin approaching or contacting the preopercle in *C. beni*).

Creagrutus melasma appears most similar to *C. lepidus* in body and fin form, premaxillary dentition and gill-raker shape. The two species differ, however, in their humeral spots (distinctly vertically elongate in *melasma* versus incorporated into midlateral stripe in *lepidus*), midlateral stripe (diffuse and tapering anteriorly in *melasma* versus broad and well developed anteriorly in *lepidus*), and dorsal-fin pigmentation (patch of dark pigmentation present in *melasma* versus absent in *lepidus*; compare Fig. 1 with Vari et al. 1993:fig. 1).

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A NEW GENUS OF FOSSIL PUFFERFISH (TETRAODONTIDAE: TETRAODONTIFORMES) BASED ON A NEW SPECIES FROM THE OLIGOCENE OF RUSSIA AND A REFERRED SPECIES FROM THE MIOCENE OF UKRAINE

James C. Tyler and Alexandre F. Bannikov

Abstract.—A new genus of tetraodontid pufferfish, *Archaeotetraodon,* is proposed for two fossil species with uniquely specialized bifurcate scale spinules: *winterbottomi,* a new species based on ten specimens from the Oligocene of Russia in which nearly all of the spinules are bifurcate; and *jamestyleri* Bannikov (1990), based on two complete specimens and a fragment from the Miocene of Ukraine in which only two scales in the middle of the body have bifurcate upright spinules. An especially long rayless pterygiophore extending forward from the dorsal-fin origin in *Archaeotetraodon* (in *winterbottomi*; condition unknown in *jamestyleri*) is similar to that found in the Recent *Lagocephalus* but this feature cannot be unequivocally polarized and may not indicate relationship between these two genera.

Expeditions by the Paleontological Institute of the Russian Academy of Sciences to the North Caucasus have discovered a rich Lower Oligocene marine ichthyofauna in the Pshekhsky Horizon of the Lower Maikop deposits. This was first described by Danilchenko (1960), with further studies more recently by the second listed author and his cooperating colleagues. Among newly excavated fossils of early Oligocene age are ten specimens, four in counterpart plates, that are unique among tetraodontids by having most of the upright scale spinules that cover the entire body bifurcate from the base and divergent distally. The bifurcate scale condition is shown to be a specialization because all Recent and one of the other fossil tetraodontids as well as all members of the diodontid sister group have undivided upright scale spinules. We describe these specimens as a new species and type of a new genus: *Archaeotetraodon winterbottomi.*

Our re-examination of the scales in materials of all previously described fossil tetraodontids based on relatively entire specimens shows that one of them, *Sphoeroides jamestyleri* Bannikov (1990), from the Miocene of Ukraine, has most of the scales with unbranched spinules but that a limited patch in the middle of the body has bifurcate spinules. We transfer *S. jamestyleri* from *Sphoeroides,* into which it was originally placed mostly for the convenience of not having to create a new genus, to *Archaeotetraodon* on the basis of its sharing with *A. winterbottomi* specialized bifurcate scales. The two species of *Archaeotetraodon* differ from one another not only in the coverage with bifurcate scales but also in several osteological features.

Methods

Length is standard length (SL) unless otherwise stated. Fossil materials are from the collections of the Paleontological Institute (PIN) of the Russian Academy of Sciences in Moscow, the Museo Civico di Storia Naturale di Verona (MCSNV), the Istituto di

Geologia della Università di Padova (IGUP), and Sammlung der Philosophie-theologie Hochschule der Eichstätt (SPHE). Comparative anatomical preparations and radiographs of Recent species of tetraodontiforms are those listed in Tyler (1980), supplemented by those of tetraodontids listed in Tyler et al. (1992).

In many derived groups of tetraodontiforms, including tetraodontids, there is a bony element in the upper midline of the body just in front of the soft dorsal fin that is thought to represent a basal pterygiophore that no longer bears dorsal-fin spines. This was called a supraneural in Tyler (1980), but is here referred to as a rayless pterygiophore, following the recommendation of Mabee (1988:836), who demonstrated that true supraneurals (predorsals) are not homologous with such pterygiophores.

For tetraodontoid phylogeny we follow the cladistic analysis of Winterbottom (1974) and the evolutionary systematics of Tyler (1980), which, respectively on the basis of specialized myological and osteological features, are in agreement that: diodontids are the sister group of tetraodontids; molids are the sister group of the tetraodontid + diodontid clade; triodontids are the sister group of the tetraodontid + diodontid + molid clade; and the Eocene eoplectids are the morphologically primitive sister group of all of these other tetraodontoids. Among other tetraodontiforms, the balistoid + ostracioid clade is the first outgroup and the triacanthoid clade the second outgroup.

There is no cladistic analysis available for the genera of tetraodontids, and Tyler (1980) simply placed the Recent genera into three groups of relative degrees of morphological specialization in what can be considered an unresolved trichotomy. The Eocene *Eotetraodon* was presumed in that work to be the morphologically primitive sister group of these three groups of Recent genera because of its retention of such plesiomorphic features as twelve principal caudal-fin rays and pleural ribs (both of which are found in triodontids); however, because diodontids and molids have no pleural ribs and fewer than twelve caudal-fin rays, it is more parsimonious to propose that the twelve caudal-fin rays and pleural ribs of *Eotetraodon* are reversals.

Although it was inconsistent with his presumed phylogeny of tetraodontid genera, Tyler (1980) continued the practice of recognizing *Canthigaster* as subfamilially distinct from other tetraodontids even though the genus *Carinotetraodon* was shown to be anatomically intermediate between *Canthigaster* and other tetraodontids in many ways, including several specialized features (e.g., skin ridge-lifting behavior, highly arched vertebral column, large haemal spines on abdominal vertebrae). This led Tyler (1980) to the conclusion that *Carinotetraodon* and *Canthigaster* had a close common ancestry. Therefore, we agree with Winterbottom (1974:99) that *Canthigaster* cannot reasonably be recognized as subfamilially distinct from (and sister group to) a polyphyletic subfamily for all other tetraodontids, including *Carinotetraodon*. With the phylogeny of tetraodontid genera so poorly known, we compare any unusual features of *Archaeotetraodon* with comparable conditions in all other tetraodontid genera, including the specialized *Canthigaster* + *Carinotetraodon* clade to which we doubt *Archaeotetraodon* is closely related.

Family Tetraodontidae (sensu Tyler, 1980)

Archaeotetraodon, new genus

Type species.—*Archaeotetraodon winterbottomi*, new species, by present designation; other species, *Sphoeroides jamestyleri* Bannikov (1990), by referral herein.

Diagnosis.—Differs from all other tetraodontids by the presence of bifurcate upright spinules on either most of the scale plates over the entire body (in *winterbottomi*) or on many of those of the middle of the body (in *jamestyleri*).

Description. — With the exception of a few species in which scales have been secondarily lost (several species of both *Sphoeroides* and *Takifugu* and single species of both *Lagocephalus* and *Tetraodon*; Tyler 1980:297–298) all Recent tetraodontids have specialized scales in which the basal plate, which has two or more processes radiating out into the skin, bears an upright spinule that protrudes through the skin as a prickle. The spinule is of varying stoutness and length, but most often is short and slender (in contrast to the larger and stouter projecting spines in diodontids), giving a shagreen-like quality to the skin (see illustrations of scales in Recent species of numerous tetraodontid genera in Tyler 1980: 291–297).

That the new species of tetraodontid from the Oligocene, *A. winterbottomi,* has an extensive covering of bifurcate scale spinules led us to re-examine the scales in the two previously described species of fossil tetraodontids based on relatively entire specimens, the Eocene *Eotetraodon pygmaeus* (Zigno 1887) and the Miocene *Sphoeroides jamestyleri* Bannikov (1990). The holotype and four other previously unreported specimens of *E. pygmaeus* are covered with unbranched spinules like those of all Recent tetraodontids. The holotype of *Sphoeroides jamestyleri* does not have the scales preserved, but the paratypic entire specimen has a complete covering of scales, most of which have unbranched spinules. However, some scales in the middle of the body (it is impossible to distinguish whether this is dorsal, ventral, or lateral) are just as distinctly bifurcate distally as those in *A. winterbottomi,* although the spinules are proportionally shorter in *S. jamestyleri.*

Because all species, both fossil and Recent, of the diodontid sister group have scale plates with unbranched upright spinules or spines like those of all Recent and one of the fossil species of tetraodontids (except more massive), we propose that spinules with undivided upright shafts are primitive for the tetraodontid + diodontid clade and that the deeply bifurcate spinules in the Oligocene *A. winterbottomi* and Miocene *S. jamestyleri* are a specialization. Therefore, the bifurcate spinule condition is a synapomorphy of *A. winterbottomi* and *S. jamestyleri.* The latter was originally placed in *Sphoeroides* because it is thought to be a morphologically relatively primitive genus (Tyler 1980) defined by a combination of what seem to be mostly plesiomorphic features, and no features that are known to be specialized. It was simply convenient to place *S. jamestyleri* in that poorly defined genus pending acquisition of better preserved materials showing more internal features which might clarify its relationships, but such materials are not yet available. However, we can state that all of the few known internal features of similarity between *S. jamestyleri* and the species of *Sphoeroides* are plesiomorphic (e.g., moderate interorbital and ethmoid widths; moderate and mostly laterally directed extensions of the lateral ethmoids, sphenotics, and pterotics) and that there are no known specialized features of similarity that unite *S. jamestyleri* with *Sphoeroides.* Because *S. jamestyleri* does share the uniquely derived feature of bifurcate scale spinules with *A. winterbottomi,* we remove *jamestyleri* from *Sphoeroides* and place it in *Archaeotetraodon* along with *winterbottomi.*

We note that in molids the basal plates of the scales are rounded to rectilinear and bear a central emargination or low spinule, and in at least smaller specimens of *Mola* some of these spinules are branched distally (see illustration in Tyler 1980:369). In all other tetraodontoids with upright spinules on the basal plate, the spinules are unbranched (a single spinule in eoplectids, the sister group of all other tetraodontoids, and several spinules in the poorly known zignoichthyids, that are most closely related to the tetraodontid + diodontid clade). In triodontids the scales bear a low spiny ridge and there are no upright spinules. Therefore, on the basis of the phylogeny of tetraodontoid families proposed by both Winterbottom (1974) and Tyler (1980), it is most parsimonious to presume that the distally branched spinules in some molids and the deeply bifurcate branched spinules in *Archaeotetraodon* are independent acquisitions.

Etymology.—From the Greek: *archaios,* old or ancient, and *tetraodon,* for the four tooth plates characteristic of the family Tetraodontidae; masculine.

Similarities of *Archaeotetraodon* to Other Tetraodontids

Rayless pterygiophore.—*Archaeotetraodon winterbottomi* has an exceptionally long rayless pterygiophore, averaging 18% SL as measured from the anterior end of the element to the anterior end of the base of the soft dorsal fin in the three specimens in which this region is preserved. We presume that this long slender element is a single piece of bone from its posterior end at the dorsal-fin origin to its anterior end at the level of the vertical through the centrum of the sixth to seventh abdominal vertebra because we cannot see any interruptions or articulations in it, although our view of the bone is somewhat obscured by the layer of spiny scales in the overlying skin. In the holotype of *A. jamestyleri* the region anterior to the dorsal fin is poorly preserved, while in the paratypic entire specimen the skeleton is much disarticulated and it is not possible to recognize a rayless pterygiophore among the mixture of bones. Thus, the condition of the rayless pterygiophore in *A. jamestyleri* is unknown and in the following discussion of the rayless pterygiophore the statements about *Archaeotetraodon* are based on the conditions in *A. winterbottomi.*

In some Recent tetraodontids with relatively long rayless pterygiophores, this element does not reach posteriorly to the dorsal-fin origin but, rather, terminates anterior to it and articulates there with an anterior process on the distal end of the first basal pterygiophore of the dorsal fin. We see no evidence of such an anterior process on the first basal pterygiophore in *Archaeotetraodon,* but that pterygiophore is not well exposed in our material. Although we cannot be absolutely sure of it, we have no reason to believe that the rayless pterygiophore in *Archaeotetraodon* does not extend as a single slender bone for the full length of the distance from its anterior end to the dorsal-fin origin. Nevertheless, it is possible that some small portion of our measurement of the rayless pterygiophore posteriorly in *Archaeotetraodon* may include part of the distal head of the first basal pterygiophore of the dorsal fin. Even with that caveat, we believe that the average measurement of 18% SL is a fair estimate of the length of the rayless pterygiophore in *Archaeotetraodon.* No other tetraodontid has a rayless pterygiophore as long as that in *Archaeotetraodon,* but a few genera contain species with rayless pterygiophores almost as long.

The rayless pterygiophore is especially long and slender in the six species of *Lagocephalus* examined, more so in some species than in others. For example, in *L. inermis* (Temminck & Schlegel), *L. laevigatus* (Linnaeus), *L. lunaris* (Bloch & Schneider), and *L. spadiceus* (Richardson) the rayless pterygiophore length averages 8–9% SL (in 2 to 12 specimens of each species examined), while it averages 12% SL in *L. sceleratus* (Gmelin) (in 4 specimens) and 15% SL in *L. lagocephalus* (Linnaeus) (in 2 specimens), the latter being the longest rayless pterygiophore of which we are aware among Recent tetraodontids. In all of these species of *Lagocephalus* the distal end of the first dorsal-fin basal pterygiophore has a prominent anterior process to which the rayless pterygiophore articulates. The rayless pterygiophore of *Lagocephalus,* even though shorter than in *Archaeotetraodon,* extends at least as far forward as in *Archaeotetraodon,* and, in *L. lagocephalus,* extends even further forward, to the level of the vertical through the region of articulation between the centra of the fourth and fifth abdominal vertebrae. The two species of *Lagocephalus* with the longest rayless pterygiophores, *L. sceleratus* and *L. lagocephalus,* are streamlined in form and have an offshore pelagic habitat; there may be a correlation in tetraodontids between a long and slender rayless pterygiophore and a strong swimming, pelagic mode of life.

The rayless pterygiophore is relatively long in the nine species of *Canthigaster* examined, averaging between 9% and 13% SL. The rayless pterygiophore of *Canthigaster* differs from the slender rod as found in *Archaeotetraodon* and *Lagocephalus* in being heavier, deeper, concave ventrally, and curved ventrally at its anterior end, following the contour of the arched back.

In most species of *Sphoeroides* the rayless pterygiophore is short, averaging about 4–5% SL, but the element is somewhat longer in such species as *S. spengleri* (Bloch) and *S. marmoratus* (Lowe), averaging 6–7% SL. In *S. formosus* (Gunther) (sometimes recognized in the monotypic *Guentheridia*) the rayless pterygiophore is far longer, heavier, and deeper than in the other species of *Sphoeroides,* averaging 12% SL (in 5 specimens) but without the slender form found in *Lagocephalus* and *Archaeotetraodon.*

Other than the species mentioned above, we know of no other tetraodontids with notably long rayless pterygiophores, i.e., of 10% SL or greater length. The condition of the rayless pterygiophore in a variety of tetraodontids can be assessed from the illustrations of representative species in Tyler (1980:figs. 195, 203, 226–244), including its absence in a few species.

The similarity in the length of the long, slender rayless pterygiophore between *Archaeotetraodon* and some species of *Lagocephalus* is difficult to interpret because of the unknown phylogeny within tetraodontids and because diodontids, their sister group, do not have a rayless pterygiophore. In the molid sister group of the tetraodontid + diodontid clade the rayless pterygiophore is either present as a short deep piece (*Mola*), absent or fused with the first basal pterygiophore of the soft dorsal fin (*Masturus*), or perhaps consolidated into a long complex structure that connects the first basal pterygiophore of the soft dorsal fin with the supraoccipital crest (*Ranzania*). In triodontids a rudimentary spiny dorsal fin, when present, of two or three spines is borne on two basal pterygiophores that are connected to the basal pterygiophores of the soft dorsal fin by two short rayless elements. These two short elements presumedly are derived from basal pterygiophores that no longer support spines at the rear of the rudimentary spiny dorsal fin. In those populations (Indian Ocean) of *Triodon macropterus* (Lesson) (the only Recent representative of the family) that usually entirely lack the spiny dorsal fin, all four of the elements in this series that extends anteriorly from the soft dorsal-fin origin therefore are rayless pterygiophores, the first of which is elongate and the more posterior three pieces short. In eoplectids a well-developed spiny dorsal fin is present and its basal pterygiophores connect with those of the soft dorsal fin without the intervention of rayless pterygiophores. Among the outgroup tetraodontiforms, the six dorsal-fin spines in triacanthoids are borne on four or five basal pterygiophores and there are no rayless pterygiophores between the basal pterygiophores of the spiny and soft dorsal fins. In balistids the three dorsal-fin spines are borne on two basal pterygiophores that form a complex carina supported by a rayless pterygial strut that braces the carina against the first basal pterygiophore of the soft dorsal fin, with the strut apparently being derived from the third basal pterygiophore of the spiny dorsal fin of triacanthoids. In monacanthids there are two dorsal-fin spines, and the less robust carina, which is formed from a single basal pterygiophore, is not supported posteriorly by a pterygial strut. In ostracioids the spiny dorsal fin is absent and a long and deep (aracanids) or short (ostraciids) rayless pterygiophore is present anterior to the base of the soft dorsal fin. Thus, when the spiny dorsal fin is absent in tetraodontiforms such as ostracioids, rayless pterygiophores are present and apparently represent basal pterygiophores of the absent spiny dorsal fin, while the reduction in number of dorsal-fin spines and their supporting basal pterygiophores from posteriorly in the series in balistids in comparison to triacanthoids is accompanied by the apparent conversion of the third basal pterygiophore of triacanthoids into the rayless pterygial strut of balistids.

Most germane, however, is the situation in triodontids, the sister group of all other Recent families of tetraodontoids, in which the distinction between basal pterygiophores and rayless pterygiophores depends simply on whether the rudimentary dorsal-fin spines are present or not. Therefore, we propose that the presence of a rayless pterygiophore, representing a rudimentary support of the now absent spiny dorsal fin, is primitive for the tetraodontid + diodontid + molid clade of tetraodontoids. However, it is equally parsimonious to hypothesize that: 1) a rayless pterygiophore was present in the ancestor of the tetraodontid + diodontid clade and that the rayless pterygiophore was independently lost by all diodontids and by some tetraodontids; or 2) a rayless pterygiophore was lost in the ancestor of the tetraodontid + diodontid clade and the rayless pterygiophore acquired by most tetraodontids as a reversal to the ancestral tetraodontoid condition. Moreover, even given that a rayless pterygiophore is primitive for the tetraodontid + diodontid + molid clade, it is not known whether that element was long or short or slender or stout. Presuming that the rayless pterygiophore of the ancestral tetraodontoid without a spiny dorsal fin was one of the four dorsal pterygial elements as found in triodontids, it could as logically be the long, stout, anteriormost first rayless pterygiophore of those *Triodon macropterus* lacking dorsal-fin spines as it could be one of the three short and heavy more posterior rayless elements. We have no way of knowing at present whether the rayless pterygiophore in the ancestral tetraodontoid without a spiny dorsal fin was long or short. Therefore, similarity in the long rayless pterygiophore of *Archaeotetraodon* and *Lagocephalus* may be plesiomorphic and not indicative of relationship.

Our surmise is that the great length and, especially, the slender form of the rayless pterygiophore is a derived feature, but since we do not know of any unequivocally derived features shared by *Archaeotetraodon* and *Lagocephalus,* it may be that the putatively derived condition of the long, slender rayless pterygiophore is independently acquired by these two genera. From what little is known of its osteology, *Archaeotetraodon* differs from *Lagocephalus* in having relatively evenly tapered neural and haemal spines on the vertebrae of the caudal peduncle anterior to the penultimate vertebra, whereas in *Lagocephalus* these are expanded anteroposteriorly, a derived condition (absent in other tetraodontids and in all other tetraodontoids).

Elongate head spines.—In at least one specimen of *Archaeotetraodon winterbottomi* the spinules on the top of the head are longer than elsewhere and many of these are not bifurcate. In only one other species of tetraodontid are the spinules on the head much longer than those on the body, this being one of the several species of *Amblyrhynchotes, A. piosae.* In *A. piosae* the body is made exceptionally prickly by spinules that are longer than in other tetraodontids, and the spinules on the top and side of the front of the head are especially elongate, up to 8% SL. These spinules are proportionally far longer than those that are slightly elongate on the top of the head in *A. winterbottomi.* In both cases among tetraodontids in which speciose genera have a few species in which spiny scales are lost, these species are not considered to be closely related within their respective genera (*Sphoeroides* and *Takifugu*) and the loss of spines has been considered to be independent (Tyler 1980: 297). With so much homoplasy in even the presence or absence of spines within tetraodontid genera, we place no phylogenetic significance on the fact that both one specimen of *A. winterbottomi* and one of the several species of *Amblyrhynchotes* have the spinules longer on the head than elsewhere, especially when the spinules in *A. winterbottomi* are otherwise so different (shorter and bifurcate) than those in *A. piosae,* and when there are no other derived features of similarity between *Archaeotetraodon* and any of the species of *Amblyrhynchotes. Archaeotetraodon* differs from *Amblyrhynchotes* not only by its short bifurcate scales but most notably also by having 18 versus 19 or 20 vertebrae (in the three species of *Amblyrhynchotes* examined) and a long (18% SL) versus short rayless pterygiophore (5–6% SL in three species of *Amblyrhynchotes*).

Generic Relationships

On the basis of its few known osteological and external features we are not able to place *Archaeotetraodon* into one of the three morphological groups recognized by Tyler (1980) for Recent genera of tetraodontids. Likewise, we do not find any special similarity between the two species of *Archaeotetraodon* and other fossil species of tetraodontids. The Eocene *Eotetraodon pygmaeus* (Zigno) has neither bifurcate scales nor a long rayless pterygiophore. The Pliocene *Sphoeroides hyperostosus* (Tyler et al. 1992) is based on skulls and anterior vertebrae but the scales and portions of the body that might include a rayless pterygiophore are unknown; it differs from *Archaeotetraodon* by the extensive hyperostosis of many skull bones at sizes as small as that of the larger specimens of either of the two species of *Archaeotetraodon.* Several other species of fossil tetraodontids have been named on the basis of pieces of jaw bones of Miocene and younger age but these cannot be usefully compared with the fossil species based on more complete specimens.

We can only call attention to the unique bifurcate scales that distinguish *Archaeotetraodon* from all other genera of tetraodontids and note that while the elongate and slender rayless pterygiophore as found in *A. winterbottomi* and some *Lagocephalus* may be a specialization for a pelagic mode of life, it seems likely to have been an independent acquisition in the few pelagic species of *Lagocephalus* and in *A. winterbottomi,* which has been found in a predominantly pelagic fossil ichthyofaunal assemblage.

Archaeotetraodon winterbottomi, new species

Figs. 1–4

Diagnosis.—*Archaeotetraodon winterbottomi* differs from the only other species of the genus, *A. jamestyleri,* by having: a vertebral formula of 8+10 (versus 7+11 in *jamestyleri*); almost complete covering of bifurcate scale spinules (versus bifurcate only on middle of body); haemal spine of penultimate vertebra with a moderately long posteroventral process under the parhypural region (versus no prolongation); supracleithrum relatively long and narrow (versus shorter and thicker).

Description.—Body moderately elongate (Figs. 1–2). Vertebrae 18 in four specimens in which total number can be counted, with eight abdominal and ten caudal in only specimen (holotype) in which proximal end of first anal-fin basal pterygiophore can be seen in association with a haemal spine; vertebral column relatively straight, only gently arched in abdominal region. Caudal skeleton relatively distinct in holotype, and having normal tetraodontid pattern of a long parhypural, a lower hypural plate fused to last centrum, an upper free hypural plate and an epural (exact shape unclear) above last centrum. Penultimate vertebra (PU_2)

Fig. 1. Photograph of holotype of *Archaeotetraodon winterbottomi,* PIN 3363/111, 90.0 mm SL, Lower Oligocene (Maikopian) of North Caucasus, southwest Russia.

with broad neural and haemal spines, the latter prolonged posteriorly under a little more than half of length of parhypural; more anterior caudal vertebrae with more slender neural and haemal spines, except haemal spines of first three caudal vertebrae short, where proximal ends of anal-fin basal pterygiophores are supported. First three abdominal vertebrae apparently with bifid neural spines and fourth abdominal vertebra with neural spine bifid anteriorly but undivided posteriorly, where it is prolonged posteriorly over base of neural spine of fifth vertebra.

Dorsal-fin rays nine in two specimens and nine or perhaps ten in one specimen. Anal-fin rays eight in only specimen in which all rays are preserved, at least basally. Basal pterygiophores in dorsal fin seven and in anal fin six in single specimen in which these can be counted. Caudal-fin rays 11 in four specimens, best preserved in holotype, with uppermost ray and two lowermost rays unbranched and other eight rays branched, four above middle of hypural plate and four below (typical tetraodontid condition). Caudal-fin length 23.3–27.3% SL (25.8% average) in three specimens. Pectoral fin not well enough preserved to describe.

A single upright spinule arising from each basal scale plate, spinules mostly short and divergently bifurcate from base (Fig. 3), length of upright spinules along top of middle of body in nine specimens 0.7–1.6% SL (1.3% average); these prickly scales present continuously over most of head and body.

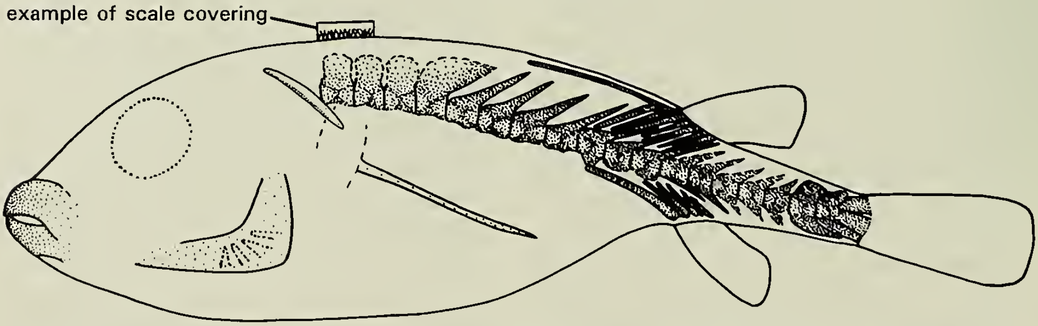

Fig. 2. Reconstruction of *Archaeotetraodon winterbottomi,* based on the holotype, data as in Fig. 1.

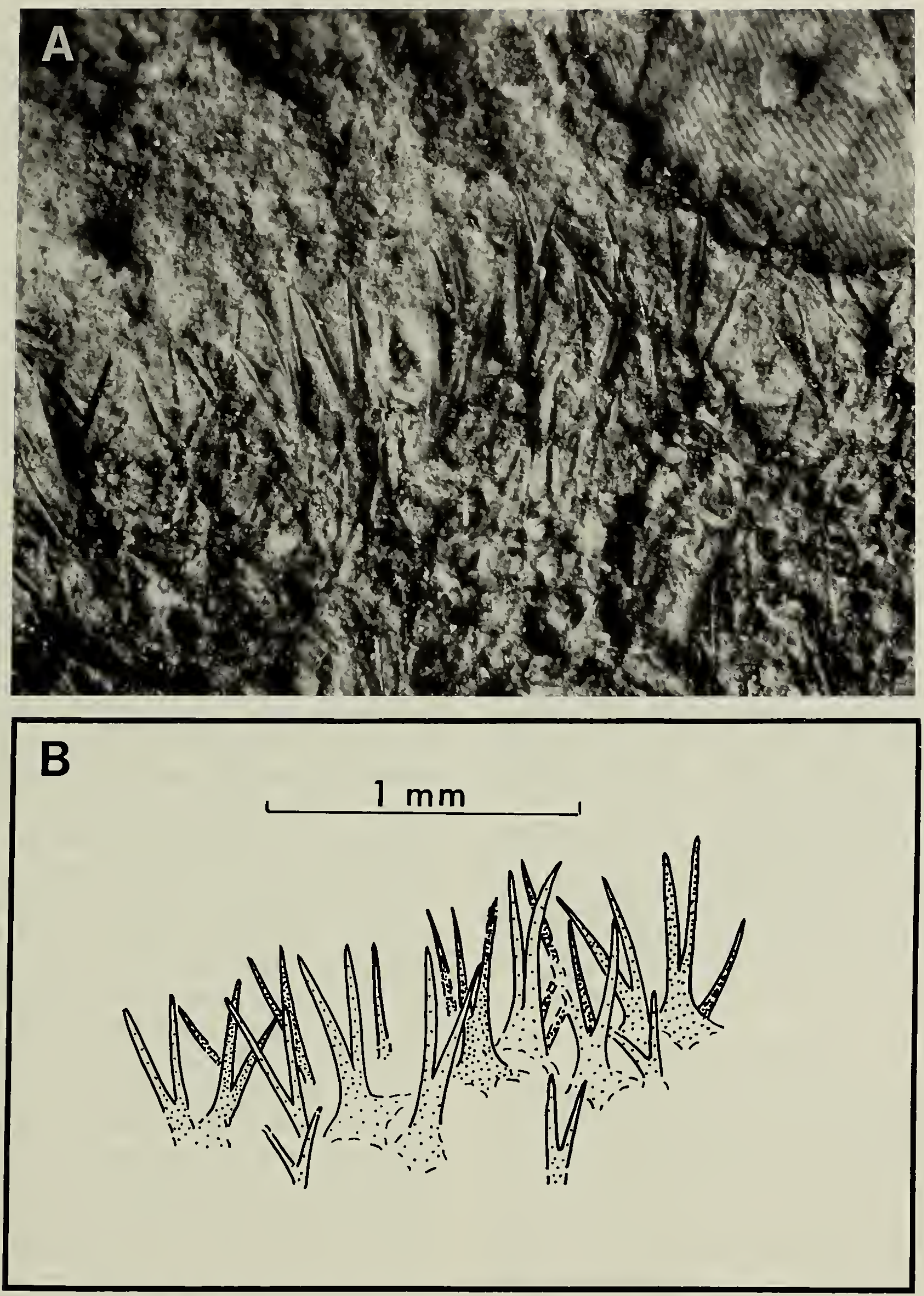

Fig. 3. A. Photograph of scales along dorsal surface of paratype of *Archaeotetraodon winterbottomi,* PIN 3363/115, ca. 40 mm SL, longest upright bifurcate spinules 0.5 mm (1.3% SL), age and locality as in Fig. 1. B. Drawing of selected scales along same dorsal surface as in A.

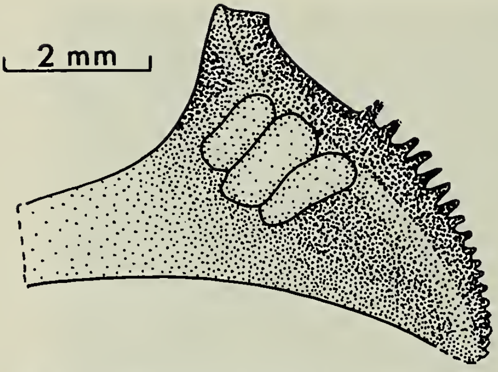

Fig. 4. Drawing of inner surface of premaxilla of holotype of *Archaeotetraodon winterbottomi,* data as in Fig. 1.

In one specimen (PIN 3363/120) a small group of about ten spinules on top of head slightly longer than those on body (1.4% versus 0.9% SL) and mostly unbranched, with all other spinules on head and body bifurcate; we presume that having a few slightly elongate and non-bifurcate spinules on top of head is normal for at least some specimens of this species (perhaps a sexually dimorphic feature).

Rayless pterygiophore long and slender, apparently a single piece, its posterior end at origin of soft-dorsal fin and its anterior end at level of vertical through centrum of sixth or seventh abdominal vertebra; its length 16.0–20.6% SL (18.1% average) in three specimens.

Inner surface of premaxilla visible in two specimens, both of which have three trituration teeth, about three times as mediolaterally wide as anteroposteriorly deep; medial edge of premaxilla with articular processes increasing in size posteriorly in series (Fig. 4), interdigitating with similar processes on apposed premaxilla. Inner surface of dentary visible in one specimen and no trituration teeth present; medial edge of dentary with articular processes like those of premaxilla.

Preopercle broad and strongly curved, with ridges in middle region. Postcleithrum long and slender. Supracleithrum long and gently curved, with a low medial flange. Interorbital width moderate, least width about 4.0–4.5% SL in two entire specimens in which it is possible to recognize the lateral edges of the upper orbit in neurocrania preserved in dorsoventral view. No other features of skeleton clearly enough exposed or preserved to warrant description.

Etymology.—winterbottomi, honoring our friend and colleague Richard Winterbottom, Royal Ontario Museum, in recognition of the excellence of his important studies on the phylogeny of tetraodontiforms and of his great help to us in our own efforts with the plectognath fishes.

Type materials.—Holotype: PIN 3363/111 (head to left) and 111a, counterpart plates, River Pshekha, 90.0 mm SL. Paratypes: PIN 3363/112 (head to right), single plate, River Belaya, 53.9 mm SL; PIN 3363/113 (head to left), single plate, River Belaya, 36.5 mm SL; PIN 3363/114 (head to left) and 114a, counterpart plates, River Belaya, 27.8 mm SL; PIN 3363/115 (dorsoventral impression), single plate, River Belaya, ca. 40 mm SL; PIN 3363/116 (head to left), single plate, River Kuban, most of head missing, length of vertebral column 32.6 mm; PIN 3363/117 (head to left), single plate, River Pshekha, fragment of most of vertebral column, whose length is ca. 33 mm; PIN 3363/118 and 118a (dorsoventral impression), counterpart plates, River Belaya, 24.7 mm SL; PIN 3363/119 (head to left) and 119a, counterpart plates, River Belaya, 52.1 mm SL; PIN 3363/120 (head to right), single plate, River Belaya, 64.2 mm SL. Except for the two specimens preserved entirely as dorsoventral impressions, all of the above are preserved as lateral impressions of the body in which, however, the neocranium is often in dorsoventral view.

Type locality.—Holotype from River Pshekha (at Gorny Luch). Paratypes from Rivers Pshekha, Belaya (upstream from the settlement of Abadzekhskaya), and Kuban (near the town of Cherkessk), all of which sites are within, respectively, 32 and 150 km of one another in the Pshekhsky (Pshekha) Horizon, lower part of the Maikop (Maikopian) deposits, Lower Khadum Formation, Lower Oligocene, North Caucasus of southwest Russia, about 35 million years ago.

Stratigraphy and ichthyofaunal associations.—About 55 other species of fishes have been collected at the localities where the type series of *A. winterbottomi* were found in the Maikop deposits of the Lower Oligocene. These fishes are predominantly pelagic forms (see table 3 in Danilchenko 1980), including the *Caprovesposus* acronurus presettlement stage of an acanthurid (Bannikov & Tyler 1992), numerous clupeids of the genera *Sardinella* and *Pomolobus* and gadids of the genus *Palaeogadus.* Several strata of the Pshekhsky Horizon bear rather numerous mesopelagic photophore-bearing fishes of the genera *Eomyctophum, Vinciguerria* and *Scopeloides.* Moreover, representatives of such apparently pelagic families as Scombridae (*Scombrosarda, Sarda*), Trichiuridae (*Lepidopus*), Palaeorhynchidae (*Palaeorhynchus, Homorhynchus*), Nomeidae (*Psenicubiceps, Rybapina*), Stromateidae (*Pinichthys*), etc., were abundant in the early Eocene of the North Caucasus. Coastal and benthic fishes were much rarer, although among those few benthic species is the only previously known Maikopian tetraodontiform, *Oligobalistes robustus* Danilchenko (1960).

We presume that the preponderance of pelagic fishes at the localities of the type series of *A. winterbottomi* is evidence that it is an offshore or pelagic species of tetraodontid, like some of the species of *Lagocephalus.*

The gray, flaky marls and calcareous clays of the Oligocene Pshekhsky Horizon cover light calcareous rocks of the underlying Upper Eocene Byeloglinsky Horizon of the North Caucasus. The only fish remains that are known from the latter horizon are isolated scales of a large elopiform of the genus *Lyrolepis.*

Comparative Fossil Materials

Eotetraodon pygmaeus (Zigno 1887): all specimens from the Lower Eocene of Monte Bolca, Italy; IGUP 6890–91, counterpart plates, holotype, 18.2 mm SL; MCSNV T137–138, counterpart plates, 16.1 mm SL; MCSNV T139, single plate, 14.2 mm SL; SPHE 1970/48, single plate, 15.5 mm SL; SPHE 1970/47, single plate, 90.5 mm SL.

Archaeotetraodon jamestyleri (Bannikov 1990): all specimens from the Tarkhanian Horizon of the Lower Miocene at Kamyshlak, Kerch Peninsula, Crimea, Ukraine; PIN 287-9, counterpart plates, holotype, 22.6 mm SL; PIN 3974-8, single plate, paratype, vertebral column distorted, cranium preserved as dorsoventral impression of 16.4 mm length from anterior end of vomer to rear of occipital region, estimated 60 mm SL; PIN uncatalogued, fragment representing part of caudal peduncle.

Sphoeroides hyperostosus Tyler, Purdy, & Oliver (1992): both specimens from the Yorktown Formation of the Lower Pliocene of Lee Creek Mine, Beaufort County, North Carolina, USA; USNM 437601, relatively complete three dimensional skull and first four vertebrae, holotype, 72.5 mm cranium length; USNM 290643, three dimensional cranium, paratype, 37.0 mm cranium length.

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PLEISTOCENE ECHINOIDS (ECHINODERMATA) FROM BERMUDA AND BARBADOS

Stephen K. Donovan and Brian Jones

Abstract.—Pleistocene fossil echinoids have been neglected compared to more ancient members of this group. Two occurrences of extant species in the Pleistocene are documented herein. *Echinometra lucunter* (Linné) from Bermuda adds to the growing list of fossil occurrences of this species, which has a durable test, but lives in areas of poor preservation potential. *Meoma ventricosa* (Lamarck) from Barbados is the first 'complete' specimen of this species from the fossil record.

Pleistocene echinoids have received less attention than those from earlier in the fossil record for a variety of reasons. For example, they are commonly poorly preserved (Gordon & Donovan 1992) and they usually belong to extant species that have already been well-studied by zoologists. The fact that these species are still extant, however, makes Pleistocene echinoids particularly suitable for investigating and testing diverse paleobiological problems and hypotheses. Gordon & Donovan (1992) used disarticulated plates to determine the distribution of echinoids on a Sangamonian (late Pleistocene) raised reef, and Donovan & Gordon (1993) tested taphonomic predictions made on the basis of living species (Greenstein 1991) against the same taxa that occurred in the Plio-Pleistocene of the Caribbean region.

The present paper records the occurrence of moderately well-preserved echinoid tests from the Pleistocene deposits of Bermuda and Barbados. The Pleistocene echinoid faunas of both islands are essentially unknown and it is hoped that the present communication may stimulate further research.

The echinoid classification used herein follows Smith (1984). Terminology of the echinoid test follows Melville & Durham (1966) and Smith (1984). Specimens described herein are deposited in the Field Museum of Natural History, Chicago (FMNH), and the University of Alberta (UA).

Class Echinoidea Leske
Superorder Camarodonta Jackson
Order Echinoida Claus
Family Echinometridae Gray
Genus *Echinometra* Gray
Echinometra lucunter (Linné, 1758)
Fig. 1

Material, locality and horizon.—A single test, FMNH PE 309, from Bermuda. The specimen label states "Echinometrid echinoid (labeled *Echinometra lucunter*). "*Cladocora* rock"—Quaternary [presumably Pleistocene]. Bermuda. Gift of Bermuda Biological Station, 1947". Quaternary deposits of Bermuda have been deposited over the past 250,000 years (Harmon et al. 1983).

Preservation.—The test (Fig. 1) is preserved in a well-indurated white limestone. Fragments of *Cladocora* are apparent in limestone adhering to the outside of the test. The Aristotle's lantern and part of the test (approximately coinciding with interambulacrum 1 and ambulacrum II) are missing, and more of the test is concealed by limestone (Fig. 1a). The apical region is poorly preserved and the apical system is

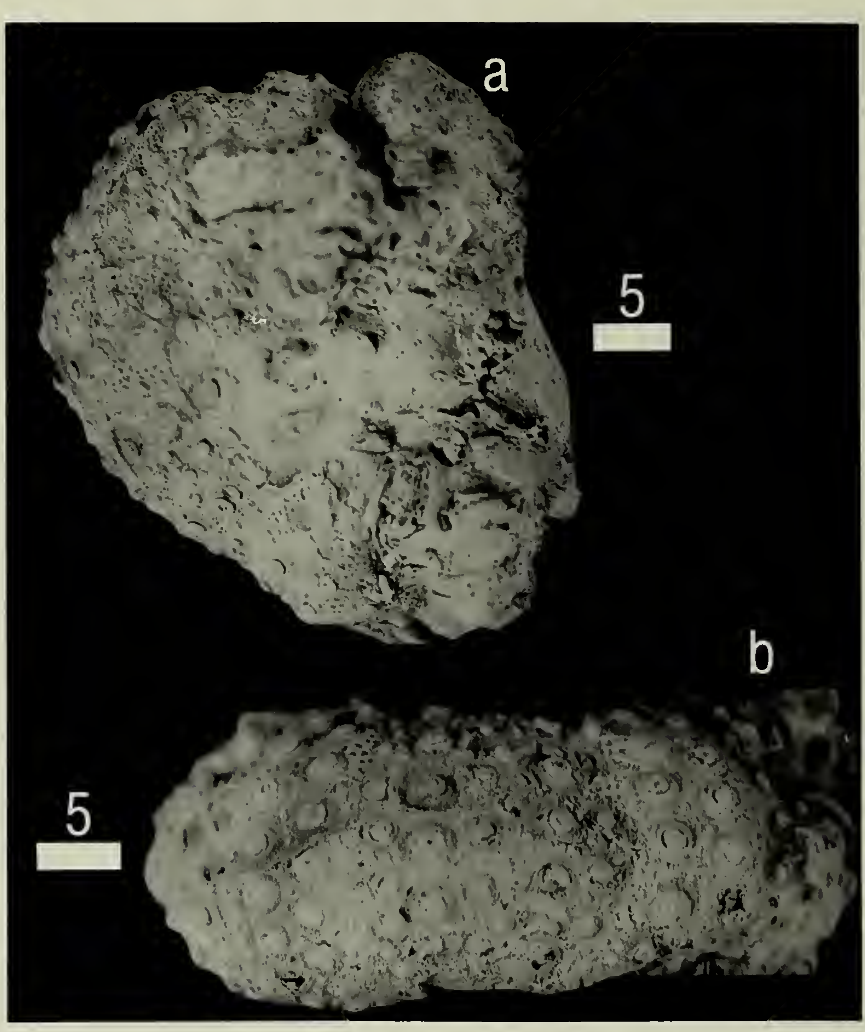

Fig. 1. *Echinometra lucunter* (Linné, 1758), FMNH PE 309. a, apical view. b, lateral view. Scale bars in mm.

missing (Fig. 1a). Parts of the test are broken and crushed, commonly across plates. Although in other regular echinoids this might mean that death was caused by predation (Smith 1984:19), the plates of extant *E. lucunter* are so well interlocked by stereom trabeculae that this breakage, associated with an essentially 'complete' test, was probably post-burial. This specimen appears to fall into disintegration state 5 of Kidwell & Baumiller (1990:249).

Description.—For a recent description of *E. lucunter,* see Donovan (1993).

Remarks.—At present, *E. lucunter* ranges from Florida to Brazil and off the west coast of Africa (Kier 1992). In particular, it occurs on hard substrates in high energy environments around Bermuda (D. L. Pawson, pers. comm.). Previously, *E. lucunter* has been reported from the Plio-Pleistocene of Jamaica, the Dominican Republic, Florida, and Angola (Gordon 1991, Kier 1992; note that in the former reference 'Dominica' in table 1 should read Dominican Republic). It is also reported from the 'middle' Oligocene (Larue 1994) San Sebastian For-

Fig. 2. *Meoma ventricosa* (Lamarck, 1816), UA 9496. a, apical view, b, oral view. Scale bar in mm.

mation of Puerto Rico (Gordon 1963), but this could be a misidentification of *E. prisca* Cotteau which is abundant at about the same level in Antigua (Poddubiuk & Rose 1985: table 1). However, this possibility was discussed by Gordon (1963:632, 635), who noted that the pore pairs of the Puerto Rico specimens are mainly arranged in arcs of six as in *E. lucunter,* but dissimilar to *E. prisca.*

The Bermudan specimen adds to the growing data base of occurrences of fossil *E. lucunter* (Donovan & Gordon 1993). Although this taxon has a high potential for preservation when compared with other regular echinoids (Greenstein 1991), Gordon (1991) noted that *Echinometra* has a poor fossil record as complete tests. This is presumably due to the preferred life habit of this taxon, on hard substrates under high energy conditions, which is usually removed from environments of sedimentary deposition (Smith 1984:22). In consequence, fossil *E. lucunter* is rarely found as 'complete' tests in Pleistocene deposits (Donovan & Gordon 1993), although *Echinometra* may be locally abundant as disarticulated plates (Gordon & Donovan 1992).

Superorder Microstomata Smith
Order Spatangoida Claus
Family Micrasteridae Lambert
Genus *Meoma* Gray
Meoma ventricosa (Lamarck, 1816)
Fig. 2

Material, locality and horizon.—A single test, UA 9496, from the Arawak Cement Quarry, northwest Barbados. The specimen came from a large boulder lying on the quarry floor. This test was preserved in moderately lithified grainstone, about 125,000 years old (Upper Pleistocene, Sangamonian; last interglacial), that accumulated in pockets between large *Montastrea annularis* colonies that are the main component of the reef at this locality.

Preservation.—This specimen is preserved largely as an internal mold, although test calcite is retained over about half of the oral surface and in part of interambulacrum 2 apically (Fig. 2). A patchy, calcareous veneer occurs over much of the internal mold that may be a remnant of the test, although individual plates are not discernable, perhaps suggesting it is possibly diagenetic in origin. The mold is composed of lithified carbonate sand. This specimen is particularly noteworthy because of its large size, about 160 mm long by 135 mm wide by 65 mm high. Although not unusual for this species, few Caribbean fossil echinoids of comparable dimensions are known.

Description.—For a comprehensive description of this species, see Chesher 1970; see also Kier & Grant 1965, Chesher 1969, and Kier 1975.

Remarks.—The only fossil echinoids previously documented from Barbados are from the Tertiary clastic sedimentary rocks exposed in the northeast of the island (Kier 1966). Kier (1966:2) commented that "It is rather surprising, considering the large numbers of echinoids known from Eocene rocks in the Caribbean . . . that . . . species from the Upper Scotland Formation are quite distinct." These rocks were previously thought to be shallow-water in origin (see, for example, Barker & McFarlane 1980). However, it is now generally recognized that siliciclastic and other rocks of northeast Barbados were of deep-water origin (Speed 1988). Eocene echinoids described from the Caribbean tend to be preserved in limestones of shallow-water origin, hence the differences between faunas. In Barbados, only the Pleistocene limestones were truly deposited in shallow-water.

Extant *Meoma ventricosa* is a sand-burrowing spatangoid found in the Caribbean, Florida, the Bahamas and the Pacific coast of Panama (Chesher 1969, 1970). It still occurs in sandy reef environments similar to that interpreted for the Pleistocene locality in Barbados (for example, the lagoon at east Discovery Bay, north Jamaica; SKD, personal observation). However, it is poorly represented in the fossil record and only appears to have been reported previously from the Upper Pleistocene of Jamaica (Donovan et al. 1994), based on test fragments.

Two subspecies of this taxon were recognized by Chesher (1970), *M. v. ventricosa* (Lamarck) and *M. v. grandis* Gray. Distinguishing between these two subspecies relies on features of the test that are not preserved in the Barbadian specimen. This test is unusually broad and could, very tentatively, be referred to *M. v. grandis,* which was originally described from the Pacific coast of Panama. If this provisional identification is correct, then either a contraction of range since the late Pleistocene or an ecophenotypic, rather than genetic, explanation for the two test morphologies in this species is indicated. However, Kier & Grant (1965: pl. 9, fig. 4) illustrated a test of *M. v. ventricosa* of comparable gross morphology to the specimen from Barbados.

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A NEW SPECIES OF *FELICOLA* (PHTHIRAPTERA: TRICHODECTIDAE) FROM A COSTA RICAN JAGUAR, *PANTHERA ONCA* (CARNIVORA: FELIDAE)

Robert M. Timm and Roger D. Price

Abstract.—A new species of chewing louse, *Felicola* (*Lorisicola*) *oncae* (Phthiraptera: Trichodectidae), is described and illustrated from a jaguar, *Panthera onca* (Carnivora: Felidae), taken in Costa Rica. Although this louse is based only on a single male specimen, its morphological distinctiveness and occurrence on a big cat of the genus *Panthera* make its discovery and description of special significance. The genus *Felicola* Ewing now contains 55 species, which can be grouped into four subgenera: *Felicola, Lorisicola, Paradoxuroecus,* and *Suricatoecus.*

Resumen.—Se describe e ilustra una nueva especie de piojo, *Felicola* (*Lorisicola*) *oncae* (Phthiraptera: Trichodectidae), de un jaguar, *Panthera onca* (Carnivora: Felidae), capturado en Costa Rica. Aunque este piojo se basa solamente en un único ejemplar macho, su distintividad morfológica y ocurrencia en un gran felino del género *Panthera* le confieren a su descubrimiento y descripción una significancia especial. El género *Felicola* Ewing contiene ahora 55 especies, las cuales pueden agruparse en cuatro subgéneros: *Felicola, Lorisicola, Paradoxuroecus,* y *Suricatoecus.*

Fifty-four species of chewing lice of the genus *Felicola* Ewing currently are recognized. Of these, 48 species occur on the felid carnivores, the families Felidae, Herpestidae, and Viverridae, 5 occur on the Canidae (Carnivora), and 1 is found on the Lorisidae (Primates). Eleven of these species occur on the cats of the family Felidae.

The trichodectid chewing louse of the genus *Felicola,* subgenus *Lorisicola* Bedford, that we describe herein was obtained from an adult male jaguar, *Panthera onca* (Linnaeus), that was shot on the night of 10 June 1988 north of Delicias de Upala, about 1 km from the Nicaraguan border in extreme northern Costa Rica. The next day, the intact jaguar was hauled in the back of the truck to Universidad Nacional in Heredia where it was skinned. The skin was frozen and stored in a freezer for four years. We were then able to thaw and wash the skin in an attempt to recover ectoparasites and obtained the single specimen of *Felicola* and a single tick. This is the first louse to be reported from a free-ranging jaguar. Although we do not generally believe that new species should be described on the basis of a single individual, in this case we feel it is warranted. The unlikelihood of our obtaining additional specimens of lice from jaguars, coupled with the extremely fortuitous collection of the type specimen, places us in the position of documenting, based upon a single individual, that a unique species of chewing louse occurs on one of the most endangered species of Neotropical mammals. Because of the significant unique characters that this louse possesses, especially its unusual genitalia and extremely large body size, we are confident that it deserves recognition as a distinct species.

Felicola (*Lorisicola*) *oncae*, new species Figs. 1, 2

Type host.—*Panthera onca* (Linnaeus).

Male.—As in Fig. 1. Head with preantennal margin straight, with shallow narrow medioanterior indentation; sparse scattered dorsal setae; antennal scape enlarged. Each side of pronotum with few short lateral setae, single median marginal seta. Pteronotum with row of short setae laterally. Abdomen with two short setae on tergum I and single row of short setae on terga and sterna II–VIII. Pleura III–VIII with single row of short setae, with those on III somewhat longer and stouter than those on V. With six pairs of large abdominal spiracles. Chaetotaxy of terminalia as shown. Genitalia (Fig. 2) with straight parallel basal apodeme lateral struts associated with large spinose sac; parameres apically tapered, blunt, and basally fused, with flat basal margin lacking indentation; mesomeral arch with prominent broad blunt apical process.

Female.—Unknown.

Dimensions of male (in mm).—Temple width, 0.59; head length, 0.52; prothorax width, 0.46; pterothorax width, 0.56; abdomen width at IV, 0.92; total length, 2.04; genitalia width, 0.22; genitalia length, 0.55; genitalia paramere length, 0.18.

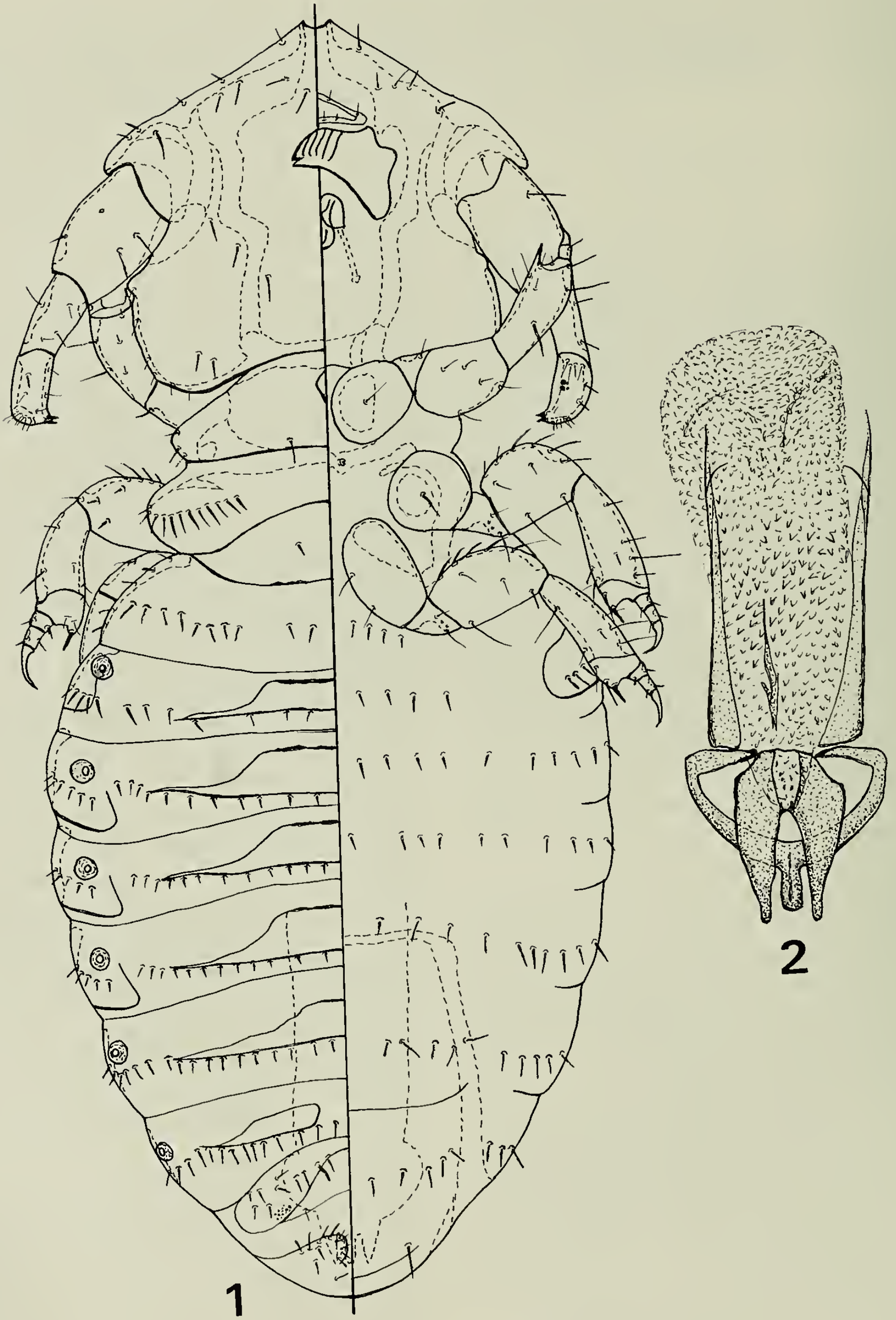
Type material.—Holotype male, ex *Panthera onca,* Costa Rica: Alajuela Province, Upala Canton, 2 km north of Delicias de Upala, 10 June 1988; in collection of Snow Entomology Museum, University of Kansas, Lawrence.

Etymology.—This species is named for the host, *Panthera onca,* the jaguar.

Remarks.—*Felicola oncae* is distinguished from the males of all other known species of the genus by the combination of its head shape, possession of six pairs of prominent abdominal spiracles, the very large dimensions, and the shape of the fused parameres and mesomeral arch of the genitalia. Although the gross head shape and spiracle number are similar to those of the majority of the species of *Lorisicola* from the Felidae, no members of the other three subgenera have more than four pairs of abdominal spiracles and most have a quite different head shape.

Within the *Lorisicola* found on felids, the largest species known previously is *F. spenceri* Hopkins from the two species of Holarctic lynx, *Lynx canadensis* Kerr and *L. lynx* (Linnaeus). *Felicola spenceri* is 1.51 mm long, with a temple width of 0.46 mm, head length of 0.45 mm, and abdomen width of 0.70 mm; *F. oncae* is considerably larger in all dimensions. *Felicola zeylonicus* Bedford, of the subgenus *Felicola,* is the largest previously known species in the genus, with a total length of 1.66 mm. Thus, *F. oncae* is by far the largest of any *Felicola* known to date. In addition to its extremely large size, the basally fused parameres of *F. oncae* are unique in shape and the mesomeral arch has a broad, blunt apical process. The apically separated parameres with the basal margin of the fusion area flattened and without an indentation were known previously only in *F. americanus* Emerson & Price, from the bobcat, *Lynx rufus* (Schreber); the two species are grossly different in dimensions and genitalia. *Felicola americanus* (subgenus *Lorisicola*), second in size to and considerably smaller in all dimensions than *F. spenceri,* is thereby much smaller than *F. oncae.*

In the Emerson & Price (1983) key to males of the New World species of the *Felicola felis* complex, *F. oncae* identifies readily with *F. americanus* in couplet 3 on the basis of the flattened basal margin of the fused parameres. If one passes through that couplet, *F. oncae* would identify further with *F. spenceri* in couplet 4. As explained above, gross differences in dimensions and genitalia separate *F. oncae* from both of these



Figs. 1, 2. *Felicola oncae.* 1. Male. 2. Male genitalia.

species, as well as from all other members of the subgenus and genus.

Lyal (1985), in his cladistic classification of the trichodectids, treated what we recognize herein as the genus *Felicola* as two genera, *Felicola* and *Lorisicola,* with each having two subgenera, *Felicola* and *Suricatoecus* Bedford, and *Lorisicola* and *Paradoxuroecus* Conci, respectively. We accept Lyal's placement of 18, 11, 12 (+ our new species), and 13 louse species, respectively, in these four subgenera. However, we believe it more appropriate that all four be recognized as subgenera of *Felicola.* We come to this conclusion because of the difficulties encountered in the key by Lyal (1985:335–338) to genera and subgenera. The longest and most complex couplets are used for *Felicola* sensu lato, character states are nondiscrete and overlapping, and separations are ambiguous. There is simply no clear break between these groups that warrants generic level distinction. This action on our part is not a severe departure from Lyal's classification, and is one that we feel is justified.

Eleven of the 12 *Felicola* now known from felids are in the subgenus *Lorisicola.* The single other species of *Felicola* reported from felids, *F. subrostratus* (Burmeister), is in the subgenus *Felicola. Felicola subrostratus* has been reported from the domestic cat complex, *Felix catus-lybica-silvestris.* These cats have been domesticated and transported by humans for at least four millennia. Domestic cats generally are treated as a man-created species, *F. catus,* that was derived from the wild cat of northern Africa and extreme southeastern Asia, *F. silvestris lybica,* although considerable interbreeding with the wild cat of Europe, *F. silvestris silvestris,* has occurred. Because we have been unable to examine lice from truly wild, non-feral cats, we are unable to evaluate the relationship of *Felicola subrostratus* to other *Felicola.*

The family Felidae, or cats, is nearly worldwide in distribution, being found in all zoogeographic regions except for the Australian and Oceanic regions, Madagascar, and the smaller oceanic islands. The family contains some four or five Recent genera and 37 extant species. Although there is little disagreement in the number of species recognized, there has been considerable debate on the number of genera and the relationships between species (Wilson & Reeder 1993). The number of genera of Recent felids recognized by various authors ranges from 4 to 19 (Ewer 1973, Nowak 1991). Four main lineages of extant cats are recognized: the cheetah (genus *Acinonyx*), the clouded leopard (genus *Neofelis*), the smaller cats (genus *Felis,* with as many as 14 subgenera in the single genus, or as many as 16 genera, including *Lynx*), and the big cats (genus *Panthera*). In *Panthera,* five species are recognized—leopard, *P. pardus* (Linnaeus); lion, *P. leo* (Linnaeus); snow leopard, *P. uncia* (Schreber) (often treated as a monotypic genus *Uncia*); tiger, *P. tigris* (Linnaeus); and jaguar.

Historically, jaguars were found from the southern United States, through Mexico, all of Central America, and much of tropical lowland South America, to central Argentina. We suspect that *Felicola oncae* is a host-specific parasite of jaguars and, as such, occurs on jaguars throughout their range. For well over two centuries, however, jaguar numbers have been declining; populations have been reduced by hunting pressure and habitat destruction and, in recent years, jaguars have been extirpated from much of their former range.

All previous bona fide records of *Felicola* from felids have been from the smaller cats of the genera *Felis* and *Lynx.* However, Ponton (1870) did describe *Trichodectes tigris* supposedly originating from a tiger. Unfortunately, he provided no illustration and the verbal description is so general as to apply to a wide range of generic possibilities. Hopkins (1949:507) suggested that the louse was ". . . almost certainly from a captive and perhaps a contamination." Hopkins and Clay (1952:354), in referring to *T. tigris,* tersely state "Type lost, description useless. Unrecognizable." Lyal (1985:247) adopts this approach and relates the name to the category of incertae sedis.

Our discovery of *Felicola oncae* on the jaguar, therefore, is the first verifiable record and recognizable description for any louse from a member of the subfamily Pantherinae and suggests that *Felicola* may be much more widely distributed on the cats than was recognized previously. Including *F. oncae,* 12 species of *Felicola* have been described from 15 species of felids. Where accurate records are available, *Felicola* appears to be quite host specific. Given that chewing lice have been found on only 15 of the 37 extant species of cats, we strongly suspect that numerous new species of *Felicola* await discovery.

Acknowledgments

We are extremely grateful to several colleagues in Costa Rica for their efforts with the jaguar that made our discovery of this louse possible. Costa Rican biologist Carlos Alberto López transported the jaguar on his back, by motorcycle, and by pickup truck from the site where it was killed to the Universidad Nacional. David Norman of the Programa Regional en Manejo de Vida Silvestre para Mesoamérica y el Caribe, Universidad Nacional, skinned the jaguar and generously made the skin available to us. Miguel Rodríguez and Eduardo López Pizarro of the Direccion de Vida Silvestre provided the permits. RMT's field work in Costa Rica was funded in part by the University of Kansas Office of Research, Graduate Studies, & Public Services; Associate Vice Chancellor Robert C. Bearse's efforts in securing funding is most appreciated. We thank Adrian Nieto for translating our abstract into Spanish for the resumen and Barbara L. Clauson for her constructive comments on an earlier version of this manuscript. This study was partially supported by Project No. Min-17-015, Minnesota Agricultural Experiment Station, St. Paul, Minnesota 55108, and has been assigned Paper No. 20,553, Scientific Journal Series.

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A NEW SPECIES OF *HYPERALONIA* RONDANI, 1863 (INSECTA: DIPTERA: BOMBYLIIDAE: EXOPROSOPINAE)

Márcia Souto Couri and Carlos José Einicker Lamas

Abstract.—A new species of *Hyperalonia* from Brazil, *H. diminuta,* is described and illustrated. Illustrations of wings of other Neotropical taxa are also included to aid in their identification.

The Neotropical genus *Hyperalonia* Rondani, 1863, comprises four species and two subspecies (Painter et al. 1978). They were revised by Painter & Painter (1968), who described a new species, *H. ater,* and presented a diagnosis of the genus, a key to species and subspecies and recorded their distribution.

Except for *H. ater,* all other known species and subspecies are represented in Museu Nacional, Rio de Janeiro collection. Studying this material, the authors found a new species of *Hyperalonia,* which is herein described. The unique exemplar of *H. ater* observed is deposited at Museu de Zoologia, Universidade de São Paulo.

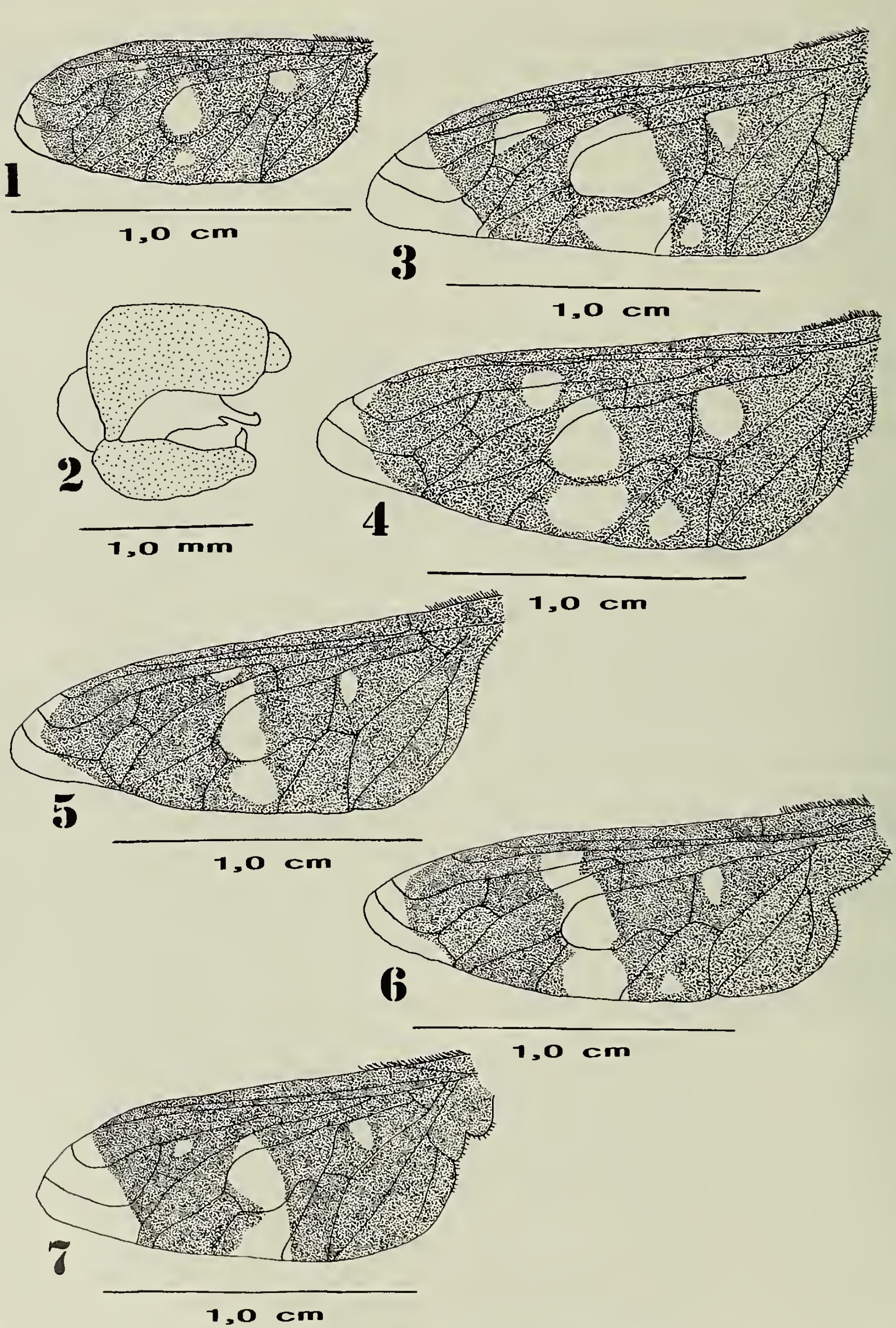
To contribute further to the identification of the genus, wing illustrations of Neotropical taxa are also presented.

Hyperalonia diminuta, new species
Figs. 1, 2

Holotype.—♂. Aragarças/Goiás Brasil, 28 Jan 1953, Moacir Alvarenga. Holotipo [red label]. *Hyperalonia diminuta* Couri & Lamas [Lamas' handwriting]. (MNRJ). In good condition; right third antennal article broken. Genital segments in glycerin inside microvial pinned with holotype.

Diagnosis.—Tip of wing hyaline, outline between black and hyaline areas straight; hyaline areas as follows: area in center of wing from near base of first posterior cell to near posterior margin of discal cell; this hyaline area is largely separated from another small one, at third posterior cell, which is round; large round hyaline area at second basal cell; a small round hyaline area crossed by R2 + 3 at its basal third (Fig. 1); hairs on costal base black; alula fringe white. Mid tibia at ventral surface with a row of about 9 short black bristles; dorsal surface with 2 bristles at basal half, one bristle at apical third and an apical bristle; hind tibia on ventral and dorsal surfaces with a complete row of short and black bristles.

Description.—Male: Body length—10 mm; wing 10 mm (Figs. 1–2). Head: orange yellow, except ocellar tubercle and a triangular area in front of it, which are both black, mouth opening brown posteriorly; frons protruded; sparse black hairs on occiput, frons and gena; occipital fringe yellowish white; a dense tuft of black hairs in the black spot on front of ocellar tubercle; antennae brown, with black hair on first article; first and second articles about the same length, both as long as broad; third article about 3 times the length of second; proboscis hardly exceeding mouth opening; palpi brown with black hairs. Thorax: black bluish; humeral and postalar callus brown; sparse minute black pubescence on notum; orange red collar of hairs on anterior part of thorax; black hairs between coxa; a tuft of orange red hairs on humeral callus and between this and wing; and another one above halter; a tuft of white hairs between base of wing and halter; halter brown and yellow; calypter dark brown; anepisternum, katepisternum and anepimeron with black hairs. Legs brown, mid tibia on ventral surface with a row of about 9 short black bristles; dorsal



Figs. 1–7. 1–2, *Hyperalonia diminuta*: (1) wing of holotype; (2) male genitalia, lateral view; 3, *Hyperalonia surinamensis*, wing; 4, *Hyperalonia morio morio*, wing; 5, *Hyperalonia morio erythrocephala*, wing; 6, *Hyperalonia chilensis*, wing; 7, *Hyperalonia ater*, wing.

surface with 2 bristles on basal half, one bristle at apical third and an apical bristle; hind tibia on ventral and dorsal surfaces with a complete row of short, black bristles. Wing: blackish brown; tip hyaline, outline between black and hyaline areas straight; hyaline areas as follows: area in center of wing near base of first posterior cell to near posterior margin of discal cell; this hyaline area is largely separated from another small one, at third posterior cell, which is round; big round hyaline area at second basal cell; a small round hyaline area crossed by R2 + 3 at its basal third (Fig. 1); hairs on costal base black; alula fringe white. Abdomen: Black bluish as thorax with small black hairs at dorsum and bristled laterally. Male genitalia in lateral view with basistylus subtriangular; dististylus with hook-shaped apex; tip of aedeagus recurved dorsally; epandrium subquadrate, with prominent ventral process. Cercus short (Fig. 2).

Discussion.—The color pattern of the wing easily distinguishes *H. diminuta* from other species in the genus. In Painter & Painter's (1968) key, this species is near *H. surinamensis,* as in both, the line between hyaline and dark parts at tip of wing is straight. The following key separates these two species.

Triangular hyaline area in the end of second basal cell; a broad hyaline area in center of wing separated by a band of black bordering the third posterior cell, this inferior part reaches margin of wing (Fig. 3) .... *H. surinamensis* Rondani

Round hyaline area at second basal cell; narrow hyaline area in center of wing, separated by a large band from a small hyaline area in third posterior cell, which does not reach margin of wing (Fig. 1) .... *H. diminuta*

The color pattern of wings of *Hyperalonia morio morio* (Fabricius, 1775) (Fig. 4); *H. morio erythrocephala* (Fabricius, 1805) (Fig. 5); *H. chilensis* Rondani, 1863 (Fig. 6); *H. surinamensis* Rondani, 1863 (Fig. 3); and *H. ater* Painter & Painter, 1968 (Fig. 7) are presented, to facilitate the identification of species.

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LOUISEA, A NEW GENUS OF FRESHWATER CRAB (BRACHYURA: POTAMOIDEA: POTAMONAUTIDAE) FOR *GLOBONAUTES MACROPUS EDEAENSIS* BOTT, 1969 FROM CAMEROON

Neil Cumberlidge

Abstract.—*Globonautes macropus edeaensis* Bott, 1969 and *G. balssi* Bott, 1959 from Cameroon are removed from the Gecarcinucidae Rathbun, 1904 and reassigned to the Potamonautidae Bott, 1970. *Globonautes m. edeaensis* is recognized as a valid species, and is established as the type species of *Louisea,* a monotypic new genus. *Louisea* is defined by a combination of characters of the mandible, third maxilliped, cheliped, and gonopods 1 and 2. *Louisea edeaensis* is compared to, and distinguished from, other freshwater crabs occurring in West Africa. *Globonautes balssi* is close to *Louisea* but is regarded here as *incertae sedis.* A key to the West African genera of the Potamonautidae is provided.

The African family Potamonautidae Bott, 1970 currently includes four genera, *Potamonautes* MacLeay, 1838, *Sudanonautes* Bott, 1955, *Liberonautes* Bott, 1955, and *Potamonemus* Cumberlidge & Clark, 1992. *Potamonautes* is widely distributed throughout sub-Saharan Africa (Bott 1955), *Sudanonautes* is found from Cote d'Ivoire to Central Africa (Bott 1955; Monod 1977, 1980; Cumberlidge 1989, 1993a), and *Liberonautes* is found in West Africa west of Ghana (Cumberlidge & Sachs 1989a, 1989b). The fourth genus, *Potamonemus,* is known only from southwest Cameroon (Cumberlidge & Clark 1992, Cumberlidge 1993b).

The present work reappraises the taxonomy of two poorly known species from Cameroon, *G. macropus edeaensis* Bott, 1969, and *Globonautes balssi* Bott, 1959. Both species are presently included in the Gecarcinucidae Rathbun, 1904 (Bott 1959, 1969, 1970) but there is some doubt as to the validity of these assignments. For example, the form of the mandible of *G. m. edeaensis* indicates that this species belongs in the Potamonautidae, while Cumberlidge (1987) examined the mandible of *G. balssi* and concluded that this taxon also belongs in the Potamonautidae.

The exact classification of *G. m. edeaensis* and *G. balssi* within the Potamonautidae is more difficult. The two species most closely resemble members of *Potamonemus,* which are also from the same part of Cameroon (Cumberlidge & Clark 1992, Cumberlidge 1993b). *Potamonemus* is characterized by a potamonautid-type mandibular palp (2-segmented, and ending in a single lobe) together with a third maxilliped which completely lacks a flagellum on the exopod. Two male specimens of *G. m. edeaensis* from Cameroon, recently discovered in the Museum für Naturkunde der Humboldt-Universitat, Berlin, Germany (ZMB), allow a complete re-assessment of this taxon. *G. m. edeaensis* has a potamonautid-type mandibular palp, together with a third maxilliped which completely lacks a flagellum on the exopod. However, differences in the form of gonopod 2 of *G. m. edeaensis* argue against its inclusion in *Potamonemus,* or in any of the other three potamonautid freshwater crab genera known from Africa. The new genus *Louisea* is therefore proposed to accommodate *G. m. edeaensis,* which is designated the type species, and a key to the West African genera of the Potamonautidae is provided.

Unfortunately, the position of *G. balssi* cannot be properly assessed because the male type specimen is in poor condition; therefore this taxon is regarded here as incertae sedis.

The following abbreviations are used: CW = carapace width at widest point; CL = carapace length, measured along median line; CH = carapace height, maximum depth of cephalothorax; FW = front width, width of front measured along anterior margin; M = male, F = female, ad = adult, juv = juvenile, ovig = ovigerous; SMF = Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt am Main, Germany; USNM = National Museum of Natural History, Smithsonian Institution, Washington, D.C.; ZIM = Zoological Institute and Museum, Hamburg, Germany; ZSBS = Zoologische Sammlung des Bayerischen Staates, München, Germany.

Methods

The holotype of *L. edeaensis* was loaned from the ZSBS; two other specimens discovered in the ZMB were subsequently loaned. The male holotype of *L. edeaenis* is in poor condition, and the entire left mandible and the palp of the right mandible are missing. Fortunately the other specimens of *L. edeaensis* are in good condition, and were collected in Cameroon less than 90 km from the type locality. The male holotype of *G. macropus* (Rathbun, 1898) was examined in the USNM.

The male holotype and the second female paratype of *G. balssi* were examined in the SMF where they were on temporary loan. The male holotype of *G. balssi* is a juvenile, and both second gonopods are missing. The female paratype of *G. balssi* was examined in the ZIM.

Four dimensions of the carapace, carapace length, carapace width, carapace height, and front width—were recorded from each specimen using digital calipers (Table 1). The relative proportions of the latter three measurements (adjusted for body size, CL) of both species were calculated (Table 1). The left mandible and the left gonopod 1 and gonopod 2 were illustrated following removal from the specimens in order to describe these structures from different angles and under magnification. Characters of the gonopods, carapace, and third maxillipeds of these specimens correspond closely with those of the holotype. The carapace, mandible and other characters of the largest of these specimens were illustrated. The length of the propodus of the right and left chelipeds of all specimens was measured along the ventral margin (Table 2).

Louisea, new genus

Globonautes Bott, 1959:995, pl. 1, figs. 1–6; 1969:359; 1970:23.

Type species.—*Globonautes macropus edeaensis* Bott, 1969:360; 1970:24, pl. 1, figs. 3–5, pl. 26, fig. 8.

Diagnosis.—Mandibular palp 2-segmented, terminal segment single (Fig. 3d, e). Third maxilliped lacking flagellum on exopod (Fig. 1c). Terminal segment of gonopod 1 directed outward, broad at base, narrowing sharply, final ⅔ almost S-shaped, tube-like, end blunt, rounded; completely lacking longitudinal groove; subterminal segment of gonopod 1 very wide at base (Fig. 1g, h). Terminal segment of gonopod 2 flagellum-like, almost as long as subterminal segment (Fig. 1i). Dactylus of right cheliped of adult male slim, propodus with large 3-peaked proximal tooth (Fig. 1e). Propodus very long, as long as carapace width. Anterior dorsal margin of merus of chelipeds with 1 large jagged tooth close to distal end, rows of small pointed teeth along rest of margin (Fig. 1a). Carapace distinctly convex, half carapace length (mean CH/CL

= 0.46), carapace, anterolateral margin, lower margin of orbit, postfrontal crest, smooth (Fig. 1a, b). Exo-orbital, epibranchial teeth small, low, distinct intermediate tooth present, vertical flank suture meeting anterolateral margin at epibranchial tooth (Fig. 1b). Small species, mature at CW = 22.0 mm.

Distribution.—Edea (3°48′N, 10°12′E) and Yabassi (4°32′N, 9°58′E) are 90 km apart, in the rain forest zone of the Littoral Province of southwest Cameroon. Edea lies on the Sanaga River, while Yabassi lies on the Wouri River.

Remarks.—This new genus of the Potamonautidae is established to accommodate *Louisea edeaensis* previously considered as a subspecies of *Globonautes macropus* in the family Gecarcinucidae.

Key to the Genera of the West African Potamonautidae

1. Terminal segment gonopod 2 very short, stump-like, $\frac{1}{10}$ length of subterminal segment 2
- Terminal segment gonopod 2 very long, flagellum-like, equal in length to subterminal segment 3
2. Third maxilliped with long flagellum on exopod .... *Sudanonautes*
- Third maxilliped lacking flagellum on exopod .... *Potamonemus*
3. Third maxilliped with long flagellum on exopod; terminal segment gonopod 1 curved, tapering to pointed tip 4
- Third maxilliped lacking flagellum on exopod; terminal segment gonopod 1 weakly S-shaped, tube-like, with rounded end .... *Louisea*
4. Terminal segment of gonopod 1 curving inward (toward medial line); intermediate tooth on the anterolateral margin between the exo-orbital tooth and the epibranchial tooth .... *Liberonautes*
- Terminal segment of gonopod 1 curving outward (away from medial line); no intermediate tooth on the anterolateral margin between the exo-orbital tooth and the epibranchial tooth .... *Potamonautes*

Louisea edeaensis (Bott, 1969)

Figs. 1–3, Tables 1, 2

Globonautes macropus edeaensis Bott, 1969: 360; Bott, 1970:24, pl. 1, figs. 3–5, pl. 26, fig. 8; Cumberlidge, 1987:table 1.

Material examined.—Holotype of *G. m. edeaensis,* adult male, CW 22.52 mm, from Edea, Cameroon, Jan 1910, ZSBS 1118/1. Two males, CWs 18.1, 13.7 mm, from Yabassi, Cameroon, coll. Riggenbach, ZMB 21575. Holotype of *G. balssi,* juvenile male, CW 12.5 mm, ZIM K-3506; 2 female paratypes, CW 22.0 mm, 13.5 mm, largest female ovigerous, ZIM K-3506. All *G. balssi* from Eosung, Bakossi highlands, Johann-Albrecht-Hohe, 1060 m, Cameroon, coll. Carl Rathke, 10 Sep 1909.

Type locality.—Edea, Cameroon.

Description of holotype.—Carapace (Fig. 1a, b): Cephalothorax ovoid, widest in anterior third (CW/CL = 1.27), relatively high, with maximum depth in anterior region (CH/CL = 0.51). Anterior margin of front straight, curving under, front relatively narrow, about ⅓ carapace width (FW/CW = 0.35). Surface of carapace smooth with no deep sutures. Postfrontal crest smooth, postorbital portions present, mid-groove broad, shallow, epigastric crests poorly defined, ending before meeting anterolateral margins. Exo-orbital tooth small, low, epibranchial tooth present but almost undetectable. Intermediate tooth on anterolateral margin between exo-orbital and epibranchial teeth. Anterolateral margin of carapace smooth. Posterolateral margin curving inward, continuous with anterolateral margin. Posterior margin about ⅔ as wide as carapace width.

Each flank with 2 sutures, 1 longitudinal, 1 vertical, dividing flank into 3 parts (Fig.

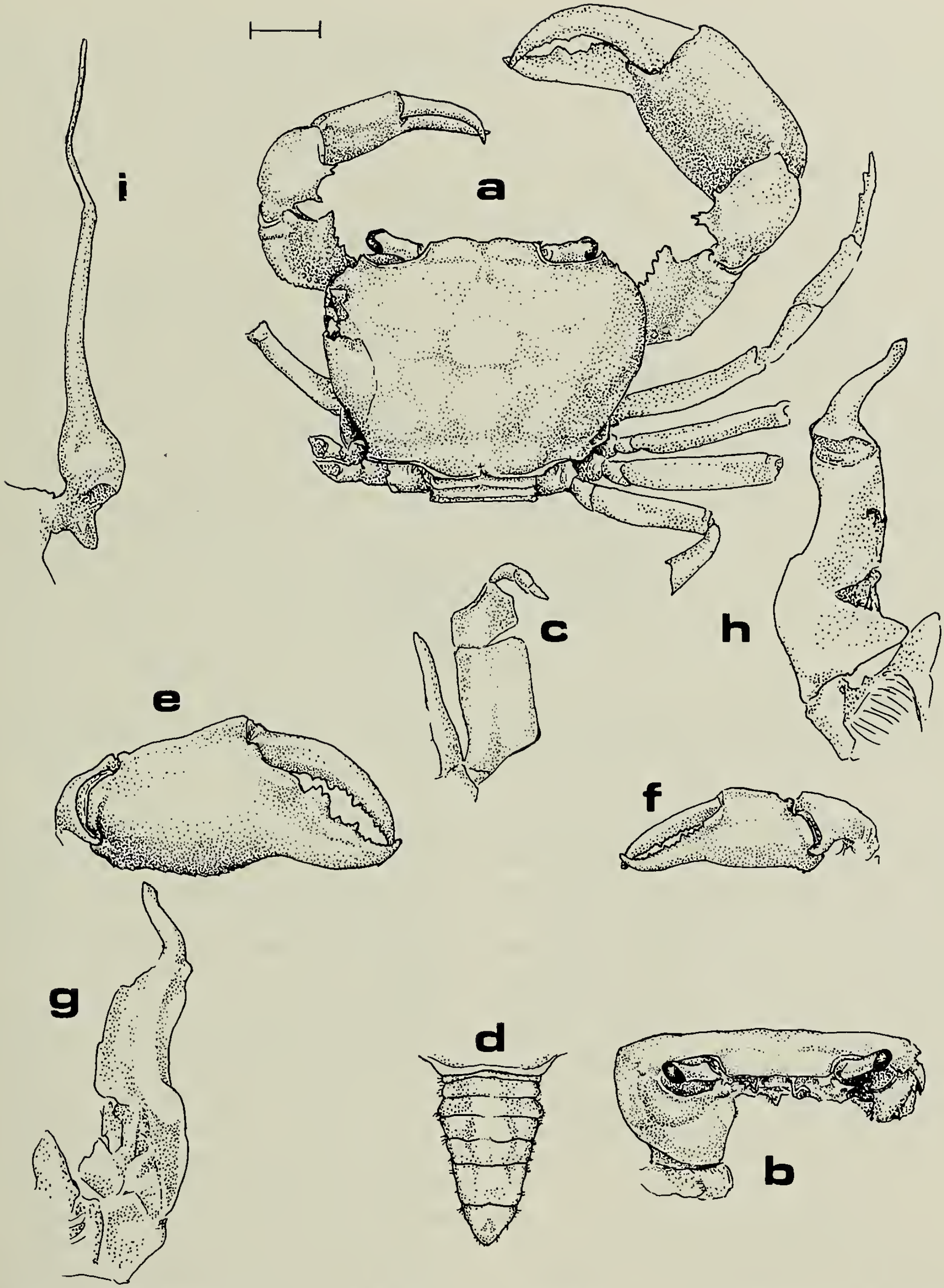

Fig. 1. *Louisea edeaensis,* holotype, adult male from Edea, Cameroon (CW 22.5 mm), ZSBS 1118/1. (a), whole animal, dorsal aspect; (b), carapace, frontal aspect; (c), left third maxilliped; (d), abdomen; (e), right cheliped, frontal view; (f), left cheliped, frontal view; (g), left gonopod 1, caudal view; (h), left gonopod 1, cephalic view, (i), left gonopod 2, caudal view. Scale bar equals 10 mm (a, b, d–f), 5 mm (c), and 2 mm (g–i).

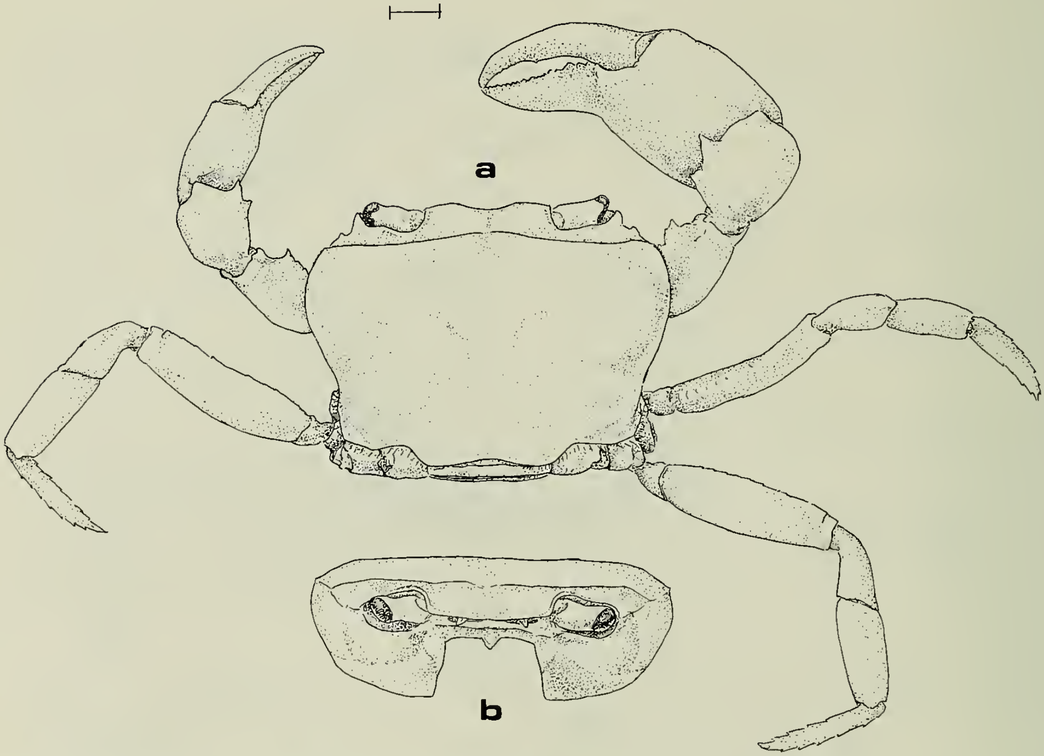

Fig. 2. *Louisea edeaensis,* from Yabassi, Cameroon male (CW 18.1 mm), ZMB 21575, (a), carapace, dorsal aspect; (b), carapace, frontal aspect. Scale bar equals 5 mm.

1b). Longitudinal suture dividing suborbital and subhepatic regions from pterygostomial region, beginning at respiratory opening and curving backward across flank. Short vertical suture dividing suborbital region from subhepatic region (Fig. 1b); suture beginning at epibranchial tooth, curving forward under intermediate tooth, then curving sharply down meeting longitudinal suture, continuing round to medical corner of lower orbital margin, marked by row of granules. Groove between sternal segments 2 and 3 complete; groove between sternal segments 3 and 4 consisting of 2 small notches at sides of sternum. Third maxillipeds filling entire oral field, except for transversely oval efferent respiratory openings in superior lateral corners. Exopod of third maxilliped lacking flagellum (Fig. 1c). Ischium of third maxilliped smooth, with faint vertical groove. Mandibular palp 2-segmented, terminal segment single, undivided, rudimentary curved flange at junction between segments, supporting fringe of long, soft hairs (Fig. 3d). Abdomen triangular, sides not indented, terminal segment rounded at distal margin (Fig. 1d).

Chelipeds (Fig. 1a, e, f) greatly unequal, right longer (22.6 mm), higher (10.2 mm) than left (14.9 mm, 5.5 mm respectively). Dactylus of right cheliped narrow, teeth small, enclosing long narrow space when closed; propodus with large 3-peaked proximal tooth, smaller teeth distally, palm swollen. Propodus very long, as long as carapace width. Anterior dorsal margin of merus of right and left chelipeds with 1 large jagged tooth close to distal end, rows of small round teeth along rest of margin, outer margin with 1 row of fainter granules. Carpus of cheliped with 2 large pointed teeth, first smaller than second. Left cheliped showing less enlargement, dactylus also narrow, enclosing narrow space, teeth smaller than those of right cheliped. Walking legs (pereiopods 2–5) slender, P4 longest, P5 shortest. Dactyli P2–5 tapering to point, each bearing rows of downward-pointing sharp bristles, dactylus of P5 shortest of the 4 legs.

Terminal segment of gonopod 1 (Fig. 1g–i) directed outward, broad at base, final ⅓ narrow, weakly S-shaped, tube-like, end blunt, rounded; completely lacking longitudinal groove and bristles; subterminal segment gonopod 1 very wide at base. Caudal face of subterminal segment forming raised triangular flap extending halfway across segment, flap tapering diagonally to point at junction with terminal segment, forming roof of chamber for gonopod 2; cephalic face of subterminal segment narrow, forming lower floor of chamber for gonopod 2, extending outward forming wide platform. Terminal segment of gonopod 2 (Fig. 1i) flagellum-like, extremely long. Subterminal segment gonopod 2 wide at base, otherwise a long, thin, slightly tapering, upright process supporting long terminal segment.

Variation.—Male from Yabassi (Fig. 2a, b) with large tooth close to distal end of anterior dorsal margin of merus of chelipeds, but this tooth not as large as in holotype. First of two large pointed teeth on carpus of cheliped larger than second in male from Yabassi. Postfrontal crest well defined, meeting anterolateral margins in Yabassi specimens, in contrast to that of holotype.

Distribution.—Between the Wouri and Sanaga rivers in the rain forest zone of southwest Cameroon.

Size.—Measurements given in Table 1.

Etymology.—The genus *Louisea* is named for my wife, Dr. Louise M. Bourgault, a Professor of Mass Communications at Northern Michigan University, Marquette, Michigan, U.S.A., in recognition of her dedicated support of African freshwater crab biology, an effort which she has maintained for more than twelve years.

Remarks.—*Globonautes macropus edeaensis* was briefly described by Bott (1969), without illustrations, and assigned to the Gecarcinucidae. A more detailed description, including photographs of the carapace and gonopod 1, appeared in a later work (Bott 1970). There have been no further reports of Bott's taxon since that time, other than brief comparison with species of *Globonautes* by Cumberlidge (1987). Bott's taxon is here elevated to specific rank, and placed in the new genus *Louisea.*

It is interesting to speculate on why *L. edeaensis* and *G. balssi* were originally assigned to the Gecarcinucidae by earlier workers. One possibility could be that the small hard flange at the junction between segments of the mandibular palp of these taxa (which is partly obscured by a fringe of long hairs) was counted as a second lobe. For example, Bott (1955, 1965) considered this feature to warrant subfamilial recognition for Madagascan crabs of the genus *Hydrothelphusa* A. Milne-Edwards, 1872, and erected the Hydrothelphusinae Bott, 1955, a subfamily of the Gecarcinucidae, to accommodate this genus. However, similar small flanges between the segments of the mandibular palp are also found in *Sudanonautes orthostylis* (Bott 1955) and *S. floweri* (De Man 1901) and this feature has not been judged to warrant familial recognition for these species which are all in the Potamonautidae (Rathbun 1921, Cumberlidge 1993a). It should be noted that the Gecarcinucidae and Pseudothelphusidae possess a mandibular palp with a large, distinct second lobe which is a separate, hardened process resting on the anterior face of the mandible.

Generic Comparisons

Differences in the length of the terminal segment of gonopod 2, the form of the terminal segment of gonopod 1, and the form of the third maxilliped are diagnostic in distinguishing between *Sudanonautes, Liberonautes, Potamonautes,* and *Potamonemus*

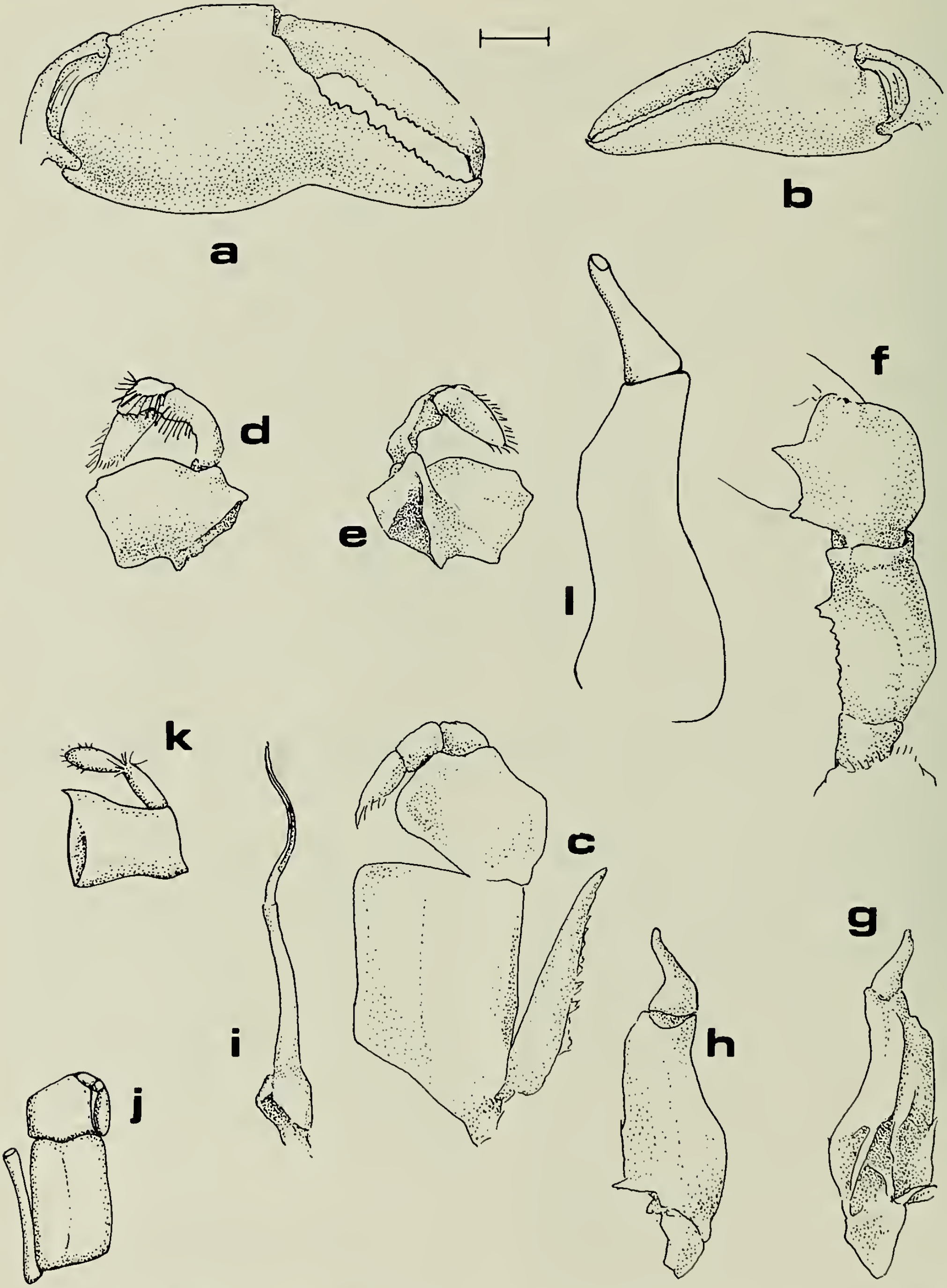

Fig. 3. *Louisea edeaensis*, from Yabassi, Cameroon male (CW 18.1 mm), ZMB 21575, (a), right cheliped, frontal view; (b), left cheliped, frontal view; (c), left third maxilliped; (d), left mandible anterior view; (e), left mandible posterior view; (f), merus and carpus of right cheliped superior view; (g), left gonopod 1, caudal view; (h), left gonopod 1, cephalic view; (i), left gonopod 2, caudal view. *Globonautes balssi* from Johann-Albrecht-Hohn, Cameroon, paratype, adult female (CW 22.0 mm), ZIM K-3506; (j), right third maxilliped; (k), left mandible anterior view. *Globonautes balssi* from Johann-Albrecht-Hohn, Cameroon, male holotype (CW 12.5

Table 1.—Carapace measurements (mm) and proportions relative to body size (CL) for all known specimens of *Louisea edeaensis* and *Globonautes balssi* from Cameroon, West Africa.

Sex	CW	CL	CH	FW	CW/CL	CH/CL	FW/CL
Louisea edeaensis							
Holotype, ZSBS 1118/1							
1. M	22.5	17.8	9.1	7.93	1.27	0.51	0.45
ZMB, 21575							
2. M	18.1	13.1	7.4	6.3	1.38	0.41	0.48
3. M	13.7	10.1	4.8	4.8	1.36	0.48	0.48
Globonautes balssi							
Holotype, ZIM K3506							
1. M (juv)	13.5	10.5	5.5	5.0	1.29	0.52	0.48
Paratypes, ZIM K3506							
2. F (ad, ovig)	22.0	15.5	10.0	7.0	1.42	0.65	0.45
3. F (juv)	12.5	9.5	5.0	4.5	1.32	0.53	0.47

(Bott 1955, Cumberlidge & Clark 1992). Of these four genera, *Louisea* most closely resembles *Potamonautes* and *Liberonautes,* since gonopod 2 in species of these genera has a long, flagellate, terminal segment, and the mandibular palp has a single-lobed terminal segment. However, characters of the third maxilliped and gonopod 1 clearly distinguish *Louisea* from these two genera. In both *Potamonautes* and *Liberonautes* the exopod of the third maxilliped possesses a flagellum, and the terminal segment of gonopod 1 curves evenly and tapers to a pointed tip (Bott 1955, Cumberlidge & Sachs 1989a, 1989b). In *Louisea* the exopod of the third maxilliped lacks a flagellum, and the terminal segment of gonopod 1 is S-shaped, tube-like, and has a blunt, rounded end. *Liberonautes* can further be eliminated on biogeographic grounds since members of this genus are not found east of Ghana (Cumberlidge & Sachs 1989a, 1989b).

The other two potamonautid genera occurring in Cameroon (*Sudanonautes* and *Potamonemus*) possess a second gonopod with a short terminal segment, and are therefore not closely related to *Louisea.* Members of *Sudanonautes* can be distinguished from *Louisea* using the same characters of the third maxilliped and gonopod 1 outlined above for *Potamonautes* and *Liberonautes.* While *Potamonemus* and *Louisea* both lack a flagellum on the exopod of the third maxilliped, they can be clearly distinguished by the length of the terminal segment of gonopod 2: it is extremely short in

Table 2.—Measurements (mm) of right and left cheliped length (RCL and LCL), and height (RCH and LCH) for all known specimens of *Louisea edeaensis* and *Globonautes balssi* from Cameroon, West Africa.

Sex	CW	RCL	LCL	RCH	LCH
Louisea edeaensis					
Holotype, ZSBS 1118/1					
1. M	22.5	22.6	14.9	10.2	5.5
ZMB, 21575					
2. M	18.1	15.4	7.3	7.5	3.9
3. M	13.7	9.9	8.7	4.7	2.7
Globonautes balssi					
Paratype, ZIM K3506					
1. F (ad, ovig)	22.0	14.0	14.0	5.5	5.0

←

mm), ZIM K-3506; (l), right gonopod 1, caudal view, based on Bott (1959, Fig. 7). Scale bar equals 5 mm (d–f, k), 2 mm (a–c, g–i), and 2 mm (j).

Potamonemus and extremely long in *Louisea.* For the above reasons, *L. edeaensis* has been removed from its former designation as a subspecies of *Globonautes macropus* in the family Gecarcinucidae, and placed in the new monotypic genus *Louisea* in the family Potamonautidae.

The single-lobed terminal segment of the mandibular palp of *G. balssi* led Cumberlidge (1987) to doubt its assignment to the Gecarcinucidae, and therefore, to *Globonautes.* Indeed, the form of the mandibular palp, and the lack of a flagellum on the exopodite of the third maxilliped of *G. balssi,* position this taxon close to either *Louisea* or to *Potamonemus.* The best way to distinguish between these two genera is by an examination of gonopod 2: a short terminal segment would place *G. balssi* in *Potamonemus,* while a long, flagellate terminal segment would place *G. balssi* in *Louisea.* However, gonopod 2 of *G. balssi* is missing on both sides in the holotype, the only male specimen. For this reason *G. balssi* is regarded as incertae sedis until more material is available.

Despite these differences the following important characters are shared by both *G. balssi* and *L. edeaensis*: (1) the mandibular palp is 2-segmented and the terminal segment is a single lobe (Fig. 3d, e, k); (2) the exopod of the third maxilliped lacks a flagellum (Figs. 1c, 3j); (3) the terminal segment of gonopod 1 is weakly S-shaped, tubular, and is not grooved (Figs. 1g, h, 3l); (4) there is a distinct intermediate tooth on the anterolateral margin between the exoorbital and epibranchial teeth (Figs. 1a, b, 2a, b); (5) the vertical flank suture on the flank begins at the epibranchial tooth, curves forward under the intermediate tooth, and finally curves sharply down to meet the longitudinal suture on the flank (Figs. 1b, 2b); (6) the postfrontal crest is smooth, poorly defined, and ends before meeting the anterolateral margins (Fig. 1a, b); (7) the groove between sternal segments 2 and 3 is complete, while the groove between sternal segments 3 and 4 consists of 2 small notches at the sides of the sternum; (8) the exo-orbital tooth is small and low, the epibranchial tooth is present but is almost undetectable (Figs. 1a, b, 2a, b); (9) the carapace is relatively high (CH/CL = 0.51 *L. edeaensis,* 0.65 *G. balssi*); and (10) both species are small, reaching maturity at CW 22.0 mm.

The following are reasons why *G. balssi* is not included here in *Potamonemus*: (1) the terminal segment of gonopod 1 of *Potamonemus* is evenly curved, with a clear longitudinal groove (Cumberlidge & Clark 1992, Cumberlidge 1993b), whereas that of *L. edeaensis* and *G. balssi* is S-shaped, tubular, and lacks a groove (Figs. 1g, h, 3l); (2) the anterolateral margin of *Potamonemus* lacks an intermediate tooth on the anterolateral margin, whereas both *L. edeaensis* and *G. balssi* possess a small but distinct intermediate tooth (Figs. 1a, b, 2a, b); (3) the carapace of *Potamonemus* is relatively flatter (CH/CL = 0.47–0.49, Cumberlidge 1993b) than that of both *L. edeaensis* and *G. balssi* (CH/CL = 0.51 and 0.65 respectively).

Finally, the most recent specimens of *L. edeaensis* were collected in 1910, and the species has not been encountered since. This is undoubtedly due in part to difficulties in the identification of freshwater crabs from Cameroon, but it may also indicate that *Louisea* is a rare, and possibly endangered, rain forest species.

Acknowledgments

I am very grateful to Dr. L. Tiefenbacher, of the Zoologische Sammlung des Bayerischen Staates, München, Germany for loaning the holotype of *Globonautes m. edeaensis.* I acknowledge the kind hospitality and helpfulness of Dr. Hartmann and Dr. G. Andre of the Zoological Institute and Museum, Hamburg, Germany. I also thank Prof. Dr. H. E. Gruner of the Zoologische Museum of the Humboldt-Universitat, Berlin for loaning specimens of *Louisea* *edeaensis*, and for his helpful cooperation during a visit. I especially thank artists Anne C. Martin and Jon C. Bedick of Northern Michigan University, U.S.A., for their skill and patience in producing the illustrations used in this paper. Part of this work was supported by a Faculty Grant from Northern Michigan University, Marquette, Michigan, U.S.A.

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FREDIUS STENOLOBUS, A NEW SPECIES OF FRESHWATER CRAB (DECAPODA: BRACHYURA: PSEUDOTHELPHUSIDAE) FROM THE VENEZUELAN GUIANA

Gilberto Rodríguez and Héctor Suárez

Abstract.—*Fredius stenolobus,* a new species of pseudothelphusid crab, is described from the Caura River basin in the Venezuelan Guiana. The species closely resembles *Fredius beccarii* (Coifmann, 1939), but can be easily distinguished by the characteristic cephalic process of the first male gonopod and by the apical spinulation of the second male gonopod. SEM microphotographs of these appendages are provided for both species.

In a recent revision of the genus *Fredius,* Rodríguez & Pereira (1992) discussed the systematics and distribution of this genus in northern South America, and advanced an hypothesis relating to the origin and radiation of its species. Recent collections in the Caura River and some of its tributaries revealed another new species of *Fredius.*

The material is deposited at the Museo de Historia Natural La Salle, Caracas (MHNLS) and the Museo de Biología, Universidad Central de Venezuela, Caracas (MBUCV). Other abbreviations used are cb for carapace breadth, and cl for carapace length.

Family Pseudothelphusidae Ortmann, 1893
Tribe Kingsleyini Bott, 1970
Genus *Fredius* Pretzmann, 1967
Fredius stenolobus, new species
Fig. 1A–D; 2A–C; 3A, B

Material.—Rio Mojagua, affluent of Rio Erebato, Estado Bolivar; E. León; 7 Mar 1992, 1 male holotype, cb 81.3 mm, cl 51.5 mm, 2 male paratypes, cl 18.8 and 25.0 mm, cb 62.5 and 38.7 mm, 3 female paratypes, cl 37.8, 35.3 and 33.5 respectively, cb 59.0, 54.4 and 51.8 mm respectively (MHNLS 1267).—Rio Caura, Entrerios, 5°57′15″N, 64°25′30″W, 350 m alt., Estado Bolivar; 25 May 1989; H. Castellanos; 1 male, cl 42.7 mm, cb 64.4 mm, 1 female, cl 54.8 mm, 86.8 mm (MBUCV XI-2923).—El Raudal, Caño Cambur, 15 km SW from Maripa, Estado Bolivar; 21 Mar 1985; J. Medina; 1 immature female, cl 35.7 mm, cb 54.5 mm (MBUCV XI-901).

Diagnosis.—Cephalic lobe of first gonopod auriculariform, narrow in cephalic view, projected distally into triangular spine; mesial border of cephalic lobe sinuous, ending proximally in rounded projection covered with spinules; lateral border of cephalic lobe ending distally in oblong rounded lobe. Mesial lobe well developed, wide, rounded, thumb-like, with bifid apex and large triangular cephalic spine on distal margin.

Description.—(based on holotype and 5 paratypes) Cervical groove deep, narrow, slightly sinuous, ending away from lateral margin. Anterolateral margin with depression behind anteroexternal angle, followed by 3–4 papillae; rest of margin behind cervical groove with approximately 15 blunt teeth, decreasing in size posteriorly. Postfrontal lobes low, wide, continued laterally as faint ridges; median groove wide and shallow between postfrontal lobes, obsolescent or absent near frontal margin. Surface of carapace in front of postfrontal lobes slightly excavated in frontal view and inclined anteriorly. Upper border of front straight or slightly bilobed in dorsal view,

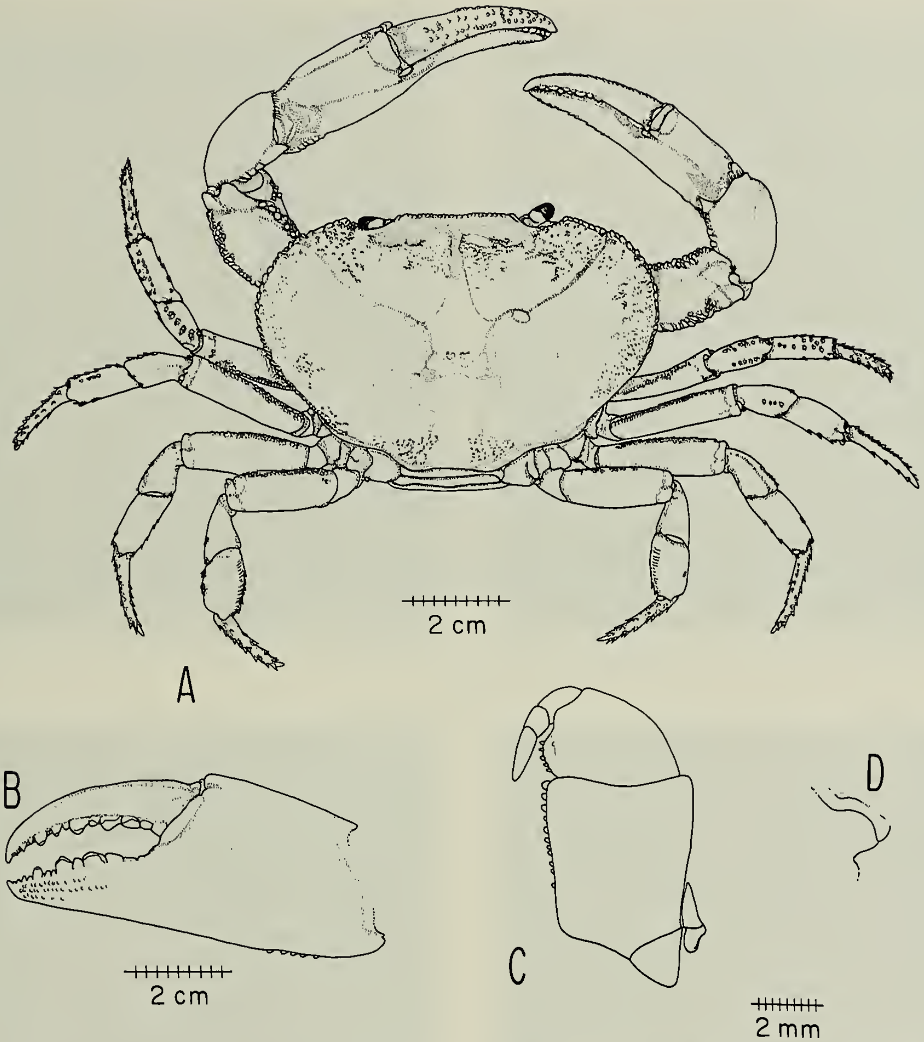

Fig. 1. *Fredius stenolobus,* new species, holotype: A, Dorsal view of carapace and pereiopods: B, Chela of largest cheliped, external view; C, Third maxilliped, left; D, Aperture of efferent channel, left.

carinated, marked with row of indistinct papillae, median notch absent or inconspicuous. Lower margin thin and strongly sinuous in frontal view. Surface of front between upper and lower borders high, excavated, retracted backwards. Surface of carapace with numerous large papillae visible to the naked eye on hepatic and branchial regions. Similar papillae present on dorsal surface of pereiopods.

Palm of larger chela elongated, not conspicuously inflated, fingers strongly arched inwards, gaping at base. Exopod of third maxilliped 0.30 length of ischium of endognath.

First gonopod robust at base, strongly tapering to subapical bulge, with marginal, cephalic, and mesial lobes well developed. Marginal lobe truncate, not extending over field of apical spines. Cephalic lobe auriculariform in cephalic view, projected distally into triangular spine (Fig. 2C, ds), mesial border sinuous, continued proximally as rounded projection with spinules; lateral

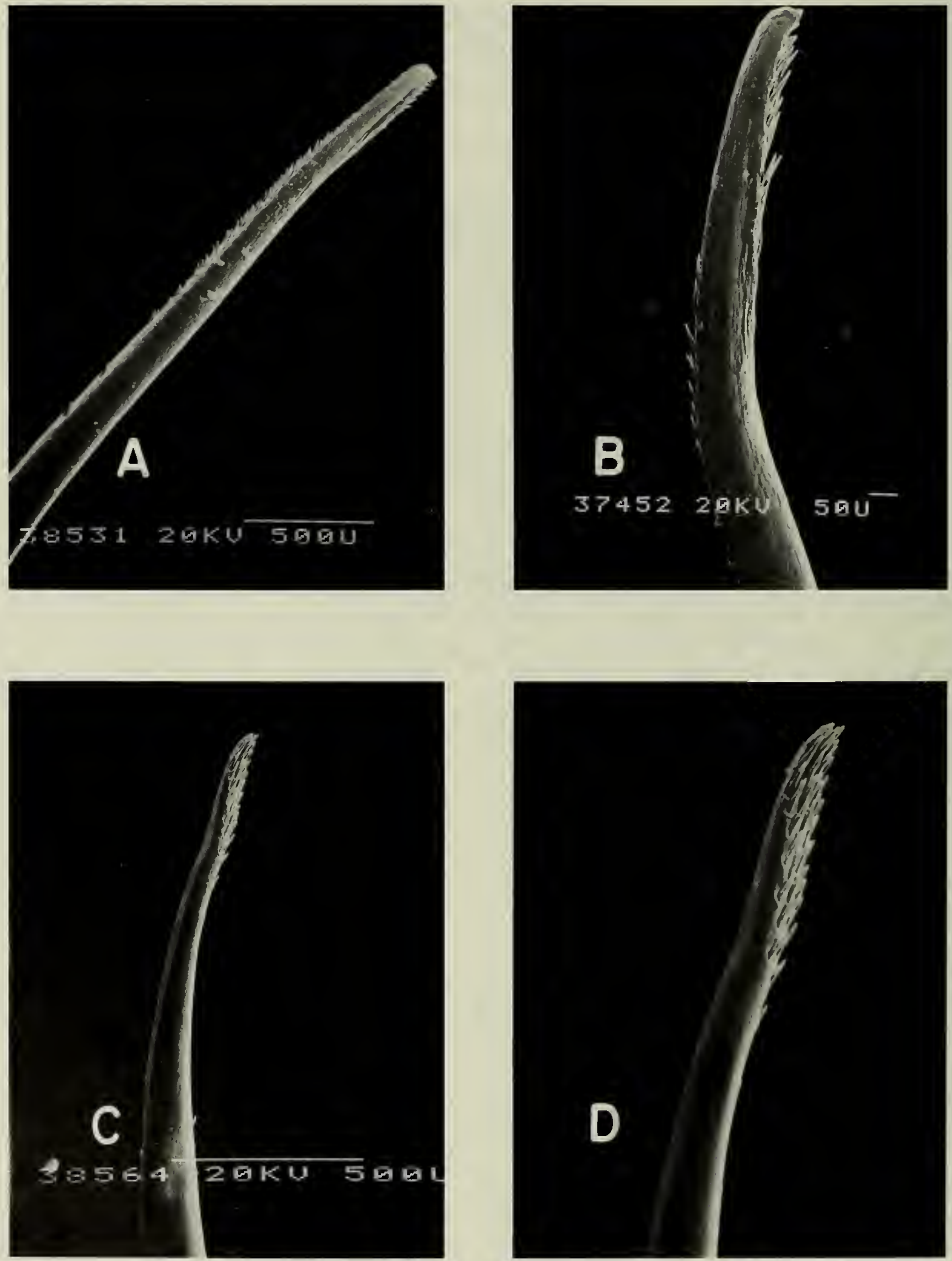

Fig. 2. Apical portion of left first gonopod: A–C, *Fredius stenolobus*, new species, holotype; D, *Fredius beccarii* (Coifmann 1939), MBUCV XI-2928. A, D, caudal view; B, meso-caudal view; C, cephalic view; al, accessory lobe; cs, cephalic spine; ds, distal spine; ml, mesial lobe.

Fig. 3. Left second gonopod: A, B, *Fredius stenolobus*, new species, holotype; C, D, *Fredius beccarii* (Coifmann 1939), MBUCV XI-2928. A, C, Terminal portion; B, D, Detail of apex. Scale in D same as scale in B.

border with rounded accessory lobe (Fig. 2A, B, al); field of apical spines wide, directed to cephalic side. Mesial lobe wide, rounded, thumb-like, with bifid apex, and large triangular cephalic spine on distal margin (Fig. 2A, cs). Marginal setae arranged in dense row over proximal half of gonopod; lateral surface with numerous long plumose setae. Second gonopod with numerous spinules on distal portion; tip cup-shaped, with relatively strong spines directed distally.

Color.—Holotype preserved in alcohol dark brown on the dorsal surface of the carapace and walking legs; anterior portion of the carapace a darker shade. The chelae are dark brown on the upper portions, brown-orange on the inner surface; the distal portions of the dactyli are black. The ventral surface of the carapace and appendages is light brown.

Etymology.—The specific name is from the Greek "stenos," narrow, and "lobos," lobe, and refers to the narrow cephalic lobe.

Fredius beccarii (Coifmann, 1939)
Figs. 2D; 3C, D

Pseudothelphusa beccarii Coifmann, 1939, p. 98, figs. 2, 4a, pl. 3, 1, 2.

Guinotia (*Neopseudothelphusa*) *beccarii*, Pretzmann, 1967, p. 24.

Eudaniela (*Aspöckia*) *beccarii beccarii*, Pretzmann, 1971, p. 16.

Eudaniela (*Aspoeckia*) *beccarii beccarii*, Pretzmann, 1972, p. 18, figs. 103–104.

Pseudothelphusa contorta Rodríguez, 1966, p. 263, fig. 3, pl. 2.

Eudaniela (*Aspöckia*) *beccarii contorta*, Pretzmann, 1971, p. 16.

Eudaniela (*Aspoeckia*) *beccarii contorta*, Pretzmann, 1972, p. 19, figs. 25–28, 73, 74.

Guinotia (*Neopseudothelphusa*) *beccarii cuyunis* Pretzmann, 1967, p. 23.

Fredius beccarii, Rodríguez & Pereira, 1992, p. 304, fig. 4M, N.

Material.—Rio Cuyuní, Estado Bolivar; 1987; A. Machado (MBUCV XI-2928). 1

male (cl 39.7 mm, cb 63.0 mm; Venezuela, without other data; (MBUCV XI-0838). [Other literature records for this species are given by Rodríguez (1982)].

Remarks.—The first gonopod of *Fredius stenolobus* closely resembles that of *Fredius beccarii,* but in this latter species the cephalic lobe is wider in cephalic view, the accessory lobe is absent, and the proximal spiny projection of its mesial margin is more developed. The cephalic spine of the first gonopod of *F. beccarii* is stronger and directed caudally, and the lateral lobe is larger than in *F. stenolobus.* The morphology of the second male gonopod has been rarely used in pseudothelphusid systematics. As our SEM photographs show, there are conspicuous differences between the second gonopods of both species. The cup-shaped tip differs in the arrangement of the spines and the conspicuous spinulation on the distal portion observed in *F. stenolobus* is absent in *F. beccarii.*

The key to the species of *Fredius* in Rodríguez & Pereira (1992) should be expanded after couplet 2 to allow for the new species as follows:

Cephalic lobe narrow, accessory lobe prominent ....
.... *Fredius stenolobus,* new species
Cephalic lobe very wide, accessory lobe absent ....
..... *Fredius beccarii* (Coifmann, 1939)

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A NEW *CALCINUS* (DECAPODA: ANOMURA: DIOGENIDAE) FROM THE TROPICAL WESTERN ATLANTIC, AND A COMPARISON WITH OTHER SPECIES OF THE GENUS FROM THE REGION

Néstor H. Campos and Rafael Lemaitre

Abstract.—A new species of a diogenid hermit crab, *Calcinus urabaensis,* is described from the Gulf of Urabá, on the Caribbean coast of Colombia. The new species is the third in the genus described from the western Atlantic, and can be distinguished from the other two known species of the genus *Calcinus* in the region, *C. tibicen* (Herbst) and *C. verrilli* (Rathbun), by differences in coloration and armature of the dactyl of the left cheliped, third pereopod, and telson. A comparison of the three species is included.

Resúmen.—Se describe una nueva especie de cangrejo ermitaño pertenecienta a la familia Diogenidae, *Calcinus urabaensis,* colectada en el Golfo de Urabá, Caribe sur. La nueva especie es la tercera conocida de este género en el Atlántico occidental, y se diferencia de las otras dos especies del género *Calcinus* de la región, *C. tibicen* (Herbst) y *C. verrilli* (Rathbun), en la coloración y espinas del dáctilo de la quela izquierda, tercer pereópodo, y telson. Se presenta una comparación de las tres especies.

Compared to other tropical regions of the world oceans, the western Atlantic contains very few species of the diogenid genus *Calcinus* Dana, 1852. Recent studies of *Calcinus* species in the Pacific, for example, have shown that nine species occur on the Hawaiian Islands (Haig & McLaughlin 1984), 11 species on the Mariana Islands (Wooster 1984), and 17 species on the Australian coast (Morgan 1991). In contrast, only two species have been described from the western Atlantic, *C. tibicen* (Herbst, 1791), broadly distributed from Florida to Brazil, including Bermuda; and *C. verrilli* (Rathbun, 1901), considered endemic to Bermuda (Verrill 1908, Provenzano 1960, Markhan 1977, Chace et al. 1986). Two other taxa also described from the western Atlantic, *Calcinus sulcatus* (H. Milne Edwards, 1836) and *C. formosus* Neumann, 1878, are considered junior synonyms of *C. tibicen* (see Provenzano 1959; McLaughlin, pers. comm.).

In 1985, during an expedition to the Gulf of Urabá, on the Caribbean coast of Colombia (Campos & Manjarrés 1988), the senior author collected a male hermit crab believed to represent an undescribed species of *Calcinus.* The coloration of the Gulf of Urabá specimen was most similar to that of *C. tibicen,* but morphologically the specimen was closest to *C. verrilli.* Because comparative material was not easily available to the senior author, the specimen was sent to the junior author who compared it with material of *C. verrilli* deposited in various museums and institutions in the United States. He too concluded that the specimen represented an undescribed species, the third in the genus *Calcinus* from the western Atlantic. Given that only one specimen existed, the preparation of a manuscript was delayed awaiting the possibility of collecting additional material. However, various collecting efforts since 1985 failed to produce any additional material, and we now describe this new species based on the male from the Gulf of Urabá.

As pointed out by Haig & McLaughlin (1984), species of *Calcinus* are morphologically very similar, and difficult to identify, particularly if color patterns have faded away. For this reason, it is appropriate to present along with the description of the new species, a comparison of the now three western Atlantic species of *Calcinus*. For this purpose, representative material of *C. tibicen* and *C. verrilli* were also examined. Illustrations of selected structures with diagnostic importance are included for all three species.

The material used remains deposited in the collections of the Indian River Coastal Zone Museum, Harbor Branch Oceanographic Foundation, Fort Pierce, Florida (IRCZM); Rosenstiel School of Marine and Atmospheric Sciences, University of Miami (UMML), and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). The following abbreviations are used: SL, shield length (to the nearest 0.1 mm), measured from the tip of the rostrum to the midpoint of the posterior margin; juv: juvenile (s); ovig(s): ovigerous; RHG, Robert H. Gore; AJP, Anthony J. Provenzano, Jr.; WLS, Waldo L. Schmitt; sta, station.

Calcinus urabaensis, new species

Figs. 1a, 2a, 3a, 4a, 5a, b, 6a, 7a, d, g

Calcinus sp.—Campos & Manjarrés, 1988: 19.

Material examined.—Holotype: ♂ SL 5.6 mm, inlet of Pinorroa, Gulf of Urabá, Colombia, on rocks, ~3 m, USNM 251886.

Description of holotype.—Shield (Fig. 1a) slightly longer than wide, with scattered short setae; anterior margin weakly concave; lateral projections obtusely triangular, with small terminal spine; anterolateral margins sloping. Rostrum produced, subtriangular, slightly in advance of lateral projections. Anterodorsal plate of branchiostegite (Fig. 2a) with acute anteroventral angle.

Ocular peduncles (Fig. 1a) long, slender (about 8.6 times as long as wide), and subequal to shield length; peduncles naked except for few short setae proximally on dorsal face, slightly curved outward (viewed laterally). Acicles terminating in strong spine; separated basally by ½ basal width of 1 acicle.

Antennular peduncles (Fig. 2a) reaching almost to base of corneae, naked except for tuft of setae proximally on penultimate segment. Ultimate segment 1.3 times as long as penultimate. Basal segment with mesial face unarmed; lateral face with distal margin armed with 4 (left) or 3 (right) small spines and 1 small submarginal spine.

Antennal peduncles (Fig. 1a, 2a) reaching to about distal ⅔ of ocular peduncles, segments with scattered setae. Supernumerary segment present. Fifth segment slightly curved outward. Fourth segment with dorsodistal spine. Third segment with strong ventrodistal spine. Second segment with dorsolateral distal angle produced, terminating in strong bifid spine, lateral margin unarmed; dorsomesial distal angle with strong spine. First segment with 4 small spines on ventrodistal margin, lateral face unarmed. Acicles slightly exceeding distal margin of fourth antennal segment, terminating in strong spine, dorsomesial margin with 2 (left) or 3 (right) spines, and 2 spines on dorsolateral margin. Flagellum almost reaching to distal end of extended left cheliped, minutely setose.

Third maxilliped with crista dentata formed of row of 25 small corneous teeth.

Left cheliped (Fig. 3a) with outer face of merus, carpus, and chela lacking setae. Fingers not leaving gap when closed, with spoon-shaped tips; cutting edges with irregularly-sized calcareous teeth and tufts of se-

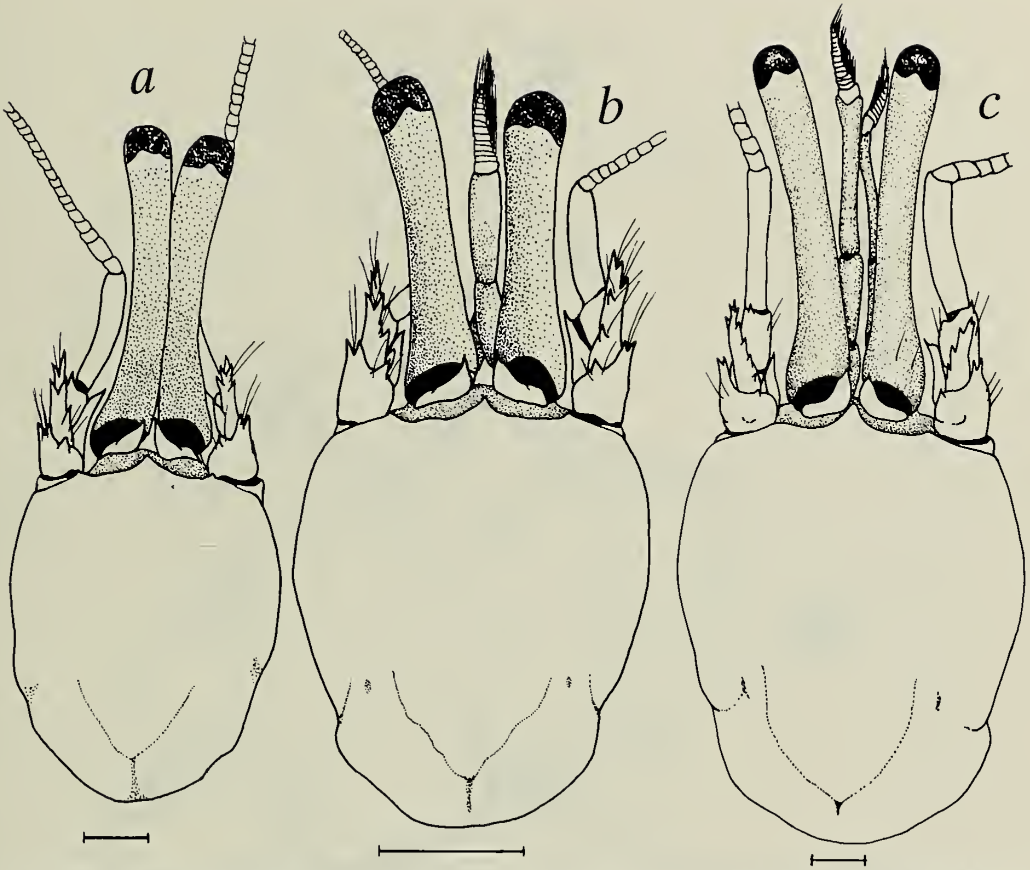

Fig. 1. Shield and cephalic appendages. a, *Calcinus urabaensis*, new species (antennular peduncles hidden under eyestalks); b, *Calcinus verrilli* (Rathbun, 1901); c, *Calcinus tibicen* (Herbst, 1791). Scales equal 1 mm.

tae. Dactyl with row of small spines on upper margin; outer face with irregular rows of low, closely-set tubercles. Fixed finger with row of corneous-tipped spines on lower margin; lower outer face with low tubercles similar to those on dactyl but smaller (spines and tubercles continued on lower outer face of palm). Palm 1.7 times as long as wide; upper margin with row of small, low protuberances; outer and inner faces smooth except for scattered tufts of short setae on inner face. Carpus with upper margin armed with 3 small spines on distal half and strong distal spine; outer distal margin with row of small tubercles on upper ⅓; outer face with prominent tubercle proximally on upper half; inner face smooth. Merus subtriangular in cross-section, upper margin with scattered short setae; inner and outer lower margins with row of 2 or 3 small spines distally; outer and inner faces smooth.

Right cheliped (Fig. 4a) slightly overreaching proximal margin of dactyl of left cheliped. Fingers with spoon-shaped tips, with scattered tufts of setae, and leaving no gap when closed; cutting edges each with 3 strong calcareous teeth. Dactyl with row of corneous-tipped spines directed anteriorly on upper margin. Fixed finger with 4 small spines on outer face proximally. Palm with upper margin raised in form of crest, and armed with 5 strong, corneous-tipped spines; outer face with scattered setae, and 2 short oblique rows of corneous-tipped spines dis-

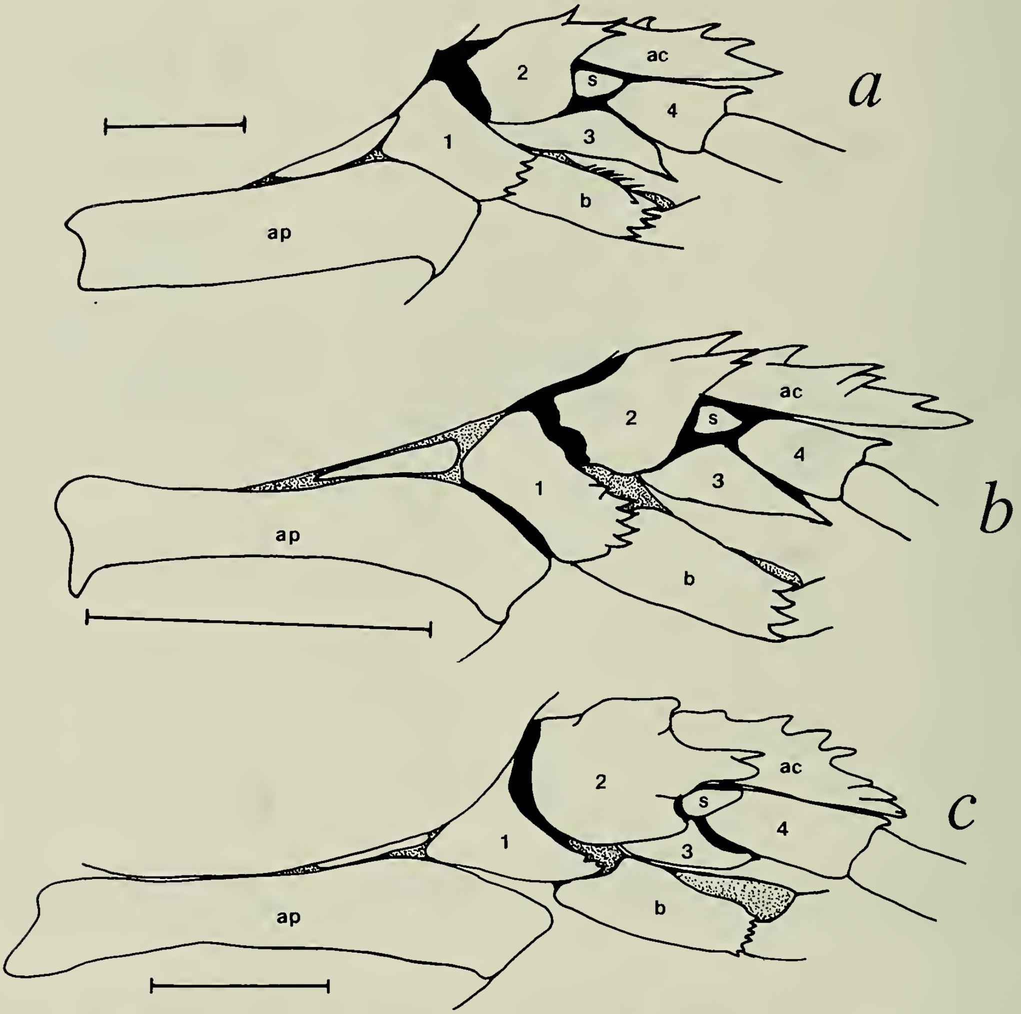

Fig. 2. Right antennular and antennal peduncle, and anterodorsal portion of branchiostegite, lateral view. a, *Calcinus urabaensis*, new species; b, *Calcinus verrilli* (Rathbun, 1901); c, *Calcinus tibicen* (Herbst, 1791). Scales equal 1 mm. (1–4: antennal segments; ac: antennal acicle; ap: anterodorsal plate of branchiostegite; b: basal antennular segment; s: supernumerary segment.)

tally; inner face smooth. Carpus armed on upper margin with 4 corneous-tipped spines, increasing in size distally; outer face with scattered minute tubercles; inner face smooth. Merus subtriangular, upper margin sparsely setose; inner lower margin with 6 spines; outer and mesial faces smooth.

Ambulatory legs slightly asymmetrical, left shorter and with propodi broader (viewed laterally) than right. Second pereopod (Fig. 5a) exceeding extended left cheliped by about ⅕ length of dactyl. Dactyl subequal in length to propodus, terminating in sharp corneous claw, and with tufts of simple setae on mesial, dorsal, and lateral faces; ventral margin armed with 7 short corneous spines. Propodus with dorsodistal, corneous-tipped spine, and ventrodistal spine; outer and ventral faces with tufts of simple setae. Carpus with strong dorsodistal, corneous-tipped spine; ventral margin with small spine at about midlength of mar-

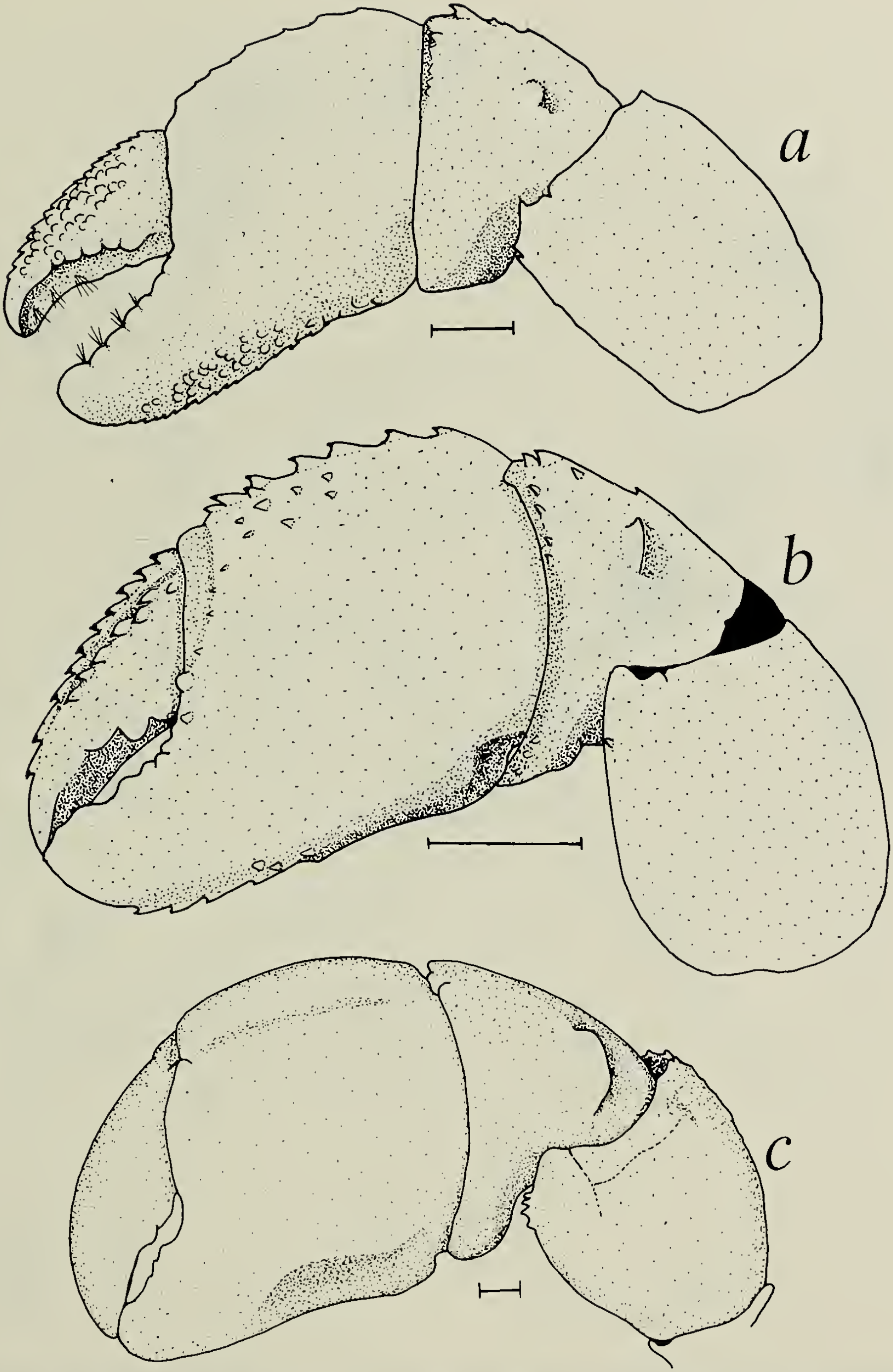

Fig. 3. Left cheliped, lateral view. a, *Calcinus urabaensis,* new species; b, *Calcinus verrilli* (Rathbun, 1901); c, *Calcinus tibicen* (Herbst, 1791). Scales equal 1 mm.

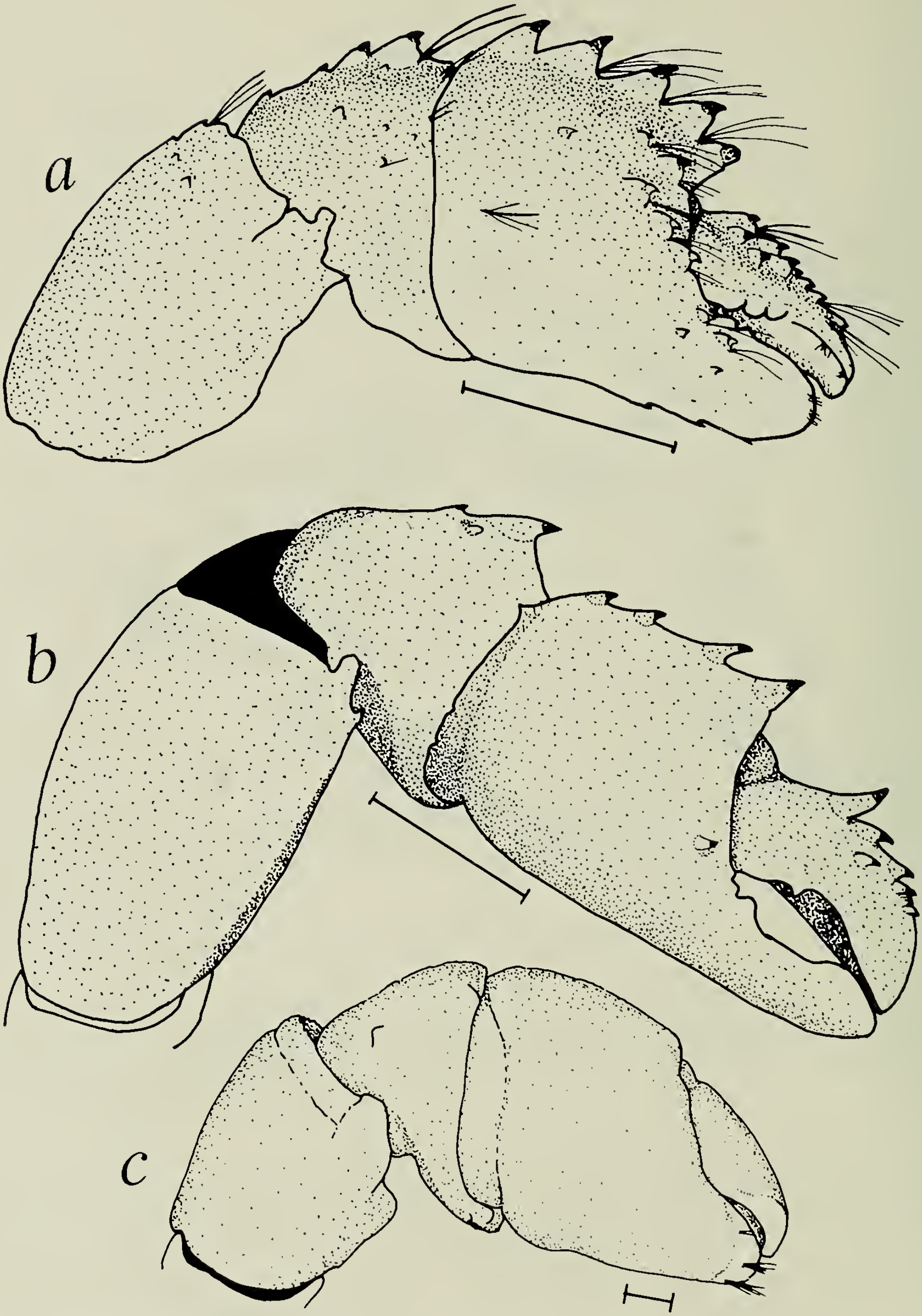

Fig. 4. Right cheliped, lateral view. a, *Calcinus urabaensis,* new species; b, *Calcinus verrilli* (Rathbun, 1901); c, *Calcinus tibicen* (Herbst, 1791). Scales equal 1 mm.

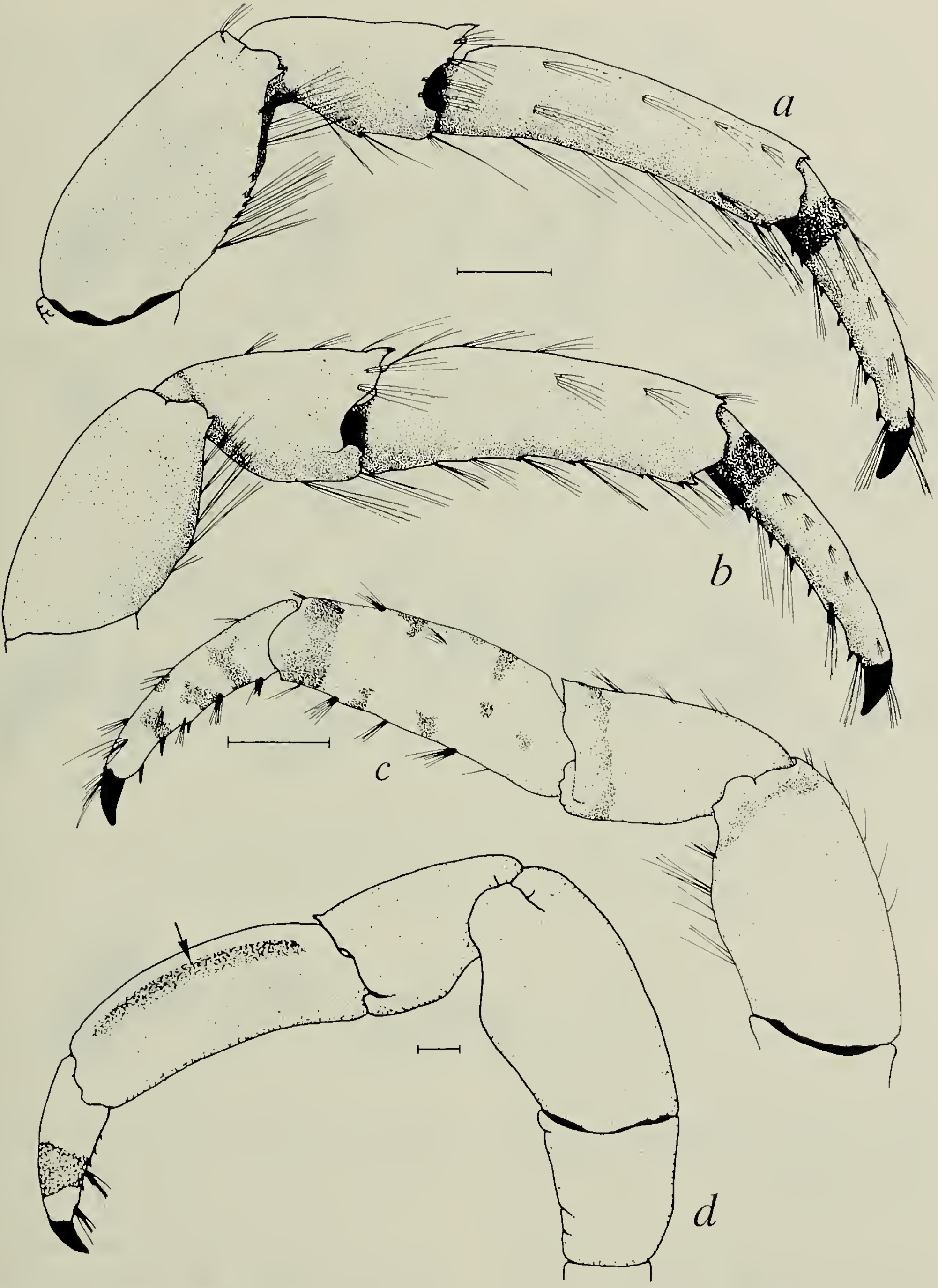

Fig. 5. Ambulatory legs, lateral view. a, b, *Calcinus urabaensis,* new species: a, right second pereopod; b, right third pereopod. *Calcinus verrilli* (Rathbun, 1901): c, left third pereopod. *Calcinus tibicen* (Herbst, 1791): d, left third pereopod. Scales equal 1 mm. (Heavily stippled areas represent color pattern, except for furrow indicated by arrow.)

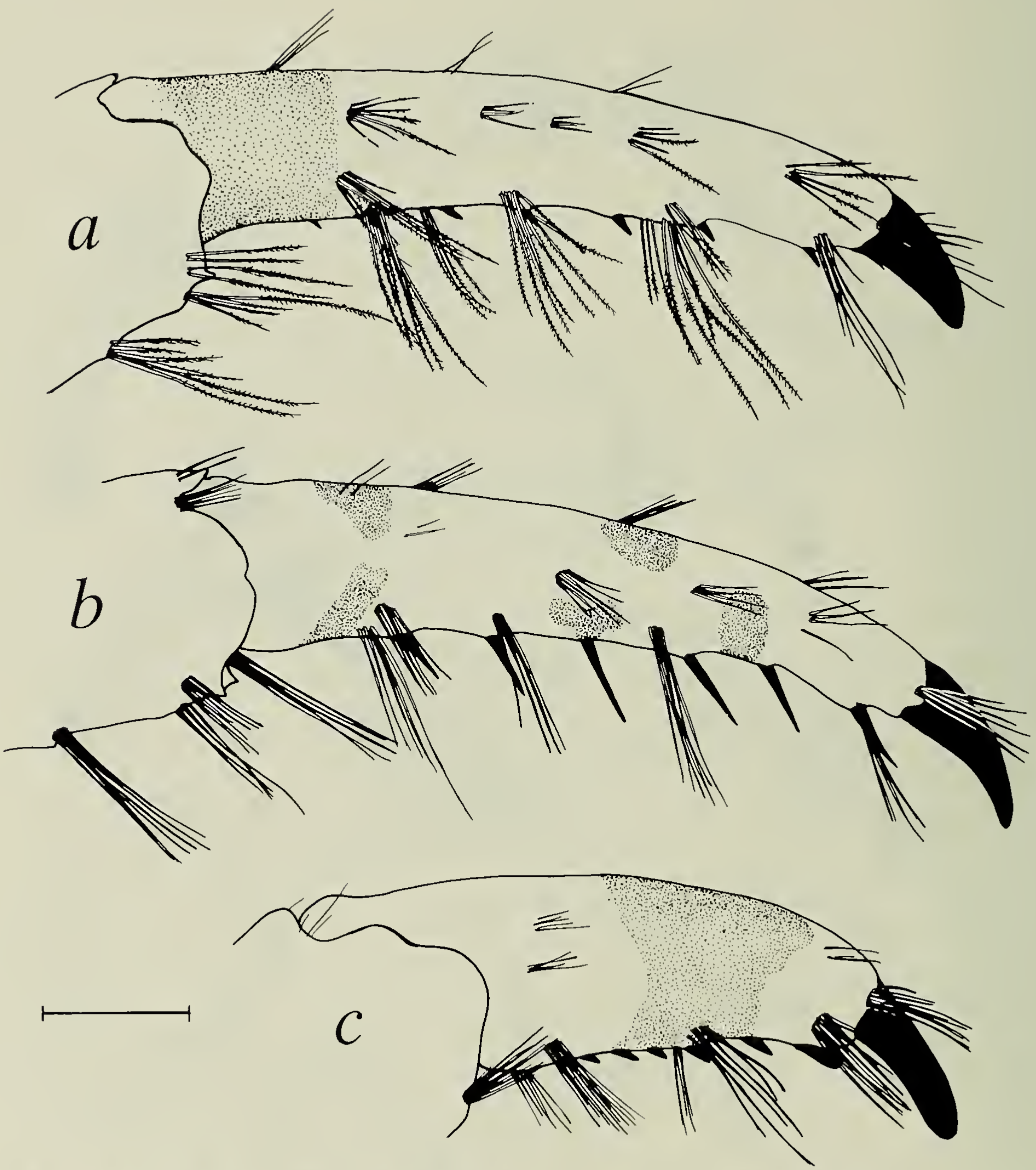

Fig. 6. Dactyl of right third pereopod, lateral view. a, *Calcinus urabaensis,* new species; b, *Calcinus verrilli* (Rathbun, 1901); c, *Calcinus tibicen* (Herbst, 1791). Scale equals 1 mm (a, c), 0.5 mm (b). (Stippled areas represent color pattern.)

gin, and long setae. Merus with spine distally on ventrolateral margin; ventral margin with row of small spines, and several tufts of long simple setae.

Third pereopod (Fig. 5b, 6a) slightly shorter, and with segments broader (viewed laterally) than second pereopod. Dactyl subequal in length to propodus. Dactyl and propodus with tufts of long plumose setae on ventral margin. Propodus with dorsodistal, corneous-tipped spine, and ventrodistal spine; outer face lacking longitudinal furrow; outer and ventral faces with tufts of simple setae; ventral margin with row of small corneous spines. Carpus with strong dorsodistal, corneous-tipped spine; ventral

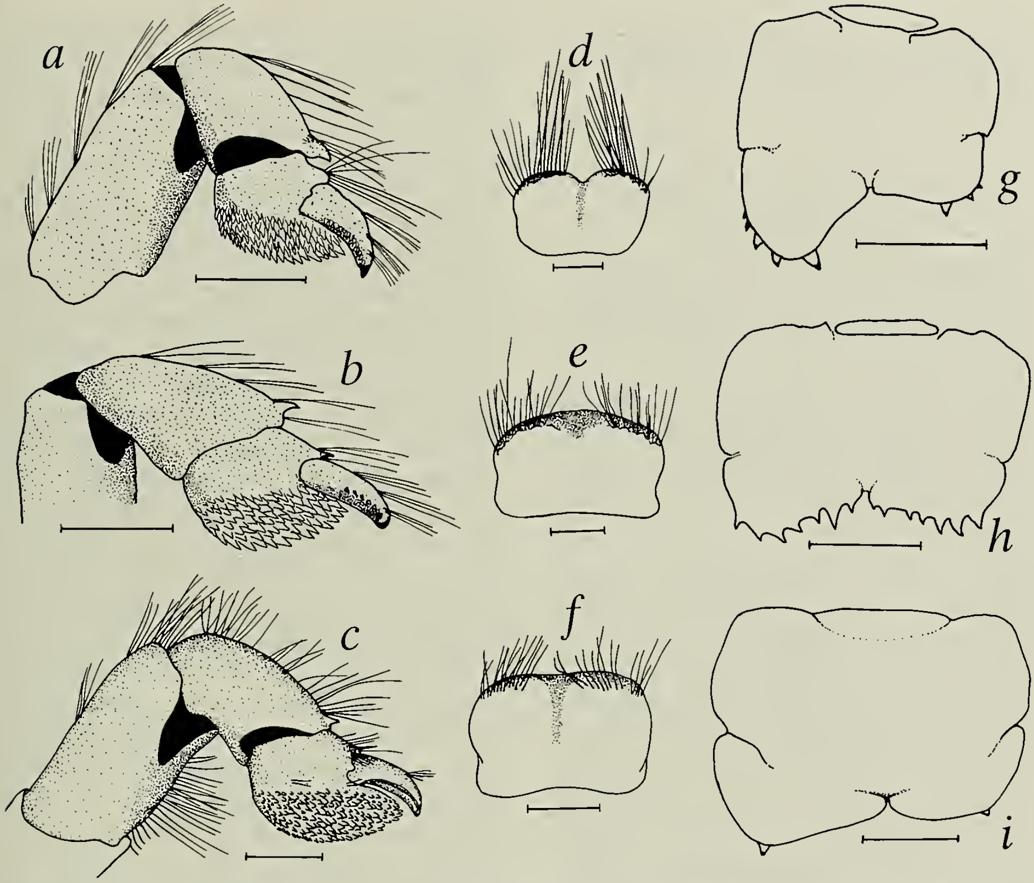

Fig. 7. Right fourth pereopod (a–c), lateral view, anterior lobe of sternite of third pereopod (d–f), ventral view, and denuded telson (g–i), dorsal view. a, d, g, *Calcinus urabaensis,* new species; b, e, h, *Calcinus verrilli* (Rathbun, 1901); c, f, i, *Calcinus tibicen* (Herbst, 1791). Scales equal 1 mm (a, c, i, g), 0.5 mm (b, d, f, h), and 0.25 mm (e).

margin unarmed, with long setae. Merus with spine distally on ventrolateral margin; ventral margin unarmed, with row of tufts of long simple setae.

Fourth pereopod subchelate (Fig. 7a). Dactyl with 13 small corneous spines ventrolaterally. Propodus unarmed dorsally. Carpus with strong dorsodistal spine.

Fifth pereopod chelate.

Sternite of third pereopods (Fig. 7d) with anterior lobe broad, subrectangular, developed as pair of subequal, rounded, setose projections divided by cleft, each projection with row of small tubercles distally.

Telson (Fig. 7g) with posterior lobes asymmetrical, left larger than right; separated by narrow, distinct median cleft; terminal margins with 5 (left) or 3 (right) corneous-tipped, subterminal spines, and fringe of long bristles (not illustrated in Fig. 7g).

Coloration in life (based on field notes).—Carapace red with tinge of purple. Ocular peduncles purple basally, fading distally, and with cream-colored band near base of cornea. Chelipeds purple, fingers white. Ambulatory legs orange; dactyl cream-colored, except for dark red band proximally (Figs. 5a, b, 6a).

Etymology.—The specific name is given for the Gulf of Urabá, where the only specimen of this species was collected.

Distribution and habitat.—Known only

from the inlet of Pinorroa, Gulf of Urabá, Colombia; on rocks exposed to strong waves, in about 3 m of depth.

Calcinus verrilli (Rathbun, 1901)

Figs. 1b, 2b, 3b, 4b, 5c, 6b, 7b, e, f

Clibanarius verrilli Rathbun, 1901:238.—Alcock, 1905:161.—Verrill, 1908:449, pl. 27, fig. 5, pl. 28, fig. 6.—Gordan, 1956: 310.

Calcinus verrilli.—Provenzano, 1960:120, fig. 1.—Hazlett & Provenzano, 1965: 617.—Markham, 1977:131, pl. 1.—Chace et al., 1986:336, fig. 111, color pl. 10.2.—Morgan, 1991:910.

Type material.—Holotype ♂ (SL 7.8 mm), paratype ♀ (SL 4.2 mm), Bermuda, coll. F. V. Hamlin, USNM 24818.

Additional material.—Bermuda: 2 ♀ (SL 2.3–2.6 mm), coll. G. Brown Goode, 1876–1877, USNM 109433.—4 ♂ (SL 1.77–3.5 mm), Three Hill Shoal, 14 Nov 1958, coll. AJP, USNM 103734.—6 ♂ (SL 3.2–5.2 mm), 2 ♀ (SL 3.2–4.1 mm), 3 ♀ ovigs (SL 3.1–4.2 mm), ~3 km north of North Rock Reef, on coral reef, 42 m, 5 Sep 1979, coll. G. Wener, USNM 265218.—2 ♀ (SL 4.4–4.8 mm), 1 ♂ (SL 4.3 mm), North Rocks Reef, 14 Nov 1958, coll. AJP, UMML 32:1643.—1 ♀ (SL 2.8 mm), 1 ♂ (SL 3.0 mm), 1 juv (SL 1.9 mm), Western Ledge Reef, 13 Nov 1958, coll. AJP, UMML 32:1644.—5 ♀ (SL 4.3–4.7 mm), 3 ♂ (SL 4.4–5.2 mm), North Rocks Reef, 14 Nov 1958, coll. AJP, UMML 32: 1645.—1 ♂ (SL 2.5 mm), Pt. at Shelly Bay, 8 Nov 1958, coll. AJP, UMML 32:1955.—1 ♀ (SL 5.2 mm), 15 ♂ (SL 3.6–4.3 mm), North Rocks Reef, 14 Nov 1958, coll. AJP, UMML 32:2216.—3 ♀ (SL 1.7–2.3 mm), 3 ♂ (SL 1.9–2.0 mm), N.E. Breakers, Sep 1966, coll. Schöne, UMML 32:5172.

Diagnosis.—Ocular peduncles (Fig. 1b) varying in relative length with specimen size, from moderately stout, about ⅘ length of shield in smaller specimens (SL $\leq$ 4.0 mm), to slender and subequal to length of shield in larger specimens; acicles terminating in strong spine. Anterodorsal plate of branchiostegite (Fig. 2b) with blunt anteroventral angle. Left cheliped (Fig. 3b) with dactyl having upper margin and outer upper face with row of corneous-tipped spines; upper margin of palm with row of strong corneous-tipped spines, and outer upper face with several small spines on distal half; outer face of carpus with prominent tubercle on upper half. Fingers of right cheliped (Fig. 4b) leaving wide gap when closed; dactyl with strong, usually upwardly curved corneous-tipped spine proximally, and distal row of anteriorly directed spines; palm with row of corneous-tipped spines on upper margin; carpus with 2 or 3 corneous-tipped spines on dorsal margin. Ambulatory legs (Figs. 5c, 6b) with dactyl subequal in length to propodus and 5 to 7 long, slender corneous spines on ventral margin of dactyl; ventral margin of dactyl and propodus with several tufts of long simple setae. Third pereopod lacking longitudinal furrow on outer face of propodus. Fourth pereopod (Fig. 7b) with small dorsodistal spine on propodus. Anterior lobe of sternite of third pereopods (Fig. 6e) subrectangular, setose, often developed as pair of low, rounded projections, with or without small tubercles distally. Telson (Fig. 7h) with posterior lobes subequal, each with 7 spines on terminal margin, outermost spines on left lobe curved ventrally; terminal margin with fringe of long setae (not illustrated in Fig. 7h).

Coloration in life (after Provenzano 1960: 120, and Chace et al. 1986: color pl. 10.2).—General color of body purple with red spots; eyestalks purple near base but with increasing red distally; area proximal to cornea white, cornea black or black spotted with white; chelipeds purple with red patches on upper distal face of carpus and merus; an irregular row of red pigment along upper margin of hand extends to dactyl; ambulatory legs with similar rows of red pigment on faces of segments (see Figs. 5c, 6b).

Distribution and habitat.—Endemic to

Bermuda; subtidal to 110 m, in attached vermetid gastropod shells of *Spiroglyphus irregularis* and *S. annulatus,* or unattached gastropod shells (Markham 1977).

Remarks.—Some specimens of this species (UMML material) exhibit sexual dimorphism in the armature of the chelipeds. The outer face of the right palm in some females is armed on the distal half with three or four small spines, whereas in some males the outer face is armed with only one distal spine. Males tend to have more spines on the right cheliped than females. The number and strength of the spines of the upper margin of the left palm and dactyl varies according to sex of the individual, being fewer and stronger in large males (SL > 4 mm) than in females of similar size.

Three male specimens were found to have both male and female gonopores. One male (SL 5.2 mm, UMML 32:1645) had female gonopores on the right and left side, and two males (SL 5.1 mm, 5.6 mm, UMML 32:2216) had only one female gonopore on either the left or right side. McLaughlin & Lemaitre (1993) have reported specimens with both male and female gonopores in the tube-dwelling hermit crab *Paguritta kroppi* McLaughlin & Lemaitre. As in *P. kroppi,* it is unclear whether the condition observed in the specimens of *C. verrilli* represents an aberration or a reproductive adaptation, such as protandry or protogyny, to a restricted mode of life.

Calcinus tibicen (Herbst, 1791)
Figs. 1c, 2c, 3c, 4c, 5d, 6c, 7c, f, i

Cancer tibicen Herbst, 1791:25, pl. 23, fig. 7.

Pagurus sulcatus H. Milne Edwards, 1836: 279.

Calcinus formosus Neumann, 1878:31.—Alcock, 1905:164.—Gordan, 1956:304.—Morgan, 1991:907.

Calcinus sulcatus.—Benedict, 1901:141, pl. 5, figs. 3, 3a.—Alcock, 1905:164.

Calcinus tibicen.—Provenzano, 1959:363, fig. 4.—Forest & De Saint Laurent, 1967: 106.—Sánchez & Campos, 1978:22, fig. 5.—Chace et al., 1986:335, fig. 111.

Material examined.—Florida: 1 ♀ (SL 5.3 mm), Fort Pierce, Dynamite Point North, beach in rocky tide pool, 18 Mar 1972, coll. R. G. Gilmore, IRCZM 89:050.—1 ♂ (SL 4.2 mm), 1 ♀ (SL 3.3 mm), 1 ♀ ovig (SL 4.4 mm), Vero Beach, 100 yards (91 m) off Sand Point, 10 ft (3 m), on coquina shelf, 28 Jun 1972, coll. RHG, IRCZM 89:219.—1 ♂ (SL 6.3 mm), St. Lucie County, Walton Rocks, in worm reef during night survey, intertidal, 27 Jan 1975, coll. RHG, IRCZM 89:2625.—1 ♂ (SL 4.6 mm), Stuart, north of St. Lucie Inlet, in worm reef by "Fish Bowl" channel, intertidal, 12 Apr 1972, coll. RHG, IRCZM 89:101.—1 ♀ ovig (SL 5.2 mm), St. Lucie County, Walton Rocks, Hutchinson Island, across from Florida Power and Light Company plant, intertidal, 9 Jul 1975, coll. J. Dudley, IRCZM 89:2302.—1 ♂ (SL 6.7 mm), Indian River, Martin County, near St. Lucie Inlet, on rocks, 4 May 1988, coll. R. S. Rox, IRCZM 89:06472.—1 ♀ (SL 3.3 mm), Tortugas, 21 Jun 1932, coll. WLS, USNM 102696.—1 ♂ (SL 4.5 mm), Tortugas, 19 Jul 1930, coll. WLS, USNM 102697.—2 ♂ (SL 3.0–6.0 mm), 1 ♀ (SL 4.9 mm), Tortugas, sta 34–32, 5 Jul 1932, coll. WLS, USNM 102698.

Virgin Islands: 1 ♂ (SL 3.3 mm), St. Croix, Christiansted, East Little Princess, intertidal under rocks, 17 Aug 1971, coll. W. E. Rainey, USNM 154541.

Jamaica: 1 ♂ (SL 4.3 mm), Port Antonio, coral reef off Navy Island, 1932, USNM 77398.

Barbados: 2 ♂ (SL 5.8–6.3 mm), 1 ♀ (SL 4.9 mm), Hasting's Reef, opposite St. Matthias Church, 20 Jul 1959, coll. A. G. Humes & R. U. Gooding, USNM 104256.

Antigua: 13 ♂ (SL 3.3–8.7 mm), 4 ♀ (SL 2.2–3.5 mm), 10 ♀ ovigs (SL 3.3–5.3 mm), Smithsonian-Bredin Caribbean Expedition 1956, sta 73–56, Charlotte Point (=Nutting's "Rocky Point"), English Harbor, 2 Apr 1956, USNM 265157.

Belize: 1 ♂ (SL 4.8 mm), 1 ♀ ovig (SL 5.5 mm), 15 Jul 1930, coll. P. W. Shufeldt, USNM 102700.—1 ♂ (SL 6.4 mm), Carrie Bow Cay, lagoon, 2–3 m, 25 Apr 1975, USNM 184516.

Isla Providencia (Colombia): 1 ♂ (SL 6.3 mm), Bahía Maracaibo, sandy-rocky beach, 28 Mar 1991, coll. G. E. Ramos, USNM 259399.

Panamá: 2 ♂ (SL 3.3–6.7 mm), Colón, Coral reef, 2 May 1911, coll. Meek & Hildebrand, USNM 44191.

Curaçao: 1 ♂ (SL 4.0 mm), 1 ♀ (SL 4.8 mm), Caracas Bay, 1920, coll. C. J. van der Horst, USNM 57513.

Diagnosis.—Ocular peduncles (Fig. 1c) slightly shorter than length of shield; acicles terminating in strong spine (occasionally bifid or trifid) distally. Anterodorsal plate of branchiostegite (Fig. 2c) with blunt anteroventral angle. Antennular peduncle (Fig. 2c) with lateral face of basal segment armed with 4 to 6 small spines on distal margin. Chelipeds lacking setae, surfaces minutely granulose. Left cheliped (Fig. 3c) with chela unarmed; outer face of carpus with prominent subrectangular lobe proximally on upper half. Right cheliped (Fig. 4c) unarmed expect for small tubercle proximally on outer face of carpus; fingers not leaving gap when closed. Ambulatory legs (Figs. 5d, 6c) each with dactyl shorter than propodus (about 0.6 times length of propodi); ventral margin of dactyl with row of 4 to 7 short corneous spines, and several tufts of short simple setae; lateral face of propodus of third pereopods each with distinct longitudinal furrow on upper half of lateral face. Fourth pereopod (Fig. 7c) with dorsal margin of propodus unarmed. Anterior lobe of sternite of third pereopods (Fig. 7f) subrectangular, setose, often developed as pair of low, rounded, unarmed projections. Telson (Fig. 7i) with posterior lobes asymmetrical, each usually with 1 submarginal spine; terminal margin with fringe of long setae (not illustrated in Fig. 7i).

Coloration in life (after Provenzano 1959: 363, and Chace et al. 1986:335).—Chelipeds red-brown to maroon, often tinged with purple, and with white fingertips. Dactyls of the ambulatory legs white or yellow, with a red band (Figs. 5d, 6c). Eyestalks orange-red fading to white near cornea. Carapace usually red, often tinged with purple (rarely green), and with white punctae.

Distribution and habitat.—Florida, Gulf of Mexico, Caribbean to Brazil, including Bermuda; lower intertidal and subtidal to 18 fms (32.9 m); commonly encountered, in hard substrates such as rocky bottoms, worm reef platforms, and coral reefs.

Remarks.—Several carcinologists have indicated that *Calcinus tibicen* is broadly distributed in the West Indian region from Florida to Brazil, including Bermuda [e.g., Alcock 1905 (as *C. sulcatus*), Verrill 1908 (as *C. sulcatus*) Schmitt 1935, Provenzano 1959, Abele & Kim 1986, Morgan 1991].

Morphological Comparison of *Calcinus* Species from the Western Atlantic

Calcinus urabaensis is similar to *C. verrilli* but differs from it in a number of attributes, and specially coloration. In the absence of coloration, the most reliable difference between *Calcinus urabaensis* and *C. verrilli* can be found on the chelipeds, the dactyls of the third pereopods, and the telson. The dactyl of the left cheliped in *C. urabaensis* has a row of small spines on the upper margin, and irregular rows of low, closely-set tubercles on the outer face; the dactyl in *C. verrilli* has two rows of corneous-tipped spines, one row on the upper margin and another on the upper outer face. The left palm in *C. urabaensis* is armed on the upper margin with small, low protuberances, whereas this margin is armed with a row of strong, corneous-tipped spines in *C. verrilli.* On the right cheliped of *C. urabaensis* the dactyl is armed with a row of spines directed anteriorly, whereas in *C. verrilli* the dactyl has a strong, upwardly curved spine proximally, followed distally by smaller anteriorly directed spines. The upper margin of the right palm in *C. urabaensis* is crest-like and armed with a row of five strong spines; the upper margin of the palm in *C. verrilli* also has spines but is not raised in the form of a crest.

Calcinus urabaensis is unique among the western Atlantic species of *Calcinus* in that dactyls of the third pereopod have several tufts of long plumose setae on the ventral margin. A similar condition is found in other *Calcinus* species, all distributed in the Indo-Pacific region: *C. vachoni* Forest, *C. sirius* Morgan, *C. spicatus* Forest, and *C. latens* (Randall) (see Morgan 1991).

The telson in *C. urabaensis* has the posterior lobes distinctly asymmetrical, left the largest, and the terminal margins of the lobes are armed with 3–5 subterminal spines. In contrast, the telson in *C. verrilli* has the posterior lobes weakly asymmetrical, and the terminal margins of the lobes are armed with 7 terminal spines.

Calcinus tibicen can immediately be separated from the other two western Atlantic species of the genus by the smooth, unarmed chelipeds, the longitudinal furrow on the lateral face of the propodus of the third left pereopod, the stout dactyls of the ambulatory legs, and the distinctive color pattern that often persists for many years in alcohol-preserved specimens. Although the coloration of *C. tibicen* generally resembles that of *C. urabaensis,* the two species otherwise differ markedly. The two can readily be differentiated by the armature of the chelipeds (armed with spines in *C. urabaensis,* unarmed in *C. tibicen*), and the setation of the dactyl of the third pereopod (plumose in *C. urabaensis,* simple in *C. tibicen*).

Acknowledgments

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PSEUDOCYCLOPS LAKSHMI, A NEW SPECIES (PSEUDOCYCLOPIDAE: CALANOIDA: COPEPODA) FROM THE LACCADIVES, INDIA

P. Haridas, M. Madhupratap, and S. Ohtsuka

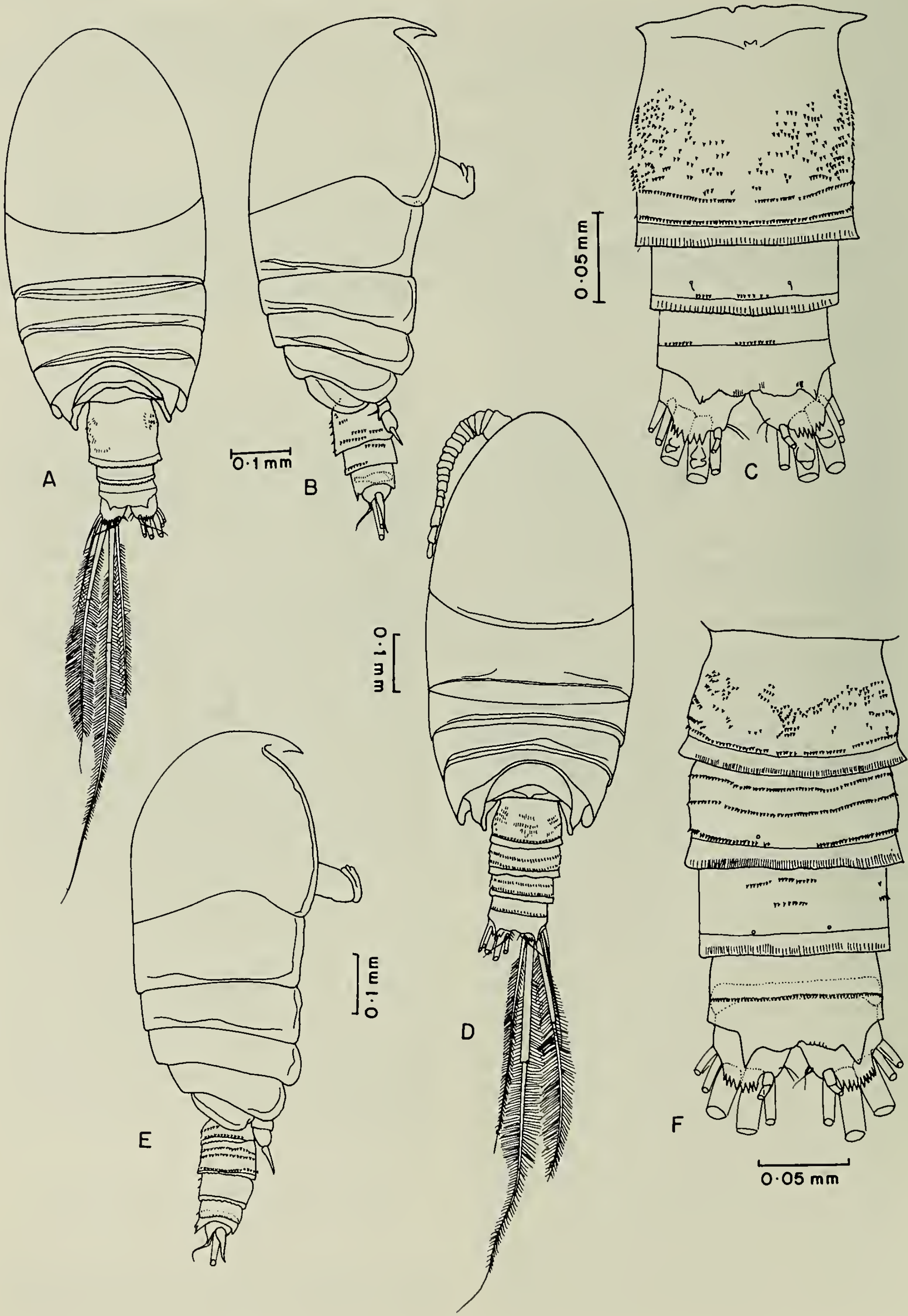
Abstract.—*Pseudocyclops lakshmi,* new species, is described from the Kadmat and Agatti atolls of the Laccadives, India, along with its dimorphic males. Characters separating the new species from the rest of its congeners are discussed. This species is epibenthic and emerges in large numbers into the water column at night.

The hyperbenthic calanoid copepod genus *Pseudocyclops* Giesbrecht, 1893 at present consists of 29 species described from shallow waters of the Atlantic and Indo-Pacific regions (Brady 1872; Brady & Robertson 1873; Giesbrecht 1893; Sars 1903, 1919; Esterly 1911; Gurney 1927; Sewell 1932; Nicholls 1944a, 1944b; Noodt 1958; Bowman & Gonzalez 1961; Vervoort 1964; Tanaka 1966; Wells 1967; Fosshagen 1968; Por 1968; Dawson 1977; Andronov 1986; Othman & Greenwood 1989; Barr & Ohtsuka 1989). Nine species of the genus have hitherto been recorded/described from the Indian Ocean including the Red Sea and Suez Canal, viz. *P. obtusatus* Brady & Robertson, 1873 from the Arabian Sea and Sri Lanka (Thompson & Scott 1903); *P. umbricatus* Giesbrecht, 1893 and *P. latens* Gurney, 1927 from the Suez Canal; *P. latisetosus* Sewell, 1932, and *P. simplex* Sewell, 1932 (type localities of these two species are not given in Sewell 1932); *P. reductus* Nicholls, 1944b, *P. gohari* Noodt, 1958 and *P. steinitzi* Por, 1968 from the Red Sea, and *P. xiphophorus* Wells, 1967 from Mozambique. Their occurrences so far are known only from type localities except *P. obtusatus* which is recorded broadly from the North Atlantic Ocean, the Mediterranean Sea and the Indian Ocean (see Thompson & Scott 1903, Rose 1933, Vervoort 1964, Othman & Greenwood 1989). *Pseudocyclops obtusatus* from the Indian Ocean was reported but not illustrated by Thompson & Scott (1903); there remains the possibility that not all of its records are correct. Similarly, *P. australis* Nicholls, 1944a, originally described from South Australia has been recorded from South Japan (Tanaka 1966) albeit with differences in the structure of exopods of antenna and mandibular palp.

During investigations on zooplankton of the atolls of the Laccadive Sea (Madhupratap et al. 1991a, 1991b), an undescribed species of *Pseudocyclops* was found to be a dominant calanoid copepod in the night-time net tows in the shallow lagoons of Kadmat and Agatti atolls. Although *Pseudocyclops* species are usually distributed near or on the seabottom, they are often found in the water column due to their vertical migration (e.g., Esterly 1911, Gurney 1927, Vervoort 1964, Fosshagen 1968, Dawson 1977, Othman & Greenwood 1989, Ohtsuka unpublished data). The present paper describes both sexes of the new species of *Pseudocyclops* including the apparently dimorphic males.

Pseudocyclops lakshmi, new species
Figs. 1–7

Material.—Specimens were collected in surface hauls at night using a square net (mesh width 200 μm) from Agatti on 10–


A
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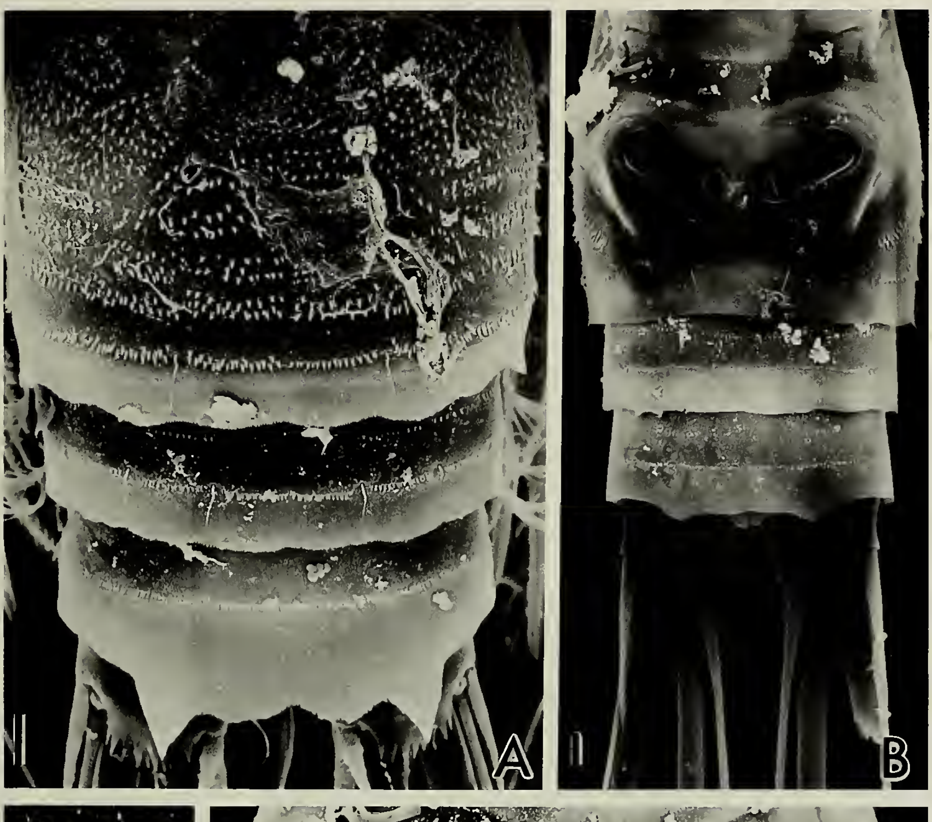

Fig. 2. *Pseudocyclops lakshmi,* Female: SEM photomicrographs. A. Urosome dorsal view; B. Urosome ventral view; C. Distal margin of genital double-somite dorsal view; D. Genital double-somite ventral view. All scale bars = 10 μm.

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Fig. 1. *Pseudocyclops lakshmi,* Female: A. Habitus, dorsal; B. Habitus lateral; C. Urosome. Male: D. Habitus, dorsal; E. Habitus lateral; F. Urosome.

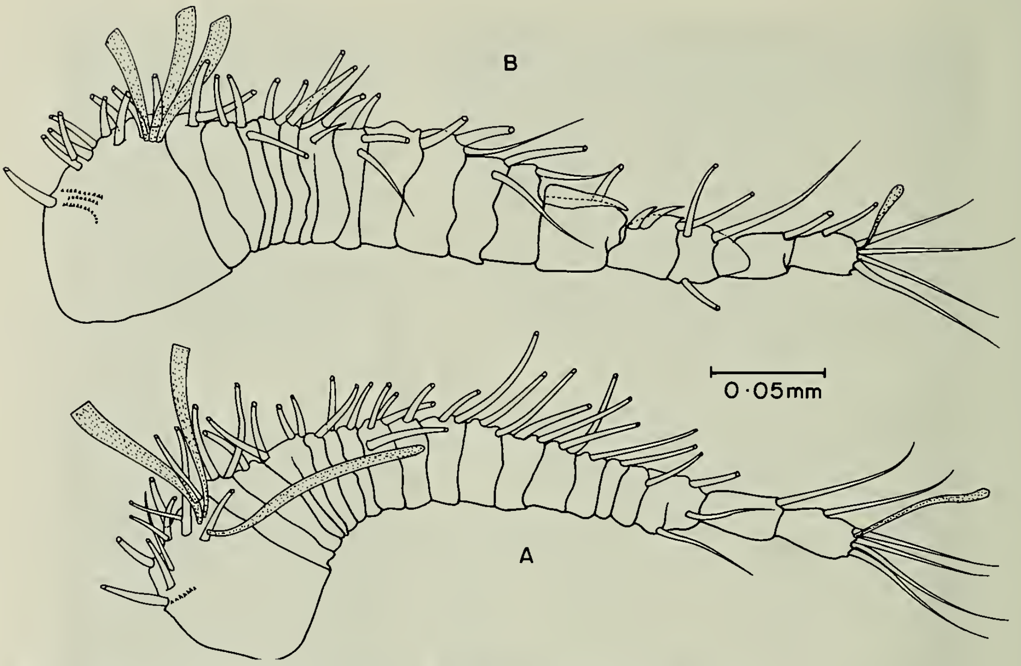

Fig. 3. *Pseudocyclops lakshmi,* Female: A. Antennule. Male: B. Right antennule.

11 Dec 1988 and from Kadmat between 14–16 Dec 1988. The morphological terminology follows Huys & Boxshall (1991). The urosomes of females of the new species were examined with a Scanning Electron Microscope (SEM-JEOL JSM T-20). All types are deposited at the Indian Ocean Biological Centre (IOBC), Cochin.

Types.—Holotype: Female, total length 0.90 mm, IOBC 0405-08-46-1992. Allotype: Male, morph "A"—IOBC 0406-08-46-1992. Paratypes: 10 females & 11 males (6 morph "A" and 5 morph "B"), IOBC 0407-08-46-1992 plus two females and four males dissected and mounted on glass slides IOBC-0408-08-46-1992.

Description.—Female. Body (Fig. 1A, B) 0.86–0.95 mm in total length (average 0.90 mm, *n* = 13). Prosome oval in dorsal view, cephalosome separate from first pedigerous somite, fourth and fifth pedigerous somites completely separate, posterior corner of fifth pedigerous somite smoothly rounded, reaching to one-third length of genital double-somite. Rostrum pointed, triangular, with a pair of minute sensilla. Urosome (Fig. 1C) 4-segmented, distal margins of first 2 somites lamellar. Genital double-somite largest, as long as following 2 somites combined and covered with numerous minute prominences (Fig. 2A, C). Gonopores and copulatory pores paired, closed off by operculum-like leg 6 (Fig. 2B, D). Second and third urosomal somites with subterminal transverse row of minute spinules; third urosomal somite produced posterodorsally into 2 triangular processes reaching beyond midlength of caudal ramus (Fig. 2A); anal somite small and telescoped into third urosome somite. Caudal ramus with serrate posterior margin dorsomedially and 1 bluntly pointed process ventromedially and with 1 dorsal, 4 terminal and 1 outer subterminal setae.

Antennule (Fig. 3A) 21-segmented, not quite reaching to posterior end of cephalosome; first segment with 3 large aesthetascs and 11 setae; fourth and fifth and eighteenth and nineteenth segments partly fused; terminal segment with one aesthetasc. Anten-

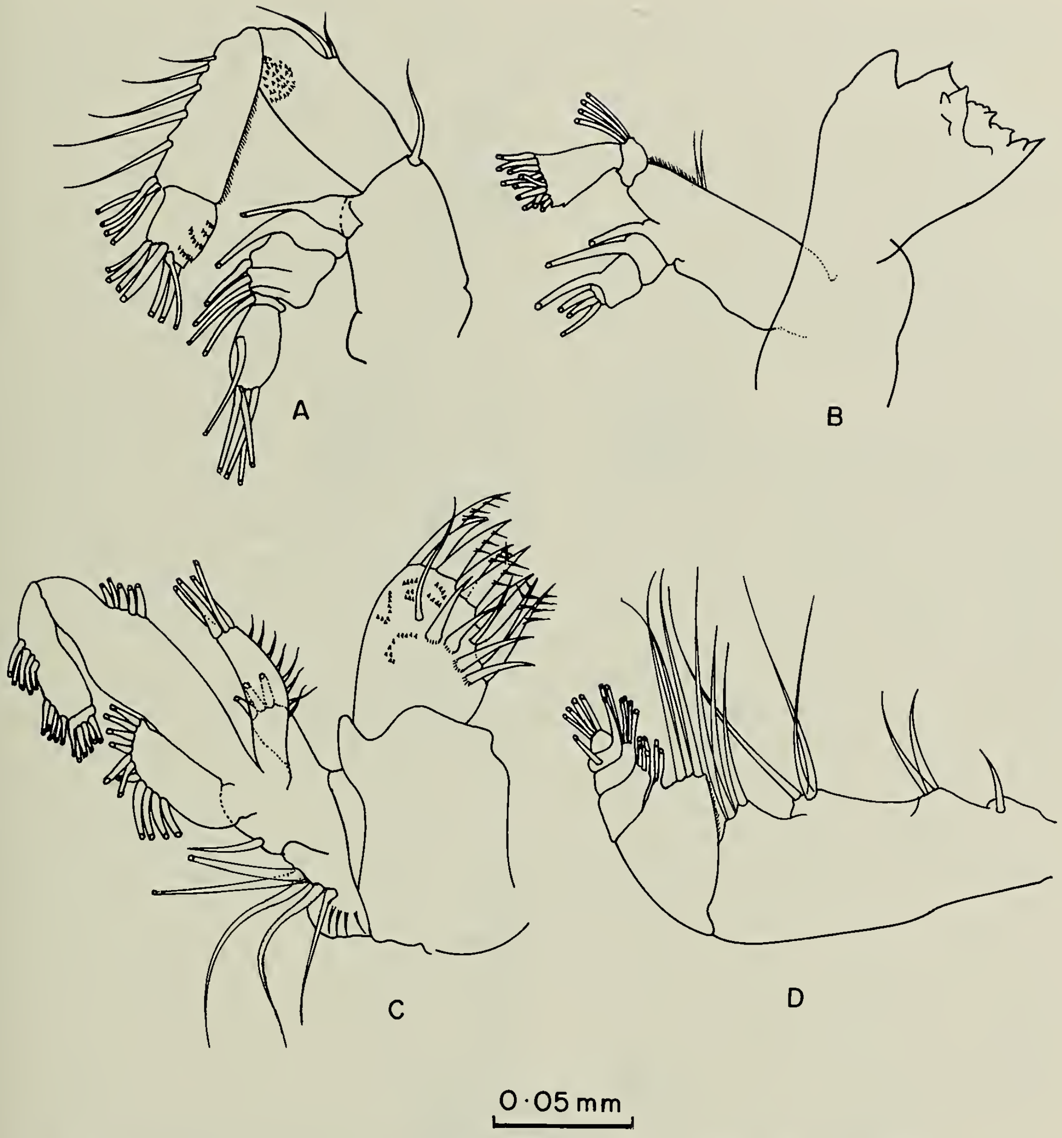

Fig. 4. *Pseudocyclops lakshmi,* Female: A. Antenna; B. Mandible; C. Maxillule; D. Maxilliped.

na (Fig. 4A) basis with seta on inner distal corner; endopod 3-segmented, first segment with 2 setae at midlength of inner margin and subterminal patch of minute spinules, second segment with 5 inner marginal and 4 terminal setae, third segment bearing 7 setae terminally and 4 rows of spinules; exopod 7-segmented, third to fifth segments incompletely fused, first 6 segments each having 1 seta, seventh segment with 1 medial and 4 terminal setae. Mandible (Fig. 4B) gnathobase with 8 blunt teeth; basis with 2 inner setae and patch of minute prominences subterminally; endopod 2-segmented, first segment small, having 4 inner terminal setae, second segment tapering proximally, with 10 terminal setae; exopod 4-segmented, first 3 segments each bearing

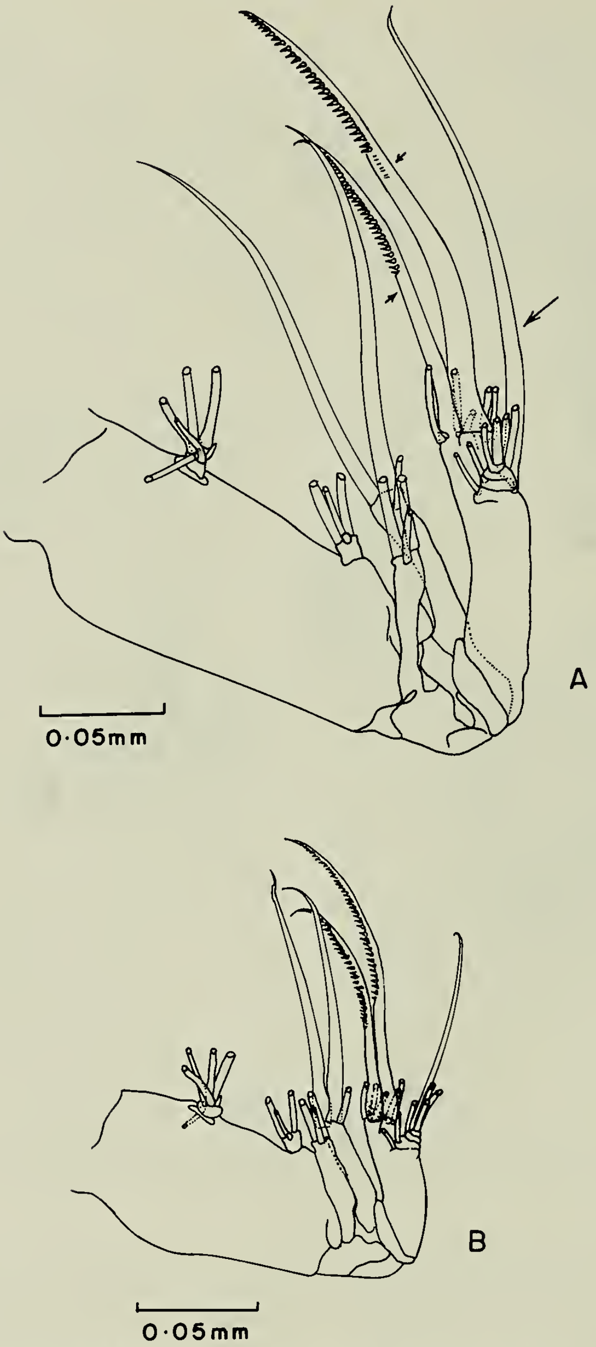

Fig. 5. *Pseudocyclops lakshmi,* Male: A. Morph B maxilla; B. Morph A maxilla.

inner seta, terminal segments carrying 3 setae. Maxillule (Fig. 4C) well developed; praecoxal arthrite with 5 setae on posterior surface and 1 weak and 8 stout spine-like setae along inner margin; coxal and 2 basal endites having 3, 4 and 5 setae respectively; coxal epipodite furnished with 9 setae of unequal lengths; basal exite having short single seta; endopod 2-segmented, first segment bearing 5 middle and 5 terminal setae along inner margin, second segment with 6 terminal setae; exopod 1-segmented, with 11 setae. Praecoxal and coxal endites of maxilla (Fig. 5B, female maxilla similar to morph A of male) having 6, 3, 3 and 3 setae respectively; basis completely fused with first endopod segment to form allobasis, furnished with 7 setae; endopod 3-segmented, first to third segments having 2, 2 and 3 setae respectively. Maxilliped (Fig. 4D) syncoxal endites with 1, 2, 3 and 3 setae respectively; allobasis with 3 medial and 2 terminal setae along inner margin; second to fifth endopod segments each with 4 setae.

Legs 1–4 (Fig. 6A–D) each with 3-segmented rami, all bearing numerous minute spinules on both anterior and posterior surfaces. Exopod segments 1 and 2 with 1 seta, exopod segment 3 with 5 setae except in leg 1 (4 setae), endopod segments 1 and 2 with 1 and 2 setae respectively, endopod segment 3 with 8 setae except in legs 1 (6 setae) and 4 (7 setae). Outer distal corners of second endopod segments of legs 2–4 each produced into bifid process; distal corners of third endopod segments of legs 1–4 acutely produced. Second exopod segment of leg 1 with bulbous process on outer distal corner; terminal spines of third exopod segments of legs 1–4 elongate but not flanged.

Leg 5 (Fig. 6E). Basis with outer subterminal seta on posterior surface; endopod 3-segmented, first segment having a small outer spinule, first and second segment with inner terminal seta, third segment having 1 inner, 1 outer 2 terminal setae; exopod 3-segmented, third segment with 4 flanged spines and 4 inner setae.

Male: Dimorphism was observed only in males. The differences between the two morphs are found in body length and maxilla. In particular, the two morphs differ in the size of maxilla (see Fig. 5A, B). In this paper, males with small and large maxillae are referred to as morphs A and B respectively. Body length of morph A 0.81–0.85 mm (average 0.83 mm, $n = 10$) and that of morph B 0.85–0.95 mm (average 0.90 mm, $n = 10$), prosome of both morphs similar to female (Fig. 1D, E).

Urosome (Fig. 1F) 5-segmented, covered with minute prominences as in the female; first 3 somites with finely striated posterior margin as in female; 2 triangular dorsal processes of fourth somite reaching to distal end of caudal ramus; anal somite telescoped into fourth somite. Caudal ramus with serrate dorsomedial margin and ventromedial blunt process.

Right antennule (Fig. 3B) 18-segmented, geniculate between 14th and 15th segments; first segment with 3 large aesthetascs and 3 rows of minute spinules; seventh and eighth segments fused or separate; 14th segment with sinuous process along whole length of anterior margin; 16th segment produced distally into triangular process reaching midlength of 17th segment; terminal segment with one aesthetasc. Left antennule 21-segmented; fourth and fifth, and eighteenth and nineteenth segments incompletely fused as in female antennule.

Antenna, mandible, maxillule, maxilliped and legs 1–4 of both morphs similar to those of the female.

Maxilla of morph B (Fig. 5A) about twice as long as that of morph A (Fig. 5B); 2 serrate setae on basis (indicated by small arrows) much stouter in morph B than in morph A; seta on second endopod segment (indicated by large arrow) longer and stouter in morph B than in morph A.

Legs 5 of both morphs (Fig. 7A–I) similar to each other except being slightly smaller in morph A. Right leg: coxa and intercoxal sclerite fused; basis separate from coxa, with 1 seta on posterior surface; endopod (Fig. 7A, D, E, F) 1-segmented with small terminal spinules and minute surface spinules, usually without terminal seta; exopod 2-segmented, first segment with stout, flanged terminal spine, second segment with 3 processes, outer long, thick, and medially curved, middle small at base of outer pro-

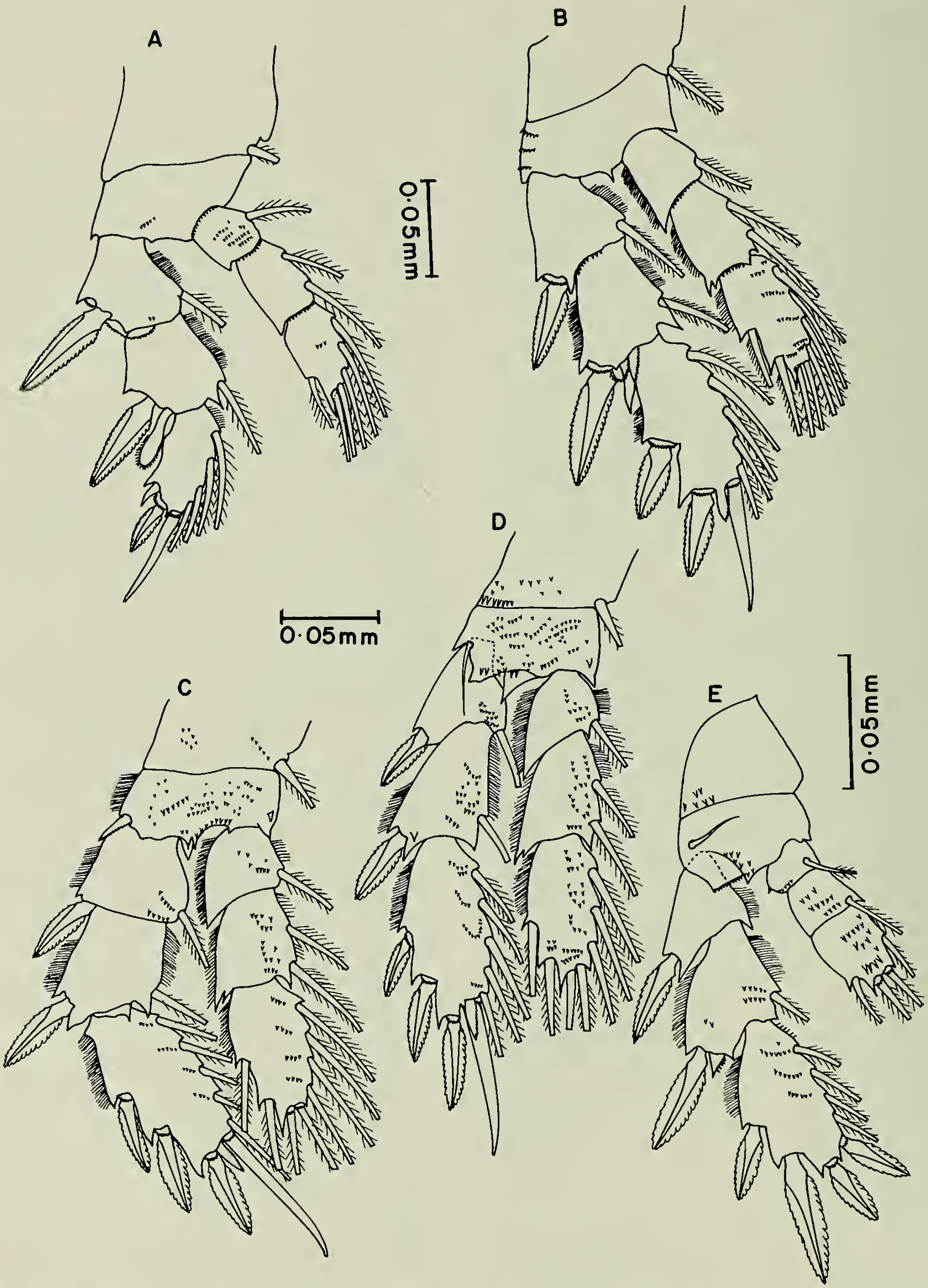

Fig. 6. *Pseudocyclops lakshmi*, Female: A. Leg 1; B. Leg 2; C. Leg 3; D. Leg 4; E. Leg 5.

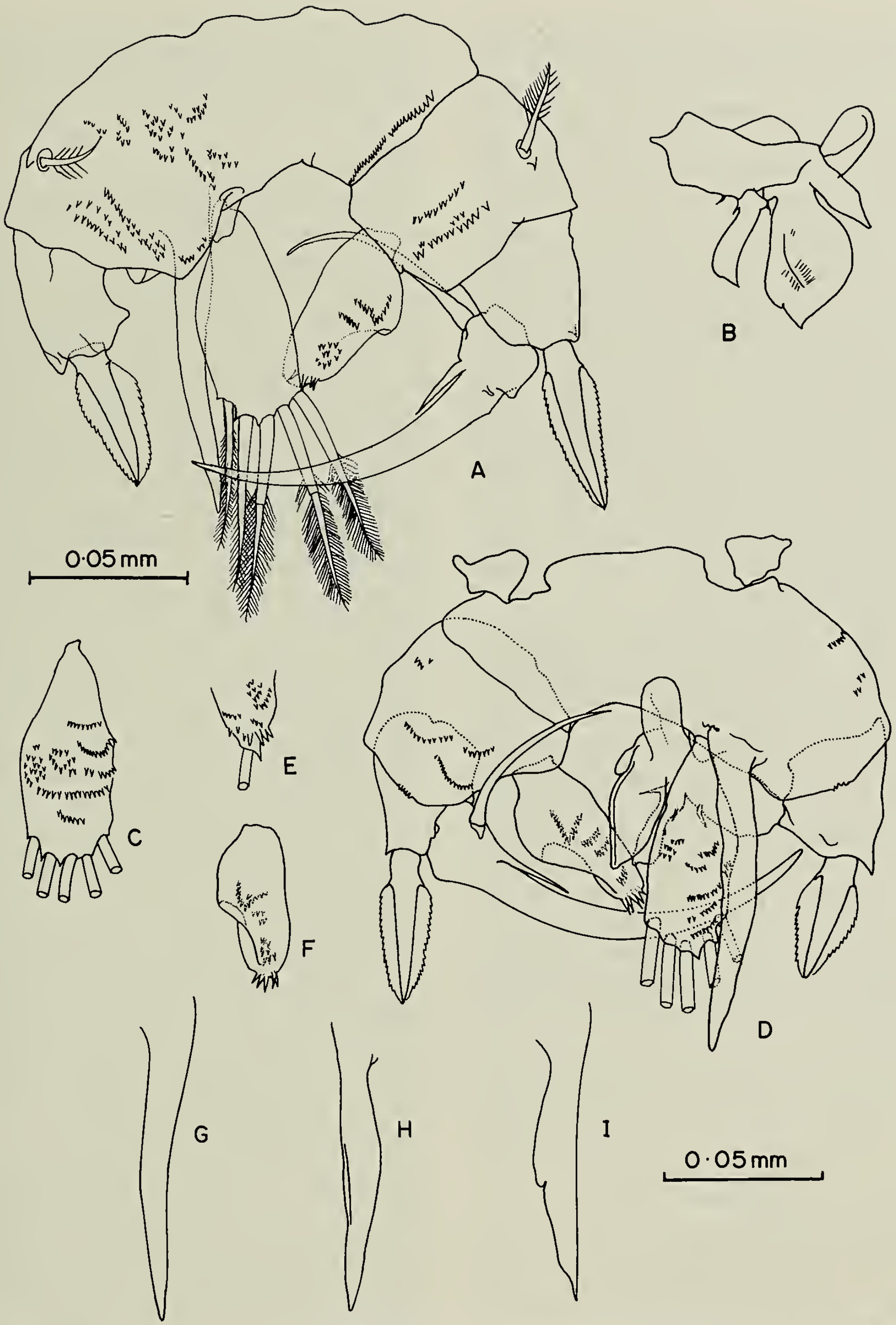

Fig. 7. *Pseudocyclops lakshmi,* Male leg 5: A. Posterior view (left exopod segment 2 omitted); B. Left exopod segment 2; C. Left endopod; D. Anterior view; E–F. Right endopod variability; G–I. Pointed process on basis of left leg showing variability in shape.

cess, inner slender and recurved appearing as chela. Left leg: coxa incompletely fused with basis on both surfaces; basis covered with minute surface prominences, with elongate, pointed process originating from anterior surface (Fig. 7A, D, G, H, I) and 1 seta on posterior surface; endopod (Fig. 7A, C) 1-segmented, with numerous surface prominences and 5 plumose terminal setae; exopod 2-segmented; first segment with outer terminal flanged spine; second segment (Fig. 7B) spoon-shaped, complex and membranous, proximal lobe oblong with 2 hemispherical hyaline processes originating from medial margin and 2 terminal processes, 2 outer processes attached on to outer margin; proximal process rod-shaped with bulbous projection and short seta at base and distal process more or less napiform with subterminal cleft.

Variation.—Segment fusion pattern is variable in right antennule of morph A male—seventh and eighth segments completely or incompletely fused. Right endopod of leg 5 of morph B male has none or 1 terminal seta. The process originating from left basis of leg 5 of morph A male is variable in shape, smoothly tapering distally or having a knob medially (Fig. 7G–I).

Etymology.—This new species is named after goddess "Lakshmi" (Hindu mythology) who symbolizes abundance and wealth. As mentioned earlier, this species is the most abundant calanoid copepod in the two lagoons.

Discussion.—The new species *lakshmi* is one of the most primitive species of the genus *Pseudocyclops,* having 5 separate pedigerous somites, 21-segmented female antennule and 7-segmented antenna exopod; it has an outer basal spine on leg 3, 3-segmented endopod in leg 5 of female and 5 plumose setae on the left endopod of male leg 5. Such primitive characters as 5 separate pedigerous somites, 3-segmented endopod of female leg 5 and 5 setae on left endopod of male leg 5 are found also in *P. australis, P. gohari, P. kulai* Othman & Greenwood, 1989, *P. lerneri* Fosshagen, 1968, *P. mathewsoni* Fosshagen, 1968, *P. reductus, P. rubrocinctus* Bowman & Gonzalez, 1961 and *P. Steinitze* although their antennules and antennae are more advanced.

The present new species, however, has several advanced morphological characters present on the urosome, leg 1 and female leg 5. The urosome is covered with minute prominences, the second exopod segment of leg 1 has an outer bulbous process, and there are 4 setae on the third endopod segment of the female leg 5 (6 setae in *P. kulai, P. lepidotus* Barr & Ohtsuka, 1989, *P. mathewsoni, P. rubrocinctus,* and *P. steinitzi*). The urosome with numerous minute prominences appears to be unique to the new species although *P. lepidotus* has foliaceous scales on the urosome. The bulbous process on the second exopod segment of leg 1 is known in *P. australis* and *P. gohari*; some congeners have a well developed process distal to the outer spine on the second exopod segment of leg 1 different in shape from that of *P. lakshmi. Pseudocyclops lakshmi* seems to be most closely related to *P. australis* from South Australia and Japan and *P. gohari* from the Red Sea in having 3-segmented endopod of the female leg 5 with 4 setae on the terminal segment and a bulbous process on the second exopod segment of leg 1. In particular, the structures of leg 5 of both sexes of *P. lakshmi* resemble those of *P. gohari.* The leg 5 of female *P. reductus* from the Red Sea also shows similarity to that of female *P. lakshmi,* but Nicholl's (1944b) description is too incomplete to compare the two in detail.

Pseudocyclops lakshmi is distinguishable from *P. australis, P. gohari,* and *P. reductus* in metasome, urosome, and legs 1 and 5 in addition to antennule and antenna. Cephalosome and the first pedigerous somite are separate in *P. lakshmi* and *P. australis,* but fused in *P. gohari.* Male *P. gohari* has 8, 8 and 6 well-developed posterodorsal processes on the second, third and fourth urosomal somites respectively; the terminal setae on the caudal ramus are extremely swollen.

The numbers of the antennular segments of the females of *P. lakshmi, P. australis* and *P. gohari* are 21, 18 and 18 respectively. The antenna exopod is 7-segmented in *P. lakshmi* while 4-segmented in *P. australis* (shown as 5-segmented by Tanaka 1966) and *P. gohari.* The mandibular exopod is 2-segmented (Nicholls 1944a) or 5-segmented (Tanaka 1966) in *P. australis* and 3-segmented in *P. gohari* while it is 4-segmented in *P. lakshmi.* The inner distal corner of the basis of leg 1 is prominent in *P. australis* but is not produced in *P. lakshmi* or *P. gohari.* The outer distal corners of the first and second endopod segments of the female leg 5 are strongly produced in *P. australis, P. gohari* and *P. reductus,* but are rather rounded in *P. lakshmi*; there are 4 setae along the inner margin of the third exopod segment of the female leg 5 except for *P. reductus* which has only 1 seta. The right endopod of the male leg 5 has 5 terminal prominences in *P. lakshmi* and 6 to 7 in *P. gohari,* in addition the 2 hemispherical hyaline processes originating along the second exopod medial margin of the left leg 5 in *P. lakshmi* are absent in *P. gohari.* The structure of the male leg 5 of *P. australis* is quite different from that of *P. lakshmi.*

Do et al. (1984) reviewed dimorphism in copepod males. According to them, dimorphism of copepod males is so far known in Calanoida, Cyclopoida, Harpacticoida and Poecilostomatoida. In Calanoida dimorphism in male is reported in families Pontellidae and Pseudodiaptomidae (Johnson 1964, Fleminger 1967, Shen & Mizuno 1984, Walter 1989) and differences occur in characters such as body size and morphology of antennule and leg 5. Dimorphic asymmetry is found in the calanoid genus *Pleuromamma* mostly in the reproductive system (Ferrari 1984). Males of the calanoid copepod *Euchaeta antarctica* produce two types of spermatophores and the same male may produce both kinds of spermatophores (Ferrari & Dojiri 1987). Variations in size ranges of both females and males without morphological differences have been observed in the poecilostomatoid copepod *Oncaea* spp. (Ferrari 1975). The pelagic harpacticoid *Euterpina acutifrons* has two forms of males, namely large and small forms, which have differences in antennule, antenna, developmental rate, sexual behavior, etc. (Haq 1965, 1972). The two forms have varying metabolic rates at different temperatures (Moreira & Vernberg 1968). Variations in the two forms of males of the poecilostomatoid *Pseudomyicola spinosus* parasitic on the blue mussel *Mytilus edulis galloprovincialis* are discernible in body length and slenderness, antennule, swimming legs and caudal ramus. Do et al. (1984) suggested that these differences are indicators of different swimming activity. Similarly, the parasitic copepod *Pachypygus gibber* has a smaller atypical male which is an active swimmer unlike the typical larger male and the former is more efficient reproductively (Hipeau-Jacquotte 1978).

Although there remains a possibility that the two morphs of male *Pseudocyclops lakshmi* may be two distinct species, the absence of females with large-sized maxilla and the co-occurrence of both morphs of males led us to the conclusion that these morphs belong to the same species. Since species of the family Pseudocylopidae usually have well-developed sexual characters in urosome, antennule and leg 5, the invariable sexual characters in both morphs of male *P. lakshmi* support this. It is possible that the feeding behaviors of these two morphs of male *P. lakshmi* may be different because maxilla plays an important role in feeding.

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NEW SPECIES OF *MARIONINA* (ANNELIDA: OLIGOCHAETA: ENCHYTRAEIDAE) FROM *SPARTINA* SALT MARSHES ON SAPELO ISLAND, GEORGIA, U.S.A.

Brenda Healy

Abstract.—Three new species of *Marionina* are described from *Spartina* salt marshes where they were associated with live and dead *Spartina* stems. All three species appear to be confined to this habitat. *Marionina spartinae* is distinguished by paired sigmoid setae, an anteclitellar origin of the dorsal vessel and elongated sperm bundles in the spermatheca. *Marionina waltersi* has 2–3 sigmoid setae per bundle, a long, narrow sperm funnel and a poorly developed seminal vesicle. *Marionina paludis* resembles *M. appendiculata* in having fan-like bundles of 3–6 sigmoid setae but differs in its larger sperm funnel and well developed seminal vesicle and the presence of a compact penial bulb. These are the first records of Enchytraeidae from the marine littoral zone of Georgia.

There have been few studies of marine littoral Enchytraeidae in the east of North America. Published records concern only the northern United States from Maine to South Carolina (Moore 1905, Welch 1917, Lasserre 1971) or Bermuda (Moore 1902, Lasserre & Erséus 1976, Giere 1979). With the exception of a single record of *Stephensoniella marina* (Moore, 1902) (Coates 1983) and some preliminary data from West Florida (Healy 1989), there is no information from more southern states. The new species described in this paper are thus the first records of *Marionina* from the southern Atlantic coast.

Sparina salt marshes, with *S. alterniflora* Loisel, 1907 (smooth cordgrass) the dominant species, cover extensive areas of the intertidal zone from Canada to mid-Florida (where they are replaced by mangroves) and on the Gulf coast as far as Texas (Reimold 1977). On the coast of Georgia, they form a belt approximately 7 km wide and the plants here grow luxuriantly, reaching 2–3 m in height with a basal diameter of 3 cm on the banks of creeks (Wiegert et al. 1981). There is extensive literature on many aspects of the Sapelo Island marshes, including their invertebrate fauna, but while oligochaetes have been shown to be an important component of the fauna of the marsh surface (Teal 1962), they have not, so far, been identified, even to family.

Preliminary investigations of salt marsh oligochaetes on the Sapelo marshes showed that Tubificidae and Enchytraeidae were present on the marsh surface, mainly in plant debris, but that both were far more abundant in the lower regions of *Spartina* stems. The three new species described in this paper, together with another enchytraeid, *Marionina appendiculata* Nielsen & Christensen, 1959 and a tubificid, *Monopylephorus parvus* Ditlevsen, 1904, were among the most abundant faunal species living in the aerenchyma of *Spartina* leaf sheaths, a microhabitat that supplies worms with food and oxygen and protection from predators (Healy & Walters 1993). The presence of aquatic Oligochaeta in plant aerenchyma has not previously been reported.

The three new species can all be referred to *Marionina* as defined by Nielsen & Christensen (1959). The genus was erected by Michaelsen (1989) to contain a group of species removed from *Pachydrilus*, but his diagnosis was inadequate to describe the new taxon. Černosvitov, in his review of the Enchytraeidae (1937), considered the systematic position of *Marionina* to be unclear but retained the taxon as a sub-genus of *Pachydrilus* in which he included 37 species. Nielsen & Christensen (1959) subsequently removed several species to other genera but admitted that *Marionina* remained heterogeneous. Their diagnosis is concerned entirely with negative or variable characters and there is, at present, no derived character that distinguishes the genus as a whole. *Marionina* species are recognized by their small size and the absence of characters that define other genera such as peptonephridia, intestinal diverticula, an anterior origin of the dorsal vessel, two kinds of coelomocytes, lobed seminal vesicles and setae with enlarged ental hooks. The genus has thus become a deposit for any small species that do not conform to other existing generic diagnoses. The 70 or so species currently included in *Marionina* constitute a heterogeneous assemblage comprising at least two lineages (Coates 1987, 1989) and some species of doubtful affinity (Nielsen & Christensen 1959; Coates 1980, 1987). Most of the marine species, however, form a homogeneous monophyly, characterized by an anterior bifurcation of the dorsal vessel in III or IV, i.e., posterior to the brain, instead of anterior to the brain as in most enchytraeids (Coates 1987, 1989, 1990). The three new species described in this paper fall into this group. They are distinguished from other marine *Marionina* by setal shape and number, the point of origin of the dorsal blood vessel, the form of the sperm funnel and development of the seminal vesicle and by characters of the spermatheca, including the arrangement of sperm in the ampulla.

Materials and Methods

Most of the material was collected in May, 1991 from the Kenan Field salt marsh on Sapelo Island (31°23′N, 81°17′W) where samples were taken from high and low marsh and creekside as part of an investigation into the microdistribution of Oligochaeta (Healy & Walters 1993). The substrate was silt and the salinity 20–30‰. A few samples containing one or more of the new species were also taken from *Spartina* marshes in other parts of Sapelo Island, and from marshes at two sites in N. Florida. The latter collections were part of a survey of intertidal and supratidal habitats in Georgia and east Florida in 1990 and 1991 (unpublished) which has provided information on the ecological limits of the species described in this paper.

Samples were taken from surface mud, roots and leaf debris and the lower stems of live and standing dead *Spartina* plants. Worms were extracted from mud by sieving and from plant material by a modified version of the wet-funnel method, using 100 W light bulbs to raise the temperature in the funnels over 40°C in 1–2 hours (Healy & Rota 1992). Leaf sheaths were shredded lengthwise before extraction. Specimens were fixed in 70% ethanol, stained in paracarmine and whole-mounted in Canada Balsam.

Type specimens and other material are deposited in the United States National Museum of Natural History, Washington, D.C. (USNM). Other whole mounts are in the collection of the University of Georgia Marine Institute, Sapelo Island (UGMI), or in the author's collection. All material was collected by the author.

Marionina spartinae, new species

Fig. 1

Material examined.—Holotype: USNM 163805, stained whole mounted specimen, Kenan Field salt marsh, Sapelo Island, May 1991. Paratypes: USNM 163806–163807, stained whole mounted specimens from the type locality, May 1991. Other material from the type locality: USNM 163808–163812; UGMI two whole mounted specimens; 98

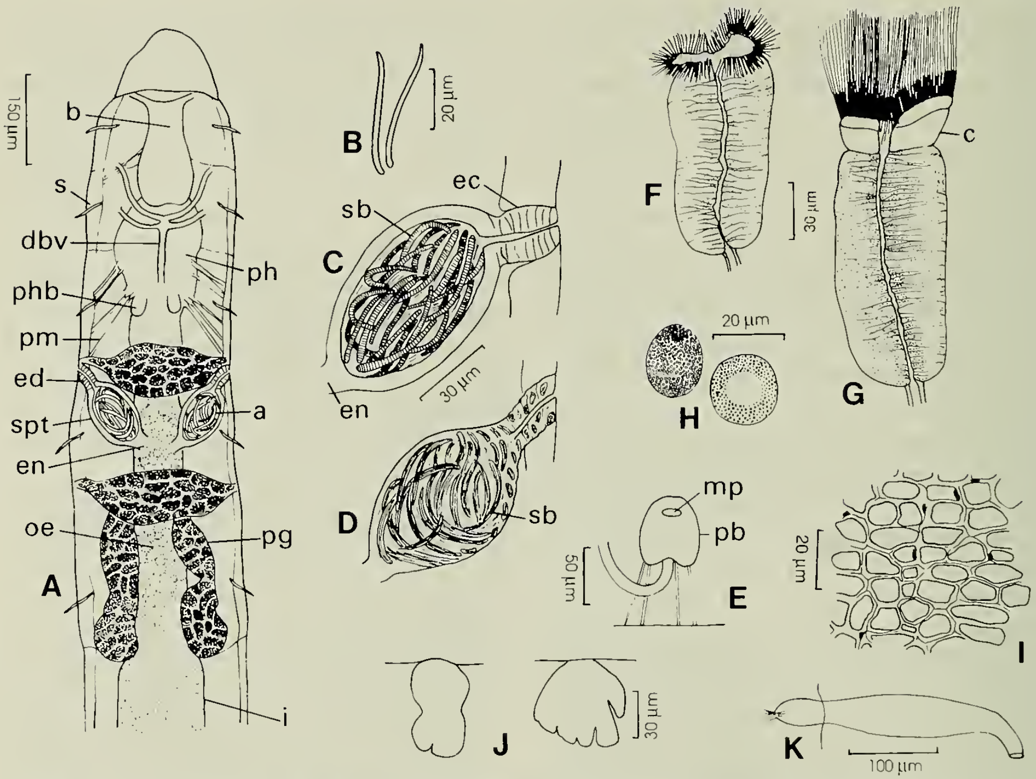

Fig. 1. *Marionina spartinae,* new species. A, schematic view of anterior region from combined observations on several fixed specimens; B, setal bundle; C, spermatheca of live specimen; D, spermatheca of fixed specimen; E, penial bulb; F, sperm funnel of fixed specimen; G, sperm funnel of live specimen; H, coelomocytes; I, clitellar glands; J, testes from two fixed, mounted specimens; K, nephridium at 8/9, live worm. a, ampulla; b, brain; c, collar of sperm funnel; dbv, dorsal blood vessel; ec, ectal duct; en, ental duct, i, intestine; mp, male pore; oe, esophagus with chloragocytes; pb, penial bulb; phb, pharyngeal bulb; pg, pharyngeal gland; ph, pharnyx; pm, pharyngeal muscles; s, setal bundle; sb, sperm bundle; spt, spermatheca.

whole mounted specimens in the author's collection. Approximately 25 live specimens examined.

Etymology.—The specific name refers to the salt marsh plant *Spartina* with which the species is almost exclusively associated.

Description.—Length of live worms 5–8 mm, width 0.27 mm at VII, 0.30 mm at the clitellum. Fixed, mounted specimens 4–5 mm long and 0.16–0.22 mm wide. Segments (22)26–32(42) (n = 130). Setae two per bundle in all segments and positions, usually absent in XII, sigmoid without ental hooks, 38–48 μm in the preclitellar region, 48–56 μm in posterior segments, of roughly equal length within a bundle (Fig. 1B). Cutaneous gland cells inconspicuous in live specimens but about three double rows may be seen in each segment in stained mounts. Clitellum extending over XII–½XIII, slightly raised, gland cells either in transverse rows, poorly developed, or irregular when well developed, absent mid-ventrally between the penial bulbs (Fig. 1I). Head pore in the middle of the prostomium.

Three pairs of pharyngeal glands, the first two united dorsally without ventral lobes, the third pair separate with elongated ventral lobes and small dorsal lobes (Fig. 1A). A pair of bulbs present on the posterior border of the pharynx (Fig. 1A). Esophageal diverticula absent. Esophagus merging gradually with the intestine from 6/7. Chloragocytes forming a dense layer from V, 5–8 cells across the intestine, containing small, sparse droplets. Coelomocytes nucleate, round or oval, sometimes with small, blunt points, filled with refringent granules, the cells appearing gray or light brown by transmitted light in live worms, length 19–23 μm (Fig. 1H). Blood colorless. Dorsal vessel originating in the preclitellar region, usually at 9/10, occasionally at 10/11, anterior bifurcation in III (Fig. 1A). Brain about twice as long as its maximum width, 115–120 μm long, indented posteriorly (Fig. 1A). Nephridia starting at 7/8, the anteseptal part ovoid with coils of the canal surrounding the nephrostome, postseptale more or less cylindrical, the efferent duct terminal, short and stout (Fig. 1K).

Testes bulky, somewhat lobed (Fig. 1J), seminal vesicle unpaired, confined to XI or extending forward asymmetrically to X or 9/10. Sperm funnel half to two-thirds the diameter of the worm, about twice as long as wide in live worms (Fig. 1G), about 1.5 times as long in fixed specimens (Fig. 1F), with a tall, somewhat flared, asymmetrical collar to which abundant, dark-staining sperm are attached. The funnel has a granular appearance and in living worms has an irregular outline. Sperm duct stout, 7–12 μm in diameter, of medium length, opening at a small, compact penial bulb, maximum diameter 25–37 μm. One to three mature eggs present at a time. Spermathecal ampulla ovoid, about twice as long as wide, 60–80 μm × 40–55 μm, thick-walled in live specimens, the wall not easily distinguishable in stained mounts, containing elongated sperm bundles (Figs. 1C, D). In live worms, the bundles are transversely striated, but striations are hard to see in stained mounts. Ectal duct short, only about 1.5 times the thickness of the body wall, without separated, projecting gland cells. Ental duct broad and short, thick-walled, uniting with the esophagus at about the level of the setae in V (Fig. 1A).

Remarks.—The distinctive characters of *M. spartinae* are its paired, sigmoid setae, the preclitellar origin of the dorsal vessel and the unusual arrangement of sperm in the spermathecal ampulla. Only a few species of *Marionina* are described as having distinctly sigmoid setae and none of these have paired setae in all segments. An anteclitellar origin of the dorsal vessel at 8/9 or in IX is unusual in *Marionina* and has only been reported for three terrestrial species from S. America: *M. ecuadoriensis* Righi, 1981, which has free spermathecae, i.e., not attached to the esophagus; *M. cana* Marcus, 1965, which has straight setae; and *M. nea* Marcus, 1965, which has 2–5 slightly sigmoid setae. In other species the origin is intraclitellar or postclitellar. The arrangement of sperm in elongated bundles in the spermatheca is unique in the Enchytraeidae, although in *Grania* and in several species of *Marionina* there are spherical sperm bundles. The bundles differ from similar shaped bundles found in some Tubificidae (Baker & Brinkhurst 1981, Erséus 1982) in lacking an outer hyaline layer which, as shown by Braidotti et al. (1980), is formed by helically wound, modified spermatozoa with degenerate nuclei and which surrounds a core of fertilizing spermatozoa. The cross striations seen in the bundles of *M. spartinae* suggest a different arrangement, but electron microscopic studies would be needed to elucidate the structure.

Habitat.—*Spartina* salt marshes, chiefly in the leaf sheaths of live and standing dead *Spartina* plants, less frequently in surface mud and decaying plant debris. One record from plant debris at the edge of a brackish lake, salinity 22‰.

Distribution.—Common and widespread

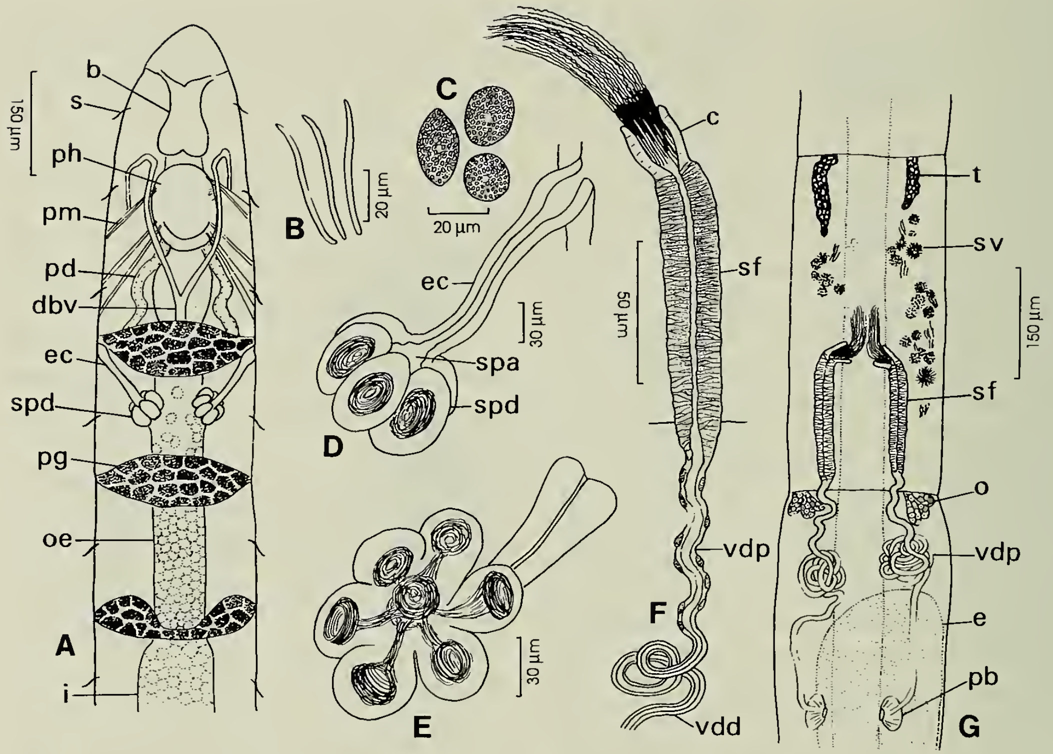

Fig. 2. *Marionina waltersi,* new species. A, schematic view of anterior region from combined observations on several fixed specimens; B, setal bundle; C, coelomocytes; D, spermatheca of live specimen; E, spermatheca of fixed specimen; F, sperm funnel and part of duct in live specimen; G, segments XI and XII. b, brain; c, collar of sperm funnel; dbv, dorsal blood vessel; e, egg; ec, ectal duct; i, intestine; o, ovary; oe, esophagus with chloragocytes; n, nephridium; pb, penial bulb with male pore; pd, duct of pharyngeal glands; pg, pharyngeal gland; pm, pharyngeal muscle; s, setal bundle; sf, sperm funnel; spa, spermathecal ampulla; spd, spermathecal diverticulum; sv, seminal vesicle, poorly defined; vdd, distal part of vas deferens; vdp, proximal part of vas deferens.

on Sapelo Island; Guana Lake, near St. Augustine, Florida.

Marionina waltersi, new species
Fig. 2

Material examined.—Holotype: USNM 163813, stained, whole mounted specimen, Kenan Field salt marsh, Sapelo Island, May 1991. Paratypes: USNM 163814–163815, stained, whole mounted specimens from the type locality, May 1991. Other material: UGMI, one stained, whole mounted specimen; 25 stained whole mounts in the author's collection. Approximately 16 live specimens examined.

Etymology.—The species is named for Dr. Keith Walters, meiofaunal specialist at the Marine Institute, Sapelo Island, who first drew my attention to the presence of enchytraeids in *Spartina* stems.

Description.—Live worms 5–6.5 mm, width 0.22 mm in the preclitellar region, 0.27 mm at the clitellum. Fixed, mounted specimens 3–4 mm long and 0.16–0.24 mm wide. Segments (21)25–29(35) (n = 25). Setae slightly sigmoid without ental hooks (Fig. 2A), (2)3(4) in preclitellar segments, 2–3 behind the clitellum, 43–56 μm anteriorly, 48–60 μm in posterior segments. Within a bundle, the outer setae are 4–6 μm longer than those near the midline. Cutaneous gland cells not apparent. Clitellum extending over XII–¾XIII, gland cells more or less in transverse rows near anterior and posterior borders, arranged irregularly in the central zone, gland cells present in the mid-ventral region. Head pore near the middle of the prostomium.

Three pairs of pharyngeal glands, the first two broadly united dorsally, the third united by a narrow band of tissue, all without ventral lobes (Fig. 2A). Pharyngeal and esophageal diverticula absent. Esophagus merging gradually with the intestine from 6/7. Chloragocytes present from V, forming a dense layer from VI, about 5–6 cells across the intestine, containing fine droplets. Coelomocytes oval, 19–25 μm, one-half to one-third the length of the setae, with coarse and small granules, appearing gray or light brown by transmitted light in living worms (Fig. 2C). Blood colorless. Dorsal vessel originating at 12/13, in XIII or at 13/14, anterior bifurcation in III or IV. Brain about 1.3–1.4 times as long as broad (fixed, mounted material), slightly indented. Nephridia starting at 7/8 or 8/9, anteseptale ovoid with coils of the canal surrounding the nephrostome, postseptale more or less cylindrical, slightly more swollen than in *M. spartinae,* efferent duct terminal, short and stout.

Testes small, unlobed, elongate, sometimes extending from 10/11 to mid XI. Seminal vesicles poorly developed (Fig. 2G) or absent. Sperm funnel long and narrow, five to six times as long as wide, roughly equal in length to the diameter of the worm (Fig. 2F). A tall, funnel-shaped collar is usually bent towards the midline while the funnel itself is straight or slightly sinuous, tapering distally as it passes through 11/12 to form a thin-walled, sinuous duct with isolated cells on its surface, about half as long as the funnel (Fig. 2F). The sinuous duct, which represents the proximal region of the vas deferens, is followed by a long, narrow, much-coiled distal region, confined to XII (Fig. 2G). Sperm attached to the funnel notably long and wavy (Fig. 2F). Penial bulb compact, 42–48 μm in diameter. One or two mature eggs present at a time. Spermathecal ampulla surrounded by a ring of five or six, more or less spherical, thick-walled diverticula on short stalks (Figs. 2D, E). Sperm present in the central chamber, in the radiating canals and in rings in the bulbous chambers of the diverticula. In live worms, the rings of sperm often rotate. Ental duct very short, the ampulla apparently closely applied to the lateral wall of the esophagus at about the level of the setae in V (Fig. 2A). Ectal duct thick-walled, about 15 μm in diameter, with a narrow canal, 2.5 times the length of the ampulla, swelling slightly near its opening where there may be a small narrow chamber.

Remarks.—*Marionina waltersi* resembles *M. southerni* (Černosvitov, 1937 pro *Enchytraeus lobatus* Southern, 1909) in having a ring of sperm-containing diverticula around the spermathecal ampulla but in *M. southerni* these are sessile and more numerous, there is a rosette of glands surrounding the orifice of the ectal duct, the seminal vesicle is large, the sperm funnel thick, the coelomocytes are dense and the paired setae are straight. *Marionina southerni* has been recorded in Massachusetts and North Carolina (Lasserre 1971). The only other *Marionina* for which a ring of spermathecal diverticula has been described is the poorly known *M. georgiana* (Michaelsen 1888) from the Antarctic, which is a larger species (around 35 segments), has up to 6 setae per bundle and a funnel only twice as long as broad. The long, narrow sperm funnel of *M. waltersi,* followed by a duct in two sections of different thickness has not been described for any other species of *Marionina.*

Habitat.—In *Spartina* salt marshes, in plant stems and occasionally in surface plant

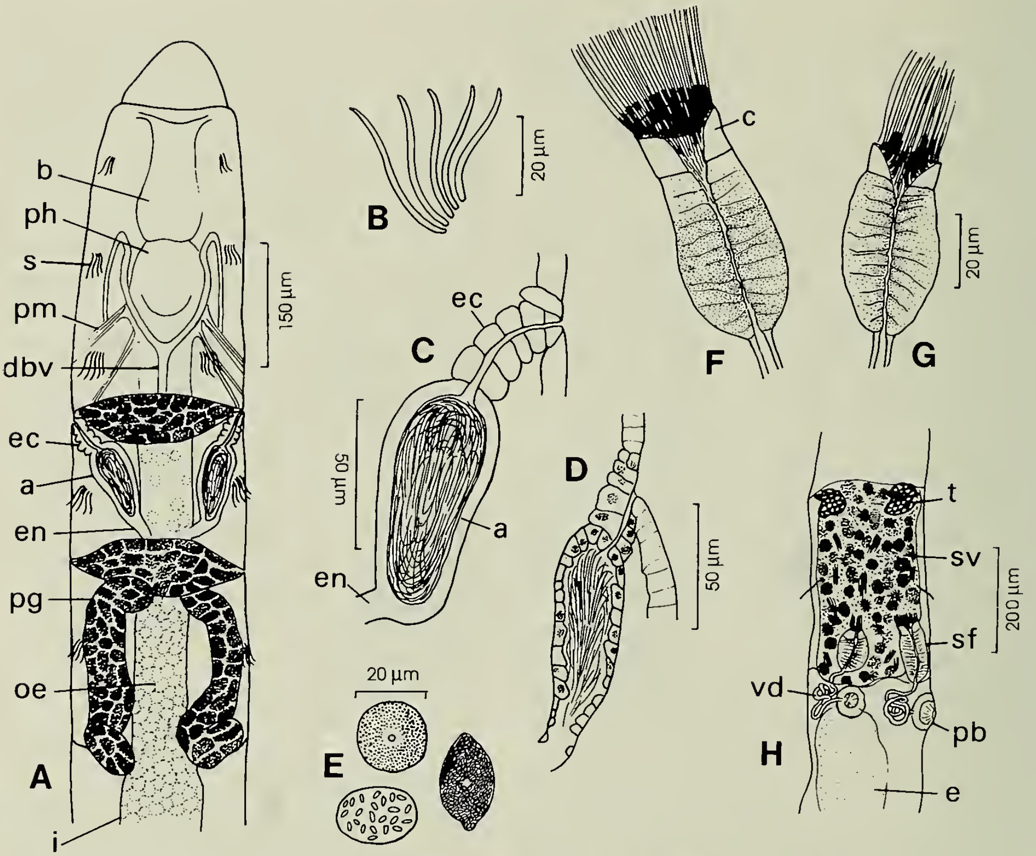

Fig. 3. *Marionina paludis,* new species. A, anterior region; B, setal bundle; C, spermatheca of live specimen; D, spermatheca of fixed specimen; E, coelomocytes; F, sperm funnel of live specimen; G, sperm funnel of fixed specimen; H, segments XI and XII. a, spermathecal ampulla; b, brain; c, collar of the sperm funnel; dbv, dorsal blood vessel; e, egg; ec, ectal duct; en, ental duct; i, intestine; oe, esophagus with chloragocytes; pb, penial bulb; pg, pharyngeal gland; ph, pharynx; pm, pharyngeal muscle; s, setal bundle; sf, sperm funnel; sv, seminal vesicle; vd, vas deferens.

debris. One record from the edge of a brackish lake, 22‰.

Distribution.—Sapelo Island, Georgia; Guana Lake, near St. Augustine, Florida.

Marionina paludis, new species
Fig. 3

Material examined.—Holotype: USNM 163816, stained, whole mounted specimen, Kenan Field salt marsh, Sapelo Island, May, 1991. Paratypes: USNM 163817–163818, two stained, whole mounted specimens from the type locality, May 1991. Other material: UGMI, three stained whole mounted specimens from the type locality; 18 whole mounted specimens from several marshes on Sapelo Island in the author's collection. Approximately 20 live specimens examined.

Etymology.—From the Latin *palus*—a marsh, because the species is associated with salt marsh habitats.

Description.—Live worms 4–6 mm, width 0.18–0.21 mm, 0.24–0.28 mm at the clitellum. Fixed, mounted specimens 3.5–4.5 mm long and 0.13–0.26 mm wide. Segments (21)24–28 ($n = 25$). Setae sigmoid, without ental hooks, usually 3–6 per bundle, (2–3)4(5) laterally and 4–6(7) ventrally in the preclitellar region, 3–4 laterally and 4–5 ventrally behind the clitellum. Setae are arranged fanwise within a bundle, those near the midline being smaller than the outer zones with a stronger curvature (Fig. 3B), size range 28–46 μm in the preclitellar region, 40–46 μm in posterior segments. Cutaneous gland cells variable, inconspicuous or in 3–8 rows of transversely elongated cells per segment. Sometimes the cells are fused to form a continuous, irregular line up to half the diameter of the worm which may possess small branches. Clitellum over XII–½XIII, clitellar gland cells irregularly distributed, absent ventrally in most specimens. Head pore at 0/1.

Three pairs of pharyngeal glands, the first two pairs broadly united dorsally without ventral lobes, the third pair free with long ventral lobes and small dorsal ones (Fig. 3A). Pharyngeal and esophageal diverticula absent. Esophagus merging gradually with the intestine from 6/7. Chloragocytes forming a dense layer from VI, 5–6 cells across the intestine. Coelomocytes mainly oval, some with small blunt points, occasionally round, 19–24 μm i.e., about two-thirds the length of anterior setae, with small granules, appearing gray or light brown by transmitted light in live worms. Blood colorless. Dorsal vessel originating at 12/13 or in XIII, anterior bifurcation at around 3/4. Brain about 1.5 times as long as wide in fixed worms, slightly indented posteriorly. Nephridia starting at 6/7, similar to those of *M. spartinae.*

Testes more or less globular, not or only slightly lobed (Fig. 3H). Seminal vesicle unpaired, confined to XI (Fig. 3H). Sperm funnel cylindrical, confined to XII, twice as long as broad, 80 × 40 μm in live worms, about half the diameter of the worm (Figs. 3F, G). Sperm duct of medium length, penial bulb compact, 30 μm in diameter. Usually only one mature egg present at a time. Spermathecal ampulla cylindrical or cone-shaped, with a rather thick wall (Figs. 3C, D), united with the lateral esophageal wall in the posterior part of V (Fig. 3A). Ectal duct about half as long as the ampulla, covered with a layer of rounded cells (Figs. 3C, D).

Remarks.—Marionina paludis closely resembles *M. appendiculata* Nielsen & Christensen, 1959 in size and general anatomy, especially in having fan-like bundles of 4–7 sigmoid setae. It differs in its much larger spermathecal ampulla with shorter ectal duct covered in a layer of large cells, in its larger sperm funnel, larger rounded testes and the presence of a well developed seminal vesicle and compact penial bulb. *Marionina appendiculata* is characteristic of muddy substrates in marine and estuarine littoral zones and is present on the Sapelo marshes. It is a widespread species and, as currently recognized, displays some variations in the size of the sperm funnel, in the development of the seminal vesicle and in the organs associated with the male pore. Some variants may indeed prove to be distinguishable as separate species. In North American material from western Canada (Coates & Ellis 1981) and from Georgia and both Atlantic and Gulf coasts of Florida (pers. obs.) the sperm funnel is always small, usually only 0.25 the diameter of the worm, the testis is small (elongated in Sapelo specimens), a seminal vesicle is absent and there are one or two free glands at the male pore which are occasionally fused around the opening. Where the species occur together, therefore, *M. paludis* can be recognized by its larger sperm funnel, larger, rounded testes and well developed seminal vesicle and penial bulb, even when the spermatheca is not clearly distinguished. Immature specimens are difficult to separate although *M. appendiculata* is generally smaller, with somewhat smaller and finer setae which may reach eight per bundle.

Habitat.—Spartina marshes, chiefly in standing dead stems, less frequently in plant debris on the marsh surface and in live stems of creekside *Spartina*.

Distribution.—Sapelo Island, Georgia.

Discussion

The three new species here described were common throughout the Sapelo marshes, *Marionina spartinae* being dominant. They were accompanied in all microhabitats except tidal debris by *M. appendiculata* and on the banks of creeks by immature *Enchytraeus*. No other enchytraeid species were found on the marshes. Two of the new species were also present at a *Spartina* marsh in N. Florida. A variety of other intertidal and supralittoral habitats have been investigated on the S. Georgia and N. Florida coasts, including *Salicornia* marshes, seagrass and other tidal debris, and plant roots near high water mark on the open coast. Other species of *Marionina* were found in these habitats but the new species appear to be confined to *Spartina* marshes.

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SUMMARY AND SIGNIFICANCE OF OVERLOOKED JAPANESE LITERATURE ON MYZOSTOMIDA

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Abstract.—The content of hitherto uncited or unreviewed Japanese scientific literature on Myzostomida is summarized with comments. The range of *Myzostoma willemoesii* von Graff has been extended to Japan, with an additional host record (a recent unpublished record from the Ogasawara Islands is also given). An associated myzostome has been reported from the hexactinellid sponge *Farrea. Myzostoma crassum* Okada, 1922 is an overlooked but available nomen dubium. Cleavage has been studied in *M. deani* McClendon. *Myzostoma echinus* von Graff has been misidentified consistently as *M. costatum* Leuckart in Japanese literature, and another species whose true identity is unclear has often been misidentified as *M. ambiguum* von Graff. Other possible recent misidentifications are pointed out herein. *Notopharyngoides* Fishelson, nomen nudum, has inadvertently been made available as *Notopharyngoides* Uchida, 1992, with the type species *Myzostoma ijimai* Hara & Okada, 1921.

Most of the original descriptions of Japanese species of myzostomidan worms (Japanese name: kyûkôchû or suikuchimushi), found as quasi-parasitic commensals or as endoparasites of crinoids and ophiuroids, were published by European or American zoologists (e.g., von Graff 1884, McClendon 1906, Jägersten 1937, Fedotov 1938). While several taxonomic and developmental papers written in English by Japanese scientists are well known (Hara & Okada 1921; Okada 1922b, 1933; Kato 1952), a considerable amount of related literature, mostly written in Japanese, seems not to have come to the attention of Western zoologists. A few such papers have been cited in bibliographies by Hartman (1951), Kato (1952), and Prenant (1959), but the findings were either not reviewed or misquoted. The contents of these largely ignored works are summarized here, with remarks on their significance. It should be noted in advance that the cited faunal encyclopedias and field guides were written and edited by eminent zoologists and are or once were in day-to-day use as reference books in Japanese laboratories; thus they are regarded here as an intrinsic part of the zoological literature. Although *Myzostoma,* not *Myzostomum,* is the correct original spelling of the main genus in question (Grygier 1992), names are spelled here following the cited Japanese authors.

Historical Review and Comments

Hara (1895) reviewed a controversy surrounding the supposed excretory organs (i.e., metanephridia) of *Myzostoma.* On p. 247 the nomen nudum *M. Ijimei* appeared in the context of histological information about an undescribed species. This was evidently a reference to the species later published as *M. ijimai* Hara & Okada, 1921.

Hara (1896) reported that 20 specimens of *Antedon inaequalis* Carpenter collected at Misaki bore galls caused by *Myzostomum willemoesii* von Graff. The supposed host now belongs to the genus *Glyptometra,* but the range of *G. inaequalis* does not extend to Japan (Clark 1950); two other nominal species of *Glyptometra* have been recorded from Misaki, *Glyptometra lata* (A. H. Clark) and *G. septentrionalis* (A. H. Clark), and presumably one of these was the host. Grygier (1990) was unaware of Hara's (1896) record and neither included *M. willemoesii* in a count of Japanese myzostome species nor took the otherwise unrecorded host into account in a discussion of host specificity. This myzostome has been known to infest eight other hosts, including four species of *Glyptometra,* and Hara's report extends its range northward from the nearest record in the central Philippines (Grygier 1990).

The Philippine record, based on specimens in the National Museum of Natural History, Smithsonian Institution (USNM 167184), is fully documented here: two galls on an arm of one *Glyptometra tuberosa* (Carpenter) (USNM 35664), "Albatross" sta. 5537, 19 August 1909, between Negros and Siquijor, 9°11'00"N, 123°23'00"E, 465 m. There is another lot of *M. willemoesii* in the Osaka Museum of Natural History (Catalogue no. Iv 1293) from an intermediate locality near the Japanese Ogasawara (Bonin) Islands: four galls formed from enlarged, twisted pinnules on one *G. tuberosa* (no. 700(2)), "Sôyô-Maru" Cruise 5 (d1–d10), 4 August 1976, 27°05.9–23.0'N, 142°03.8–05.8'E, 165–345 m.

Komai (1919) briefly introduced the Myzostomida as a whole, summarized McClendon's (1906) taxonomic paper, and reproduced figures from it.

Okada (1920) reported four specimens of *Myzostoma* collected from the hexactinellid sponge *Farrea* sp. He assigned the specimens to *Myzostoma antennatum* von Graff based on morphological resemblance, although they were of a different color. This is the only report of myzostomes collected from a sponge, although it might be suspected that the worms had been lost accidentally from a crinoid or ophiuroid during collection.

Okada (1922a) published a key to the Myzostomida of Japan preceded by a long, literature-based, general introduction of the group. The key included 13 nominal species of *Myzostoma,* one of which, *My.* (sic) *crassum* seems never to have been fully described. In the accompanying table, this species was referred to as *M. crassum* H. (for Hara), but I have been unable to locate any published description by Hara. Inasmuch as this name appeared in a key, it was accompanied by a diagnosis and is available with Okada as its author; however, it is an unrecognizable nomen dubium. According to the relevant couplet, in *Mg.* (sic) *antennatum* the position of the female (i.e., male; lapsus or misprint of a Japanese kanji character) genital opening is directly outside the third parapodium while in *M. crassum* the male opening lies between the third parapodium and (which?) sucker (i.e., lateral organ). This is a very subtle distinction. The host of *M. crassum* is *Antedon macrodiscus* Hara (i.e., *Tropiometra afra macrodiscus*) from near-coastal waters off Misaki, Kanagawa Prefecture. My own extensive survey (Grygier 1990) turned up only three species of myzostomes on this host, *M. bocki* (Jägersten), *M. nasonovi* Fedotov, and *M. ijimai,* all of which can be distinguished from *M. antennatum* by gross morphology and are thus unlikely to be synonymous with *M. crassum.*

Okada (1930) briefly described the early cleavage of embryos of *Myzostoma deani* McClendon, misspelled as *M. cleani* when reviewed by Kato (1952), from Enoshima, Tateyama Bay, Chiba Prefecture. This is the only report about developmental biology in this species.

Much more recently, Utinomi & Kogo (1965) recorded: 1) *Myzostomum* sp. from *Comanthus* (*Cenolia*) *japonica* (Müller) (i.e., *Oxycomanthus japonicus*), 2) *Myzostomum* sp. and *M. costatum* Leuckart from *Comanthus* (*Comanthus*) *parvicirra* (Müller), and 3) *Myzostomum* sp. from *Comanthina schlegeli* (Carpenter). All were from the southwestern part of the Kii Peninsula (especially Tanabe Bay), Wakayama Prefecture. The worms from *C. schlegeli* were found in sub-epidermal cysts on the arms or discs, with openings to the ambulacral grooves.

The collections of the Seto Marine Biological Laboratory, where Kogo did this work, include four catalogued vials labelled *Myzostomum costatum,* but all are misidentified. Poly 138 was isolated from *Comanthus parvicirra* but now the vial contains only a dry crinoid arm fragment. Poly 139, host unstated, contains four *M. fissum* von Graff and seven small specimens that may also belong to that species or to an undescribed, closely related species. Poly 140, host unstated, contains two individuals of a probably undescribed species in the *M. crosslandi* species-group sensu Grygier (1990). Poly 137, host unstated, contains one specimen which is similar to the Japanese myzostome, host unknown, which Jägersten (1940) identified as *M.* cf. *insigne* Atkins and which was reexamined by the author in the Zoological Museum in Copenhagen in 1986. Being unpigmented, both specimens more closely match Atkins's (1927) original description of *M. pottsi.* Grygier (1990) considered *M. insigne* and *M. pottsi* to be junior synonyms of *M. echinus* von Graff. Photographs of so-called *M. costatum* in some handbooks (Utinomi 1964; Imajima 1975a, 1983a) actually show *M. echinus* with the color pattern described by Atkins (1927) for *M. insigne.* Uchida (1992) mentioned that *M. costatum* was found on *Lamprometra palmata* (Müller) and *Comanthina schlegeli* in Japan, but did not include an illustration by which to judge his identification.

The species referred to as *M. ambiguum* in all Japanese primary and secondary literature is also misidentified. Treatment of it as *M. ambiguum* dates to Jägersten (1937), who showed that it was distinct from *M. antennatum,* and whose opinion was followed by Fedotov (1938), Kato (1952), and the compilers of several field guides and faunal encyclopedias (Kato 1960; Okada & Kato 1965, 1979; Nishimura & Suzuki 1971; Imajima 1975b, 1983b). Grygier (1990) considered the Japanese "*M. ambiguum*" to be a different species, but whether some of the earlier records actually correspond to *M. longimanum* (Jägersten), *M. vastum* von Graff (sensu von Graff 1884), or an undescribed species is still uncertain. True *M. ambiguum* has a wide tropical distribution and can easily be recognized on the basis of von Graff's (1887) illustration, particularly with regard to the rather narrow and truncated rear end of the body and the barely submarginal location of the proboscis pocket opening. In Japan, true *M. ambiguum* does occur in Okinawa, based on specimens identified by the author in the Department of Marine Sciences, University of the Ryukyus.

A recent guide to marine invertebrates of Okinawa Prefecture, southern Ryukyus Islands (Iwase et al. 1990:91) included photographs of living *Myzostomum elegans* van Graff (sic) and *Myzostomum ijimai* Hare et Okada (sic), the former on an arm of *Comanthus parvicirra,* the latter removed from the mouth of *Tropiometra afra macrodiscus.* The bull's-eye color pattern of the former corresponds to that of *Myzostoma polycyclus* Atkins (cf. Atkins 1927), which was (implicitly) treated as separate from *M. elegans* by Grygier (1990). Uchida (1992) labelled other photographs of perhaps the same individuals as *Myzostomum polycyclus.* The supposed *M. ijimai,* the same individual of which appears in a photograph in Uchida (1992), has a series of discrete submarginal lappets like those of *M. platypus* von Graff and *M. aruense* Remscheid, unlike the continuous, wavy-edged, submarginal brim of *M. ijimai* (cf. Hara & Okada 1921, Jägersten 1937, Kato 1960, Okada & Kato 1965; the species is called *Myzostomum ijimae* in the last two references). The specific identification of the Ryukyuan specimen is thus questionable despite its occurrence on the proper host.

Noting that the proboscis protrudes from the dorsal surface in *M. ijimai,* Uchida (1992) remarked that the genus *Notophar-*

yngoides had been proposed for that reason. For lack of a diagnosis, *Notopharyngoides* was a nomen nudum when introduced by Fishelson (1974, 1976), but Uchida's (1992) remarks constituted a diagnosis for it, and its use in connection with a single species name constituted a type species designation. Therefore, Uchida (1992) inadvertently validated this former nomen nudum and must be recognized as the author of *Notopharyngoides,* with the type species *Myzostoma ijimai. Notopharyngoides* may be considered equivalent to the *M. platypus* species-group sensu Grygier (1990).

Uchida (1992) presented a photograph of *Myzostomum bocki* on its host, *Tropiometra afra macrodiscus,* but the banded color pattern of the worm strongly suggests that it is really *Myzostoma nasonovi.* Grygier (1990) considered these two species to be synonymous, but after examining specimens of both found that they can be distinguished unambiguously by the banding and the parapodial hook apparatus (Grygier 1992).

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SCIURODENDRIUM GARDNERI, NEW SPECIES (NEMATODA: TRICHOSTRONGYLOIDEA: HELIGMONELLIDAE), A PARASITE OF *SCIURUS CAROLINENSIS* GMELIN, 1788 (MAMMALIA: SCIURIDAE), WITH COMMENTS ON THE BIOGEOGRAPHY OF *SCIURODENDRIUM* DURETTE-DESSET, 1971

Ricardo Guerrero

Abstract.—*Sciurodendrium gardneri,* new species, is described from an eastern gray squirrel, *Sciurus carolinensis,* collected in Virginia, U.S.A. A nearctic origin for the genus *Sciurodendrium* is proposed on the basis of the paleobiogeography of the host.

Sciurodendrium Durette-Desset, 1971, is a genus found only in New World squirrels (Sciuridae). There are five known species (Durette-Desset & Justine 1992): one nearctic, *Sciurodendrium hassalli* (Price 1929); and four neotropical, *S. oliverai* (Lent & Freitas 1938), *S. hepaticum* (Lent & Freitas 1938), *S. aripense* (Baylis 1947), and *S. landauae* (Durette-Desset 1970). *Sciurodendrium hassalli* is the name that has been used for heligmonellid parasites of squirrels in the United States (Harkema 1936, Chandler 1942) on the assumption that there was only one species of this genus in the Northern Hemisphere. However, a routine examination for parasites in an eastern gray squirrel from Virginia revealed an undescribed species.

The parasites were collected in an isotonic solution of NaCl, preserved in ethanol (70%), and clarified in lactophenol. All measurements are in microns and given as the mean followed by the range in parentheses. Types are deposited in the US National Parasite Collection, USDA, ARS Beltsville, Maryland (USNP), and the Colección de Parasitología, Museo de Biología, Universidad Central de Venezuela, Caracas (CPMBUCV).

Sciurodendrium gardneri, new species

Description.—Heligmonellidae, Pudicinae; small slender worms, reddish in color when fresh. Cuticle of the anterior end dilated and coarsely striated. The mouth opening is triangular and bears an internal ring of six small papillae and an external ring consisting of the amphids and four well-developed papillae (Fig. 1A). Synlophe with a well-developed carene consisting of two continuous ridges (Fig. 1C). In addition, the synlophe includes nine dorsal discontinuous ridges arranged in nonalternating interrupted longitudinal lines and eight ventral discontinuous ridges in alternating lines (Fig. 1D) resulting in the doubled number of ventral ridge "tips" seen in cross-sectional view (Fig. 1C).

Male (10 specimens): Body 3720 (3179–4493) long by a maximum width of 82 (74–94) near mid body. Cephalic vesicle is 52 (47–57) long and 32 (28–38) wide. Esophagus is simple, 250 (208–288) long. Nerve ring and excretory pore located 146 (132–165) and 169 (154–184), respectively, from the anterior end. Caudal bursa is type 2-2-1 and the dorsal ray is deeply cleft to the level of the origin of 8th ray; ray 9 shorter and

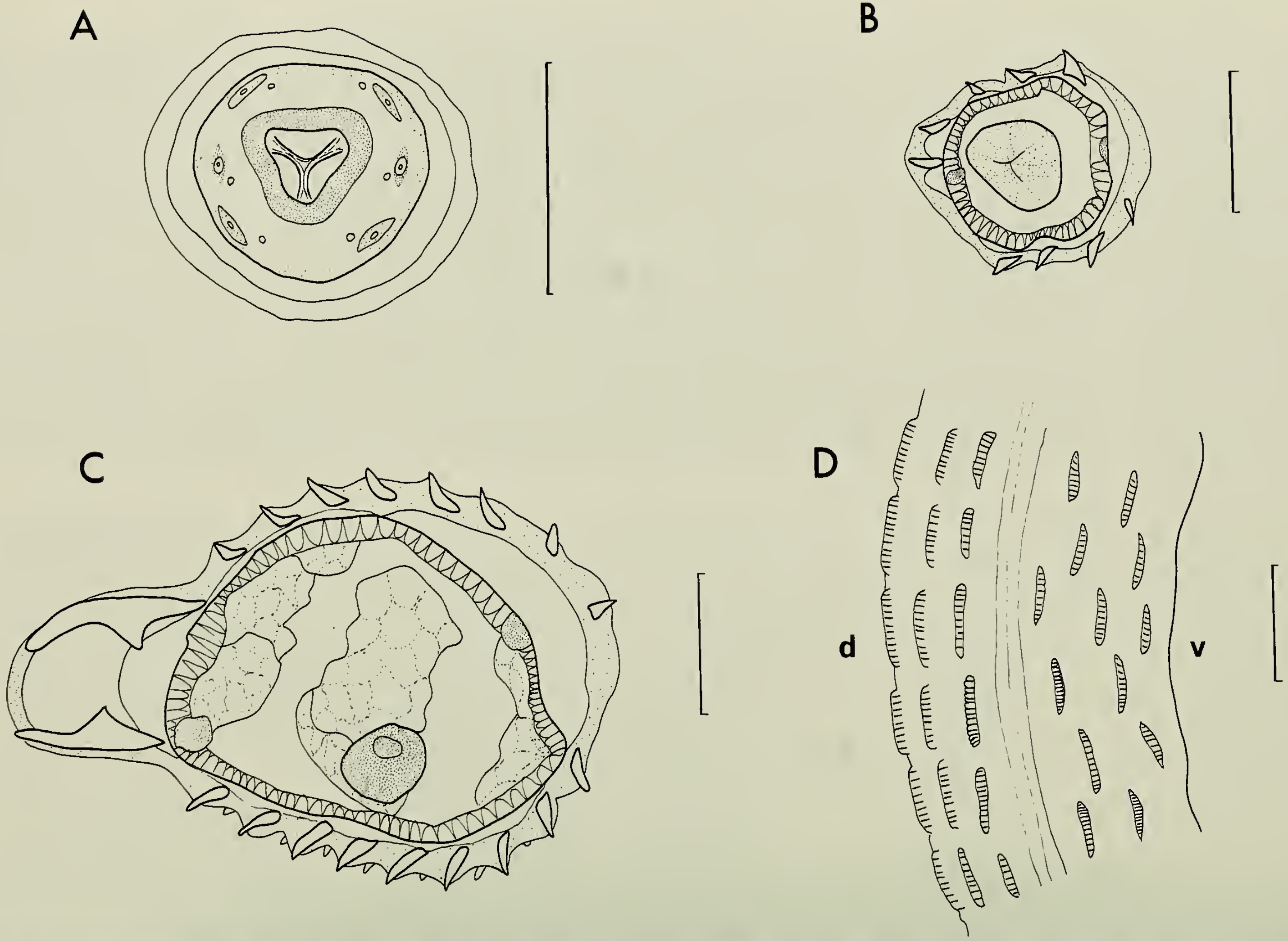

Fig. 1. *Sciurodendrium gardneri,* new species: A, ♀, apical view; B, ♀, cross-section showing synlophe at level of base of cephalic vesicle; C, ♀, cross-section showing synlophe near mid-length of body; D, ♀, view of longitudinal ridges from right side (d = dorsal, v = ventral surface). Each bar equals 25 μ.

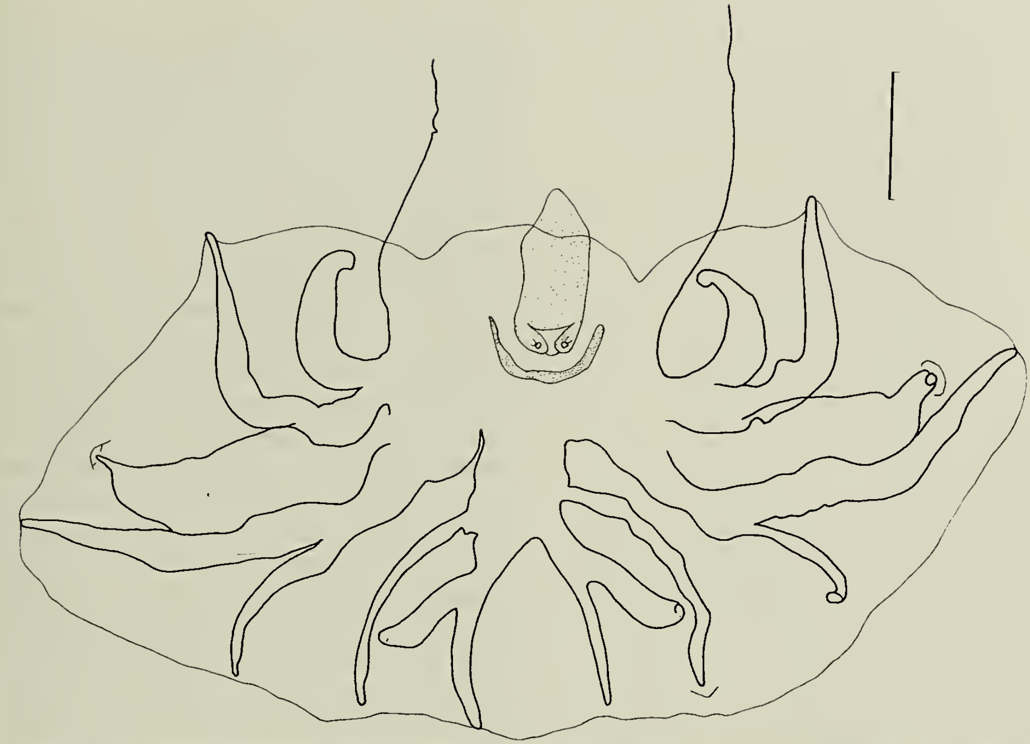

Fig. 2. *Sciurodendrium gardneri,* new species: ♂, posterior end showing characteristics of bursa and rays. Bar equals 25 *μ*.

thicker than ray 10; ray 4 gross and with papilliform end; ray 6 arises from basal third of ray 5 (Fig. 2). Spicules are subequal, filiform, alate, fused at the tips, and measure 370 (334–420) long and 4–5 wide. Telamon is elongated, weakly cutinized, and located close to cloacal papillae. A gubernaculum is absent.

Female (10 specimens measured): Body 5360 (4801–5881) long with a maximum width of 98 (92–104). Cephalic vesicle is 54 (48–60) long and 33 (30–37) wide. Esophagus is simple, 272 (246–298) long. Nerve ring and excretory pore situated 187 (156–210) and 221 (200–254), respectively, from the anterior end (Fig. 3).

Vulva located 173 (156–188) from the posterior end of the body, and followed by a vagina vera 31 (24–40) in length, a vestibule 87 (76–100) long, a sphincter 33 (28–40) long, and an infundibulum 140 (94–210) long (Fig. 4). Uterus measures 316 (220–490) in length and contains 6 (4–7) thin-shelled eggs, each measuring 73 (68–84) by 38 (36–42). Tail is 84 (59–108) in length.

Host: *Sciurus carolinensis* Gmelin, 1788 (Rodentia: Sciuridae)

Location: Small intestine.

Locality: Oakton, Fairfax Co., Virginia, U.S.A.

Type specimens:

Holotype: CP-MBUCV No. 3942 (male).

Allotype: CP-MBUCV No. 3943 (female).

Paratypes: CP-MBUCV No. 3109 (19 males and 11 females); USNM Helm. Collection No. 82704 (2 males and 2 females).

Etymology.—Patronym, in honor of Alfred L. Gardner, of U.S. National Biological Survey, due to his very important contributions to Neotropical mammalogy.

Remarks.—*Sciurodendrium gardneri* is

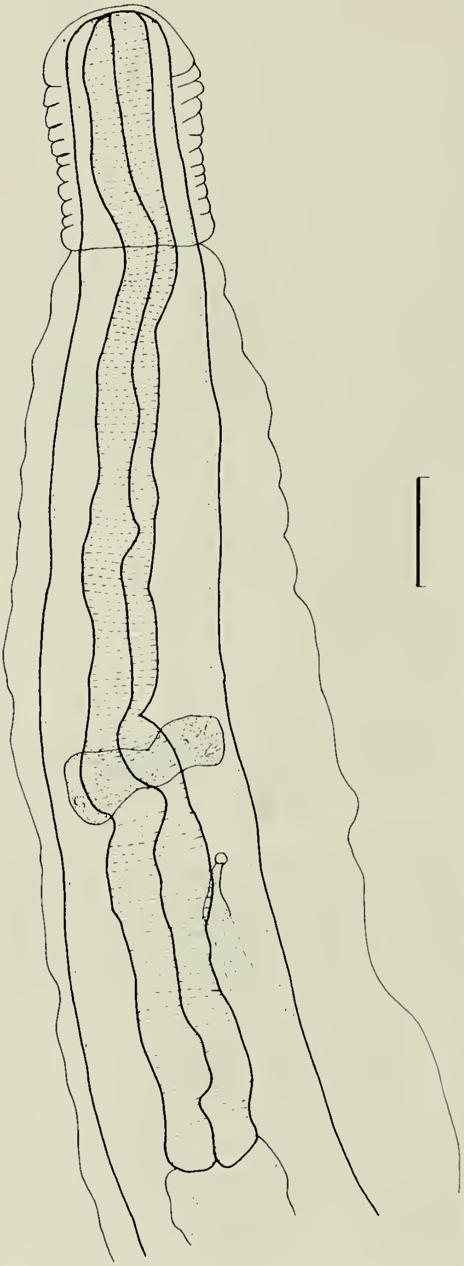

Fig. 3. *Sciurodendrium gardneri*, new species: ♀, anterior end of body showing positions of nerve ring and excretory pore. Bar equals 25 μ.

similar to *S. hassallii* and *S. oliverai* and differs from other known congeners on the basis of small body size and deeply cleft dorsal ray of caudal bursa (cleft to level of origin of ray 8). It differs from *S. hassalli* and *S. oliverai* in that rays 4 and 9 are conspicuously gross and broader than the other rays. All rays in *S. hassalli* are thin as is usual in other members of the group. Also, *S. gardneri* is smaller than *S. hassalli* in size and differs from *S. oliverai* in having a telamon (absent in the latter).

Discussion.—Durette-Desset (1985:290) stated "Trichostrongyloids of Neotropical Sciuridae belong to a single genus, *Sciurodendrium,* a Pudicinae derived from forms in Caviomorph rodents." "It is therefore likely that the Sciuridae lost their brevistriatine parasites during their migration into North America [from the Old World] and were reinfected after contacting South American pudicines."

Durette-Desset (1971) introduced this hypothesis in her revision of heligmosomes, and has repeated it in subsequent papers (Durette-Desset 1982, 1985; Durette-Desset & Chabaud 1977, 1981; Durette-Desset & Justine 1991). However, my finding another species of *Sciurodendrium* in a North American squirrel and a review of holarctic heligmonellids does not support Durette-Desset's (1985) hypothesis on the origin of pudicine parasites of squirrels.

The Sciuridae are known in Europe from the Lower Oligocene (±35 million years ago [mya]; Hartenberg 1985), in North America from the Hemingfordian (±16 mya; Webb 1985), but only recently in South America from the Lujanensian (<1 mya; Reig 1981). Two major intercontinental migrations, first across Beringia into North America and then across the Isthmus of Panamá (Moore 1961), occurred before squirrels became established and radiated in South America. Durette-Desset (1985:290) wrote "We believe that sciurids were devoid of trichostrongyloids when they moved into South America. Trichostrongyloids are rare in holarctic Sciuridae and those that exist belong to a recent family, the Heligmosomidae." According to the cladistic analysis of Durette-Desset & Justine (1992), *Sciuro-*

dendrium must have appeared only a few hundred thousand years ago and evolved from parasites of the caviomorph families Dasyproctidae, Echimyidae, and especially the Capromyidae. An alternative explanation is that sciurids entering South America carried brevistriatine heligmonellids, and that pudicines subsequently acquired from caviomorph rodents quickly displaced brevistriatines in all New World squirrels.

My research suggests, however, that neither of these hypotheses is supported by the evidence. Other Recent mammals that entered South America from North America retained their trichostrongyloid parasites. For example, *Longistriata,* a genus of parasites of holarctic Soricidae also is present in South American shrews (Guerrero 1982). The same is true for *Vexillata,* a parasite (Guerrero 1984) of the Heteromyidae, a New World rodent family that has its greatest diversity in North America. It seems unlikely that the Sciuridae were without trichostrongyloids throughout their 16-million-year history in North America before they were able to disperse across the Panamanian isthmus. If derived from caviomorph rodents, how did *Sciurodendrium* reach temperate North America? There is no evidence of a "reverse" migration of sciurids from South America northward.

Durette-Desset (1971) commented that *Brevistriata* (Brevistriatinae), a parasite of Oriental Sciuridae, and *Sciurodendrium,* a parasite of New World sciurids, are quite similar. This she attributed to convergence, pointing out that in the former the cuticular ridges are discontinuous and in alternating lines, and ray 4 is equal to or longer than the 5th. The characteristics I describe above for *S. gardneri* show that discontinuous alternating cuticular ridges are not diagnostic only of *Brevistriata.* Relative lengths of rays 4 and 5 may be the only remaining major diagnostic character distinguishing the two subfamilies.

I suggest that *Sciurodendrium* is nearctic in origin and closely related to some Brev-

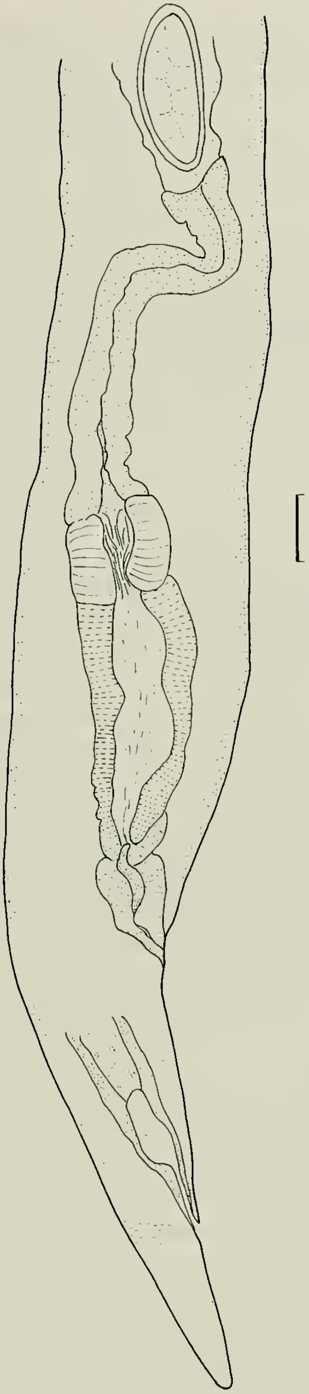

Fig. 4. *Sciurodendrium gardneri,* new species: ♀, posterior end of body. Bar equals 25 μ.

istriatinae such as, for example, *Calypsostrongylus* Schmidt, Myers & Kuntz, 1967, sensu Durette-Desset (1976). Relationships between Old World Brevistriatinae and Western Hemisphere Pudicinae need to be reexamined.

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DESCRIPTION OF THE NEW GENUS *ALLOPATHES* (CNIDARIA: ANTIPATHARIA) AND ITS TYPE SPECIES *CIRRIPATHES DESBONNI*

Dennis M. Opresko and Stephen D. Cairns

Abstract.—The rarely collected species originally described as *Cirripathes desbonni* is redescribed based on two specimens. A neotype is designated because the type is presumed to be lost. A new genus, *Allopathes,* is proposed for this species based on its unusual colony form: numerous elongate, mostly unbranched stems originating from a short, trunk-like base. *Antipathes robillardi* Bell is also placed in this genus, which gives the genus a range of western Atlantic and Mauritius at 129–161 m.

In September, 1989 the second author participated in a cruise of the *Johnson-Sea-Link I* research submersible (stations 2582–2595) off the southeastern coast of Louisiana. Eight species of Antipatharia were observed, photographed, and collected (Cairns et al. 1994), one of which was *Allopathes desbonni.* This species is composed of numerous long, slender, mostly unbranched stems arising from a stout, trunk-like base. We consider the distinctive nature of the corallum of this species and one other, *A. robillardi,* to justify establishing a new genus, and include a redescription of the species.

Allopathes, new genus

Diagnosis.—Corallum consisting of numerous elongate stems arising from a short trunk-like base. Stems generally straight but may be slightly coiled at their distal end; mostly unbranched, but occasionally with first and second-order branches arising from the lowermost parts of the stems. Spines typically arranged in verticils around circumference of axis. Polyps in a single row along length of axis.

Discussion.—As was noted by Duchassaing & Michelotti (1864) the generic affinites of *Cirripathes* (=*Allopathes*) *desbonni* are not clearly defined. The individual stems resemble those of *Cirrhipathes* and *Stichopathes,* and the arrangement of the polyps in a single row would tend to associate the species more with *Stichopathes.* The latter was treated as a subgenus of *Cirrhipathes* by some (e.g., Van Pesch 1914). However, the morphology of the spines of *Allopathes,* and its tendency to develop long branches, would suggest an affinity with *Antipathes verticillata* (Brook 1889). Placing *Antipathes desbonni* in *Stichopathes* or *Cirrhipathes* would substantially alter the major diagnostic character of those genera, i.e., the unbranched growth form of the corallum, which we do not believe to be justified. Likewise, placing *A. desbonni* in *Antipathes* would diminish the significance of the unique morphology of the corallum. Although the genus *Antipathes* currently is a heterogeneous assemblage of species, it is our view that natural groupings of species tend to center around distinct types of skeletal morphology which, when evaluated in association with characteristics of the spines and polyps, are likely to define generic or subgeneric taxa. Therefore, we consider it appropriate to establish a new genus for *desbonni* and also include in it *Antipathes robillardi* Bell, 1891.

Etymology.—From Greek *allos,* other +

Fig. 1. *Allopathes desbonni,* neotype (USNM 88327). a, Basal section of corallum showing the origin of the stems, ×0.75; b, Section of stem with polyps, ×6.

pathes, second component of *Antipathes,* in allusion to its taxonomic relationship. Gender: feminine.

Type species.—*Cirripathes desbonni,* here designated. *Cirripathes* is an incorrect spelling of *Cirrhipathes.*

Allopathes desbonni (Duchassaing & Michelotti, 1864), new combination

Figs. 1–4

Cirripathes Desbonni Duchassaing & Michelotti, 1864:142.

Not *Antipathes* (*Cirrhipathes*) *Desbonnii.*—Pourtalès, 1874:46.—1878:209 (=*Stichopathes pourtalesi* Brook).

Antipathes (*Cirrhipathes*) *Desbonni.*—Pourtalès, 1880:114, pl. iii, figs. 6–7.

Stichopathes? *desbonni.*—Brook, 1889:92.

Material examined.—Gulf of Mexico, off southeastern Louisiana, 27°44.62′N, 91°07.9′W, 129–144 m, *Johnson-Sea-Link I* Stn 2585, USNM 88327, neotype.—Off Montserrat, Lesser Antilles, *Blake* Stn 155, 88 fm (=161 m), one specimen in the Museum of Comparative Zoology, Harvard University.

Diagnosis.—Corallum large, about 1 m in height, with numerous mostly unbranched stems arising from a short trunk-like base (Fig. 1a); stems generally straight and stiff, but flexible and somewhat coiled near apex; occasionally branched near base. Spines typically conical, acute, and usually 0.10–0.14 mm (but up to 0.20 mm) from midpoint of base to apex; with cone-shaped tubercles on upper two-thirds or more of surface. Spines arranged in verticils of varying regularity and in longitudinal rows with 3 or 4 spines per millimeter in each row. Polyps arranged in one row along stems and branches; 1.0–1.2 mm in transverse diameter (from proximal side of proximal lateral tentacles to distal side of distal lateral tentacles); interpolypar space about 0.4–0.5 mm; from 5 to 7 polyps per centimeter (Fig. 1b).

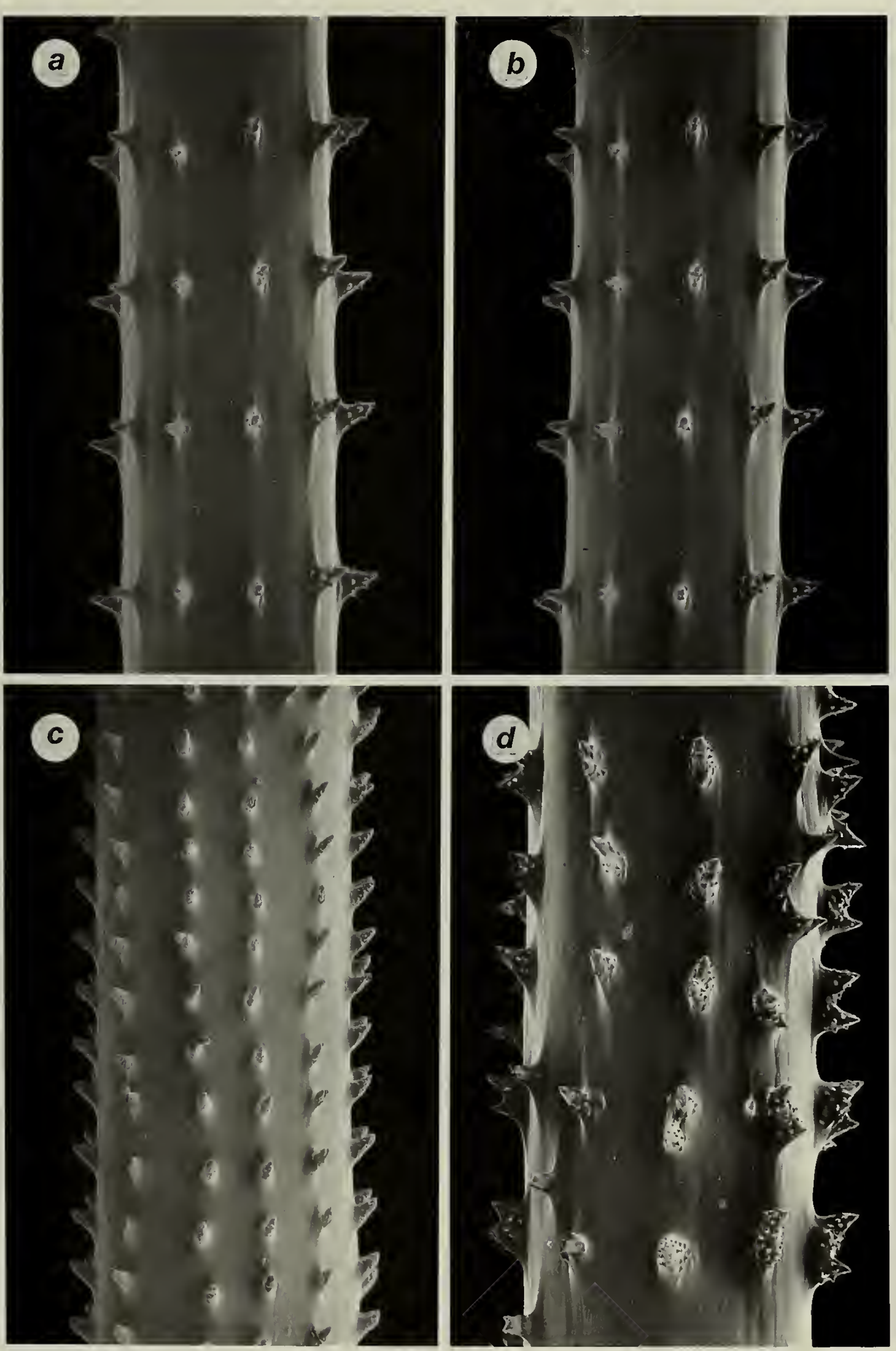

Fig. 2. *Allopathes desbonni,* neotype (USNM 88327). a, b, Section of stem 0.5 mm in diameter, showing arrangement of spines, stereo pair, ×59; c, Section of stem 1.5 mm in diameter, ×25; d, Section of stem 0.85 mm in diameter with bifid spines, ×46.

Description.—The neotype consists of a cluster of about 40 stems attached to a 4 cm long "trunk," as well as several dozen detached pieces. This specimen was only part of a much larger colony, the remainder of which was not collected. Individual stems reach a maximum length of about 90 cm and are 0.5–2.3 mm in diameter at their base (average 1.47 mm, $n = 24$). Stems 46, 53 and 75 cm long have basal diameters of 1.1, 2.3, and 1.5 mm, respectively. All stems arise directly from the base (Fig. 1a) and most are unbranched; however, a few have a single branch that originates not more than 1 centimeter above the basal end of the stem. The branches are unbranched and can be as long as the stem from which they arise. The axial diameter of a stem or branch decreases regularly from base to apex, e.g., for one 52-cm long stem, the diameter is 2.3 mm at the base, 1.7 mm at a height of 10 cm, 1.1 mm at 30 cm, 0.7 mm at 40 cm, and 0.3 mm at its distal end.

The stems and branches of the corallum radiate upward from the base. They are relatively straight and stiff for most of their length; however, near the apex (i.e., upper 10 cm or more) they curve and even form a loose coil. This occurs regardless of the overall length of the stem or branch, and is associated with an increased flexibility of the axis due to a very thin sclerenchymal layer and a relatively wide central axial canal (0.20–0.36 mm). Because of these factors the tips of the stems and branches collapse when dried.

Axial spines (Figs. 2, 3, 4a–c) are arranged in longitudinal rows and also in verticils, although the regularity of the verticils varies considerably from point to point. Six or seven longitudinal rows of spines can be seen in viewing one side of the axis and 13 rows were counted around the entire circumference of one segment of axis having a diameter of 1.6 mm. The distance between the spines in each row varies on different parts of the axis and ranges from 0.24 to 0.40 mm; however, in general, there are usually 3 or 4 spines per millimeter in each row.

Spines are generally uniform in size at any given point on the corallum, though they vary in size and appearance along the length of the axis, as well as around the circumference. Spines on the polyp-side of the axis are generally larger than those on the abpolypar side. The spines also increase in size from the distal end of a stem or branch to the basal end; however, the rate of increase is not uniform from one stem or branch to another. About 1 cm from the distal end where the axial diameter is about 0.2 mm, the spines are quite small, 0.04–0.06 mm from the tip to the center of the base, somewhat compressed laterally, triangular in shape, and have only a few small conical protuberances on their surface. With increasing axial diameter the spines become larger; i.e., 0.07–0.09 mm (axial diameter about 0.3 mm), 0.10–0.12 mm (axial diameter 0.4–0.7 mm, Fig. 3a), 0.10–0.16 mm (axial diameter 0.7–1.0 mm, Fig. 3b), and 0.12–0.20 mm (axial diameter over 1.0 mm). Overall, the typical polypar spine is 0.10–0.14 mm tall, conical in shape, with an acute to slightly rounded apex, and with cone-shaped tubercles scattered over the surface. The corresponding abpolypar spines are generally 0.02 to 0.06 mm smaller and usually have fewer surface tubercles. For example, at the midpoint of one 30-cm long stem (axial diameter about 0.9 mm) the polypar spines measure 0.10–0.12 mm and the abpolypar spines 0.08 mm. The spines on the lowermost portion of each stem (usually within 5 to 10 cm of the basal end and regardless of total length of the stem) differ from the typical spines in being almost smooth-surfaced (Figs. 2c, 3c). These spines are large (usually 0.16–0.20 mm), have a sharp apex and tend to be directed distally. In addition, on some stems, and particularly where the axial diameter is 1.0 mm or more, the polypar spines can become rather wide and blunt with numerous surface tubercles (Figs. 4b, c). The location and abundance

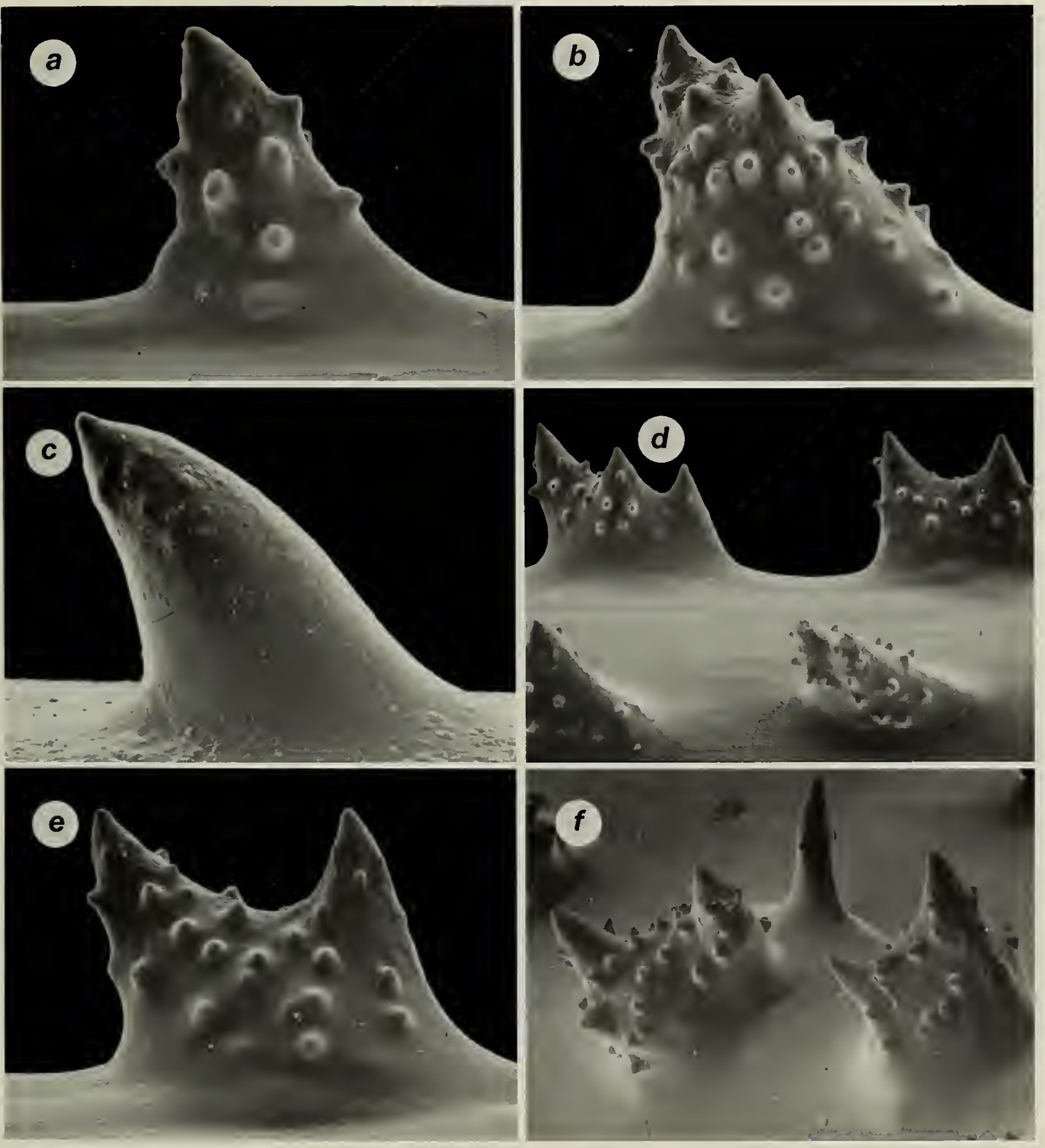

Fig. 3. *Allopathes desbonni,* neotype (USNM 88327). a, Spine from section of stem about 0.5 mm diameter, ×365; b, Spine from section of stem about 0.8 mm in diameter, ×245; c, Smooth spine from lowermost portion of stem, ×240; d–f, Bifid and trifid spines from stem 0.85 mm in diameter, ×115, ×245, ×170, respectively.

of these blunt spines varies from stem to stem, but they are never found at the distal or basal ends of the stem. A very atypical condition was found on sections of one stem where the primary polypar spines were bifurcated and trifurcated and occasionally accompanied by an acicular secondary spine (Figs. 2d, 3d–f).

Polyps are arranged in a single row along the entire length of the stems and branches (Fig. 1b). They are generally 1.0–1.2 mm in transverse diameter (from the distal side of the distal lateral tentacles to the proximal side of the proximal lateral tentacles), and separated by a space of 0.4–0.5 mm, resulting in about 6 or 7 polyps per centi-

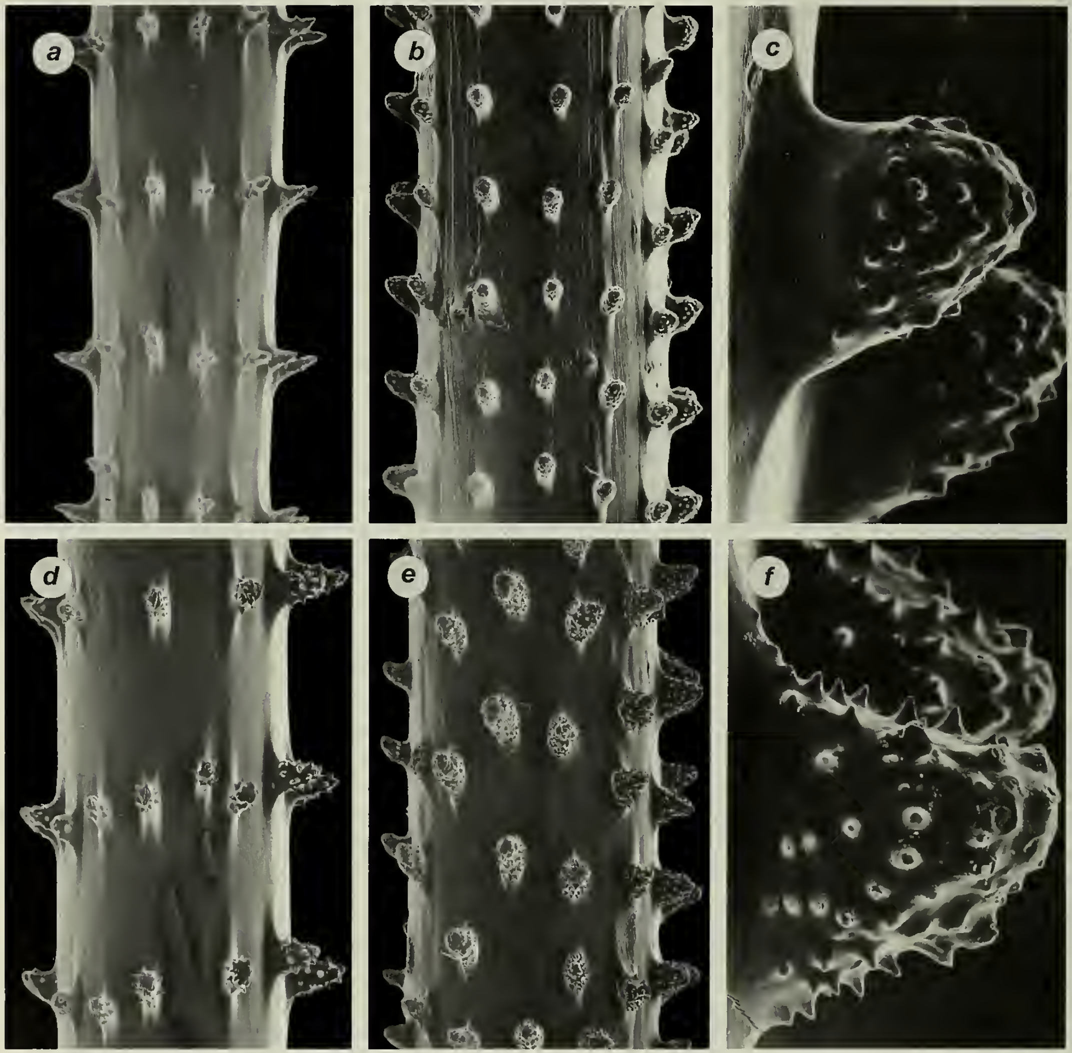

Fig. 4. *Allopathes desbonni* (a–c, neotype, USNM 88327; d–f, *Blake* Stn 155). a, Section of stem 0.3 mm in diameter, ×70; b, Section of stem 0.9 mm in diameter, with large, blunt spines, ×31; c, Blunt spine, ×250; d, Section of stem 0.4 mm in diameter, ×69; e, Section of stem about 0.8 mm in diameter with large, blunt spines, ×34; f, Blune spine, ×25.

meter. Near the base of the stems there can be as few as 5 polyps per centimeter. In a preserved state the sagittal tentacles are about 1.5 mm long and appear about twice as long as the lateral tentacles.

Remarks.—Duchassaing & Michelotti's (1864) original description of this species is as follows: "Simplex filiformis, caudata, nigra, spinis minutis, confluentibus. Species lenta, nec flexuose spiralis . . ." None of Duchassaing & Michelotti's antipatharian types are in the collections of the Turin Museum (Rossi, pers. comm.), and it is unlikely that they still exist. For this reason a neotype is designated.

Pourtalès (1874, 1878) originally confused Duchassaing & Michelotti's species with a single-stemmed *Cirrhipathes,* but in the *Blake* collection Pourtalès (1880) found one cluster of stems joined at the base which he recognized as the true *C. desbonni.* He noted that the axial spines on the younger parts of the corallum were arranged in verticils, as well as in longitudinal rows; however, he did not provide a detailed description of the spines and made no mention of surface sculpturing.

We re-examined the *Blake* specimen and found it to consist of about twelve stems, the longest of which is about 46 cm in length and about 1.5 mm in basal diameter. Most are broken at their distal end and also broken off from the trunk. Neither the size of the spines (0.10–0.18 mm) nor their density (3 or 4 per mm in each row) are appreciably different from the *Johnson-Sea-Link* specimen and, as in the latter case, the spines on the basal end of the stems are relatively smooth and acute, whereas others slightly higher up are rather wide and blunt. However, on many of the stems from the *Blake* specimen, the spines have much more strongly developed surface sculpturing than the *Johnson-Sea-Link* specimen. The surface tubercles are larger and more distinct, even on spines on the abpolypar side of the axis (Figs. 4d–f). Polyps are not present on the *Blake* specimen.

Whether the differences in surface sculpturing of the spines is indicative of a species level differentiation is difficult to determine in view of the condition and limited amount of material available.

Comparisons.—A species of antipatharian from Mauritius, *Antipathes robillardi* Bell, 1891, is very similar in general appearance to *A. desbonni.* The type specimen of *A. robillardi* could not be located in the collections of the British Museum so a direct comparison with *A. desbonni* was not possible. However, from Bell's description and illustration, it can be determined that the two species are of comparable size (stems about 1 m long), and both have spines arranged in verticils. Bell reported that the corallum of *A. robillardi* consisted of several trunks which gave rise to numerous stems, many of which were simple, but some were said to "divide at once two or three times," and one was said to divide at a height greater than 7.5 cm from the base. In the neotype of *A. desbonni* very few of the stems divide, and none at a height greater than 1 cm. Bell reported that the spines of *A. robillardi* were blunt and his illustration shows eight rows in lateral view; however, the spines were not described as having any surface sculpturing, and the illustration is not detailed enough to indicate whether they have conical tubercles like those in the neotype of *A. desbonni.* There is, however, another species from Mauritius, *Antipathes verticillata* (Brook), that has verticillated spines that are very similar in appearance to those of *A. desbonni*; i.e., they are conical, acute, and covered with sharp, conical tubercles (Brook 1889: plate XII, figs. 25 and 25a). Significantly though, the corallum of *A. verticillata* differs from that of *A. desbonni* and *A. robillardi* in being branched, with long simple, mostly unilaterally arranged branchlets, a condition not unlike that occurring in the western Atlantic species *Antipathes pedata.* Spines in the latter species are not arranged in verticils; however, they do have distinct surface tubercles not unlike those occurring in *A. verticillata.*

Distribution.—Gulf of Mexico off southeastern Louisiana; off Montserrat, Lesser Antilles; 129–161 m.

Acknowledgments

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DIVERSITY OF METAZOAN OVARIES AND VITELLOGENIC MECHANISMS: IMPLICATIONS FOR LIFE HISTORY THEORY[1]

Kevin J. Eckelbarger

Abstract.—Metazoan life histories are diverse and the selective pressures that have shaped them have resulted in wide interspecific variation in egg size and energy content, fecundity, the age of first reproduction, and the number of and interval between reproductive episodes. Metazoan ovaries show wide morphological variation and a number of mechanisms have evolved by which yolk is synthesized within growing oocytes. The ovary and associated vitellogenic mechanisms play a direct role in the rate of egg production, the frequency of breeding, and the size and energy content of the egg and resultant consequences for larval dispersal. Evolutionary discussions of semelparity vs. iteroparity, r-selected and K-selected species, and the significance of interspecific variability in egg size, energy content and resultant larval mode, should consider the role of oogenesis because the developmental pathways established during oogenesis have a direct effect on subsequent life histories. Reproductive success in both pelagic and benthic marine communities is influenced by a species' capacity to convert food into egg production. The vitellogenic phase of oogenesis is generally the longest phase of egg growth but its duration varies by orders of magnitude between species due to interspecific differences in vitellogenic mechanisms. Metazoans can be viewed on a continuum from slow to fast egg producers, each utilizing physiologically distinct vitellogenic pathways that limit the rate of egg production. Reproductive responses to food vary widely among species and are probably correlated with interspecific differences in digestive kinetics and vitellogenic mechanisms. So-called opportunistic species have evolved specialized vitellogenic pathways for the rapid conversion of food into egg production while many other species (e.g., annual spawners) utilize slower pathways. There exist complex interrelationships between habitat, food, feeding strategies, digestive constraints, and vitellogenic mechanisms that need to be appreciated if marine community dynamics are to be fully comprehended. This review discusses the adaptive significance of metazoan ovaries and vitellogenic mechanisms and their possible life history consequences.

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[1] The eighth presentation in the Riser Lecture Series: In 1985 the annual Riser Lecture was initiated by members, alumni and friends of Northeastern University's Marine Science Center, at Nahant, Massachusetts. The occasion was the official retirement of Professor Nathan W. Riser. As teacher, biologist and founder of the facility, "Pete" Riser endowed the laboratory with a legacy, that being the importance of considering one's special focus within the context of the whole organism. The Riser Lecture is dedicated to that principle.

> "Though some of the very essential features of oogenesis, such as cytology of maturation divisions, have remained almost the same throughout the animal kingdom, differences exist among various groups in details of structure, chemistry, and physiology of the female gamete and its spawning behavior; others are directly traceable to varied demands imposed by the habitat and life cycle (Adiyodi & Adiyodi 1983)."

One goal for undertaking life history studies is to predict what kind of life history pattern an organism will display in any given habitat. Such a predictive ability should lead to a better understanding of the selective forces that shape the evolution of life histories and produce the diversity of patterns observed in nature. The reproductive biology of any species represents a collection of traits that have been subject to selection and presumably represent adaptive features (Gould 1977, Raff & Kaufman 1983, Ghiselan 1978). Many of these reproductive traits act as covariables and often evolve in concert. To determine a species' "fitness" and to better understand marine community structure, life history theorists have tried to understand the evolution and ecological significance of numerous reproductive traits including the number, size, and quality of offspring, the age distribution of reproductive effort, the interaction between reproductive effort and adult mortality, the timing of reproduction, and the variability of these traits among the offspring (Cole 1954, MacArthur & Wilson 1967, Pianka 1970, Stearns 1976).

The consequences of metazoan life history variations for population dynamics were first explored by Cole (1954) and, since then, many clusters of life history traits have been analyzed (Levin & Haggett 1990). Life history theorists generally study population regulation and marine community structure from the point of view of dispersal, predator-prey interactions, and competitive coexistence (Levin 1984). However, many life history traits are constrained by ovarian structure and by species-specific vitellogenic mechanisms that determine the quantity, quality, and rate of energy (yolk) incorporation into the egg during oogenesis. The rate of egg production, the frequency of breeding, the size and energy content of the egg, and the resultant consequences for larval dispersal (e.g., planktotrophy vs. lecithotrophy), are strongly influenced by the ovary. For successful reproduction to occur, maternal mobilization, biosynthesis and bioaccumulation of nutrients must occur within the egg in a programmed manner during oogenesis. The impact that ovarian evolution has had on metazoan reproductive success is exemplified dramatically by arthropods, which account for more than 90% of the total number of species on earth. A major reason for their success has been the evolution of specialized ovaries and vitellogenic mechanisms that enable them to manufacture, sometimes in a single day, an egg mass exceeding half their body weight (Yamashita & Indrasith 1988). However, many other species have far less capacity for rapid egg production due to constraints that impose limits on the vitellogenic phase of oogenesis. Thus, the length of oogenesis may vary by orders of magnitude from one species to another depending upon the mechanism of vitellogenesis employed during the yolk acquisition phase of oogenesis.

Larval ecologists and life history theorists have focused special attention on the invertebrate egg and the contrast between species that undergo a single reproductive episode during their lifetime (semelparous species) and those that undergo multiple reproductive episodes (iteroparous species). Variability of egg dimensions, energy content, and subsequent larval developmental mode (e.g., lecithotrophy vs. planktotrophy) have evolutionary significance and influence the distribution and abundance of marine species (see Young 1990). Even though yolk is believed to play a pivotal role in larval nutrition and has been the subject of many theoretical discussions (Emlet et al. 1987), oogenesis has rarely been considered. To understand the relationship between ovarian structure and function, energy investment per egg, and larval biology, one must consider oogenesis because interspecific variations in yolk content are established during the vitellogenic phase of egg ontogeny.

Studies of semelparity vs. iteroparity generally focus attention on the spawning event while the period of egg maturation and vitellogenesis, which may have preceeded it by weeks or months, is less appreciated. Although many ecologists may be unaware of the diversity of metazoan vitellogenic mechanisms, they are acutely aware of the ecological implications of these mechanisms. For example, species differ in their ability to rapidly respond to open, unexploited, or organically enriched habitats. Species that do respond rapidly have been labeled "opportunistic" (MacArthur 1960, Hutchinson 1967) or "r-selected" (MacArthur & Wilson 1967). Species with opportunistic life histories mature early and undergo frequent reproductive episodes, enabling them or their offspring to adapt through short-term selection (Grassle & Grassle 1974). For egg production to proceed at an accelerated rate, the egg must incorporate nutrients quickly. For other species, however, oogenesis is often an annual event, requiring months of egg maturation resulting in a relatively predictable seasonal reproductive episode. Such slow egg production is usually preceeded by a programmed energy transfer from somatic storage sites to the ovaries as exemplified by most echinoderms (Pearse & Cameron 1991). Semelparity and iteroparity, therefore, represent life history manifestations of different vitellogenic mechanisms, some of which are adapted for the rapid synthesis of yolk, while others are not (Eckelbarger 1983). In recent years, comparative studies of oogenesis have revealed a correlation between life histories and patterns of oogenesis in cnidarians (Eckelbarger & Larson 1988, 1992; Eckelbarger 1994), ctenophores (Greve 1970), polychaetes (Eckelbarger 1983), oligochaetes (Jamieson 1991), nematodes (Stark 1984), rotifers (Bentfield 1971), ectoprocts (Reed 1988, 1991), insects (Davidson 1986), and crustaceans (Blades-Eckelbarger, pers. comm.). Therefore, developmental pathways established during oogenesis have a direct effect on subsequent life histories.

A number of excellent reviews on oogenesis are available but most have targeted specific events of cell differentiation and the processes that regulate developmental pathways (see Wourms 1987, for review). Few investigations have addressed the ecological significance oogenesis has played in life history evolution. This review will examine the diversity of metazoan ovaries and vitellogenic mechanisms and assess their possible life history consequences.

Invertebrate Ovaries and Accessory Cells

Invertebrate ovaries range from loose associations of germ cells to morphologically complex organs. Two types of oogenesis have evolved in the invertebrates (Eckelbarger 1983). *Extraovarian* oogenesis involves the release of oocytes from the ovary early in their development (often before vitellogenesis begins) and the subsequent completion of development elsewhere, frequently within a coelomic space (e.g., polychaetes). *Intraovarian* oogenesis, the more common pattern, involves the retention of oocytes in the ovary until late in development or just prior to spawning (e.g., echinoderms and molluscs). In either case, oocytes may or may not be associated with accessory cells during oogenesis. The majority of invertebrates possesses distinct (localized) ovaries in which the oocytes are closely associated with accessory cells that fall into one of four general categories: 1) follicle cells, 2) nurse cells, 3) nutritive eggs, or 4) other miscellaneous accessory cells (Wourms 1987). Accessory cells are commonly assumed to play a trophic role but supportive evidence is usually lacking. Although the topographic, structural, and functional interrelationships between germ cells and accessory cells are poorly understood in most species, numerous examples are available that demonstrate that some ovarian accessory cells may have ecological significance because they enable the organism to accelerate egg production through trophic support of the growing oocyte.

Follicle cells are somatic in origin (non-germ cell line) and partially or completely encompass individual oocytes or groups of oocytes. They are believed to have at least four distinct functions: 1) mechanical support or protection of oocytes during early oogenesis, 2) the production of secondary, compound, or cellular egg envelopes around oocytes, 3) the synthesis of metabolites or yolk precursors, and/or 4) the resorption of atretic oocytes (Wourms 1987). Nurse cells are abortive germ cells that are associated with oocytes through confluent cytoplasmic bridges resulting from incomplete cytokinesis (Huebner & Anderson 1976). They have been reported from many invertebrate phyla. In general, nurse cells replace or supplement the biosynthetic activities of the oocyte. They may have a trophic function by contributing organelles (i.e., mitochondria), ribonucleoproteins, and/or pre-yolk or fully formed yolk bodies to the oocyte, or they may play a role in determining oocyte polarity (Wourms 1987). Nurse cell-oocyte complexes are most highly developed in insects. The more primitive species possess panoistic ovaries that contain only follicle cells while the higher insects have meroistic ovaries with well-developed nurse cell-follicle cell complexes that contribute significantly to oocyte development (Telfer 1975).

In some species (e.g., sponges, hydroids, some polychaetes, and *Artemia*), a few germ cells abort their development and are phagocytized as "nurse eggs" by one or more oocytes. Neoophoran turbellarians are unique because yolk is not synthesized in the egg but rather in special accessory cells (vitellocytes) that are deposited within the alecithal eggs and later engulfed by developing embryos (Gremigni & Falleni 1991). Therefore, the egg acquires yolk during embryonic development rather than during oogenesis. Prosobranch gastropods, particularly the neogastropods, show additional examples of post-oogenic yolk transfer in that non-viable, nutritive eggs are deposited within egg capsules to serve as supplemental sources of nutrition for the developing embryos (Rivest 1983).

In echinoids, large vesicular cells called nutritive phagocytes appear to sequester nutrients prior to vitellogenesis and transfer them via a diffusional process to the oocytes (Pearse & Cameron 1991). A number of recent studies on echinoids has also implicated the intestine, ovary and coelomocytes as sites of yolk protein synthesis but these results warrant further investigation (reviewed in Pearse & Cameron 1991). Among anthozoans, specialized gastrodermal cells collectively referred to as the trophonema, become intimately associated with developing oocytes and are believed to play a nutritional role by mediating the movement of yolk precursors from the coelenteron to the egg (Fautin & Mariscal 1991). Within the Scyphozoa, specialized gastrodermal cells termed trophocytes serve a nutritive role during oogenesis in a manner similar to that described in anthozoans (Eckelbarger & Larson 1988, 1992; Eckelbarger 1994). Figure 1 summarizes the potential sources of yolk precursors available to metazoan oocytes during vitellogenesis.

Phyletic Constraints on Vitellogenesis

Organisms display a variety of life history traits that can be correlated with unique morphological constraints determined by ancestry. To understand the significance of diversity in metazoan ovaries and vitellogenic mechanisms, one must first consider the bewildering variety of architectural themes observed in the Metazoa. Although

Fig. 1. Sources and routes of yolk precursor entry into developing oocytes in different metazoans. 1) low molecular weight precursors enter oocyte through surface microvilli; 2) large molecular weight yolk precursors enter oocyte via receptor-mediated endocytosis; 3) yolk precursors derived from coelomic eleocytes enter oocyte via endocytotic uptake; 4) follicle cell-derived yolk precursors enter oocyte via endocytotic uptake; 5) nurse cells provide metabolites and/or organelles to oocyte via intercellular bridges; 6) both follicle cells and nurse cells are involved in support of oocyte growth; 7) oocyte phagocytizes germ or somatic cells during growth phase; 8) blood vessel-derived precursors are incorporated into oocyte via endocytic uptake.

all oocytes require an external source of energy for yolk synthesis, the options for acquiring yolk precursors are constrained by the body plan of the organism in which they reside. For example, lower metazoans (e.g., placozoans, sponges, cnidarians, small-bodied, interstitial species) are structurally simple, lack well-developed circulatory systems, fluid-filled body cavities and complex ovaries that could provide nutritional support to the growing oocyte. They also have fewer and less specialized cell types so oocytes often grow autonomously without the aid of accessory cells. Germ cells in the sponges and cnidarians are often motile and capable of actively migrating toward their own sources of nutrition. Simple diffusion or active transport of precursors to the oocytes from digestive cells may be adequate to support oocyte growth in many small-bodied infaunal organisms particularly since few eggs are produced at one time. The direct transport of dissolved organic materials (DOM) from the external environment through the body wall also may play a role in oocyte nutrition (Manahan et al. 1982). In contrast, species in the higher phyla (e.g., vertebrates) deliver yolk precursors from extraovarian sources via the circulatory system to a static oocyte growing within a relatively complex ovary.

Oocytes often depend to some extent on the trophic support of cells and tissues that are spatially close to the ovary or can communicate with the ovary via the circulatory system or adjacent fluid-filled cavities. Therefore, similar mechanisms of oocyte nutrition have arisen independently in different taxa when there are structural similarities in their body plans. Nurse cells, for example, play some role in support of oocyte growth in many species and may have arisen independently within many phyla because early germ cells initially undergo mitotic division within the ovary. In most instances, the cytoplasmic continuity between sibling germ cells is lost and each cell develops into an independent, viable egg. In other cases, intercellular bridges remain intact and some germ cells are restricted to only a trophic role. The extent of nurse cell involvement in oocyte nutritional support is significant in ctenophores, rotifers, and insects. Follicle cells are perhaps the most ubiquitous ovarian accessory cell. They are particularly common among coelomates because they are derived from the peritoneum which is intimately associated with the ovary. In some annelids, molluscs, crustaceans, insects and ectoprocts, the follicle cells often undergo hypertrophy prior to or during vitellogenesis and contain abundant proteosynthetic organelles that are probably involved in yolk precursor production.

It is likely that yolk precursors often pass directly or indirectly from the digestive system to developing oocytes, particularly in small-bodied species that produce only a few eggs at a time. The intimate association of oocytes with digestive systems is a common theme in cnidarians, nemerteans, and molluscs, for example and this method of nutrient acquisition has been proposed for gastrotrichs (Rieger & Rieger 1980) and interstitial polychaetes (Eckelbarger 1983). Stricker (1986) suggested that yolk precursors originating from the gut may be passed to the ovary through intervening accessory cells in the ectosymbiotic nemertean *Carcinonemertes epialti,* a species that rapidly produces eggs while feeding on the eggs of host crabs. In nematodes, yolk proteins are produced by the gut and transferred through the pseudocoel to the ovary allowing some species to be among the most fecund on earth (Kimble & Sharrock 1983). In some species, close apposition of oocytes to the digestive system may be adequate for the transfer of nutrients during oocyte growth (e.g., polychaetes and coronate scyphozoans) while in other species, specific digestive cells have assumed a trophic role (e.g., anthozoans and semaeostome and rhizostome scyphozoans). In vertebrates, the circulatory system is an efficient means of transfering vitellogenin to the oocytes. In some invertebrates, notably the polychaetes and cephalopod molluscs, the circulatory system is also used to transfer yolk precursors to the ovary. The funicular system in bryozoans has been cited as a possible means of precursor transport to the ovaries of individual polypides, analogous to that observed in polychaetes (Reed 1988). Many invertebrates have fluid-filled cavities surrounding the ovaries that enable precursors to be transferred to developing oocytes from their extraovarian sites of production. Thus the hemocoels of crustaceans and bivalve and opisthobranch molluscs, the pseudocoel of nematodes, the coelom of annelids, and the perivisceral coelom of echinoderms all serve potentially as reservoirs for precursor storage and a means of inter-organ nutrient transfer to the oocytes from the extraovarian site of precursor synthesis. These cavities also permit the accumulation and storage of large numbers of eggs prior to spawning.

Mechanisms of Yolk Synthesis (Vitellogenesis)

The egg cell is typically the largest cell within an organism due to incorporation of substantial quantities of ooplasmic energy reserves collectively called "yolk." The biosynthesis and accumulation of yolk represents a substantial energy investment by the female and is a complex and highly regulated process under both genetic and endocrine control. Vitellogenesis is usually the longest period of oocyte differentiation but it varies in length by orders of magnitude from one species to another. The rate of yolk synthesis is dependent on the capacity of the oocyte or other mediating cells to obtain and convert yolk precursors into yolk bodies. That, in turn, is dependent on the structure of the ovary and the mechanism(s) of vitellogenesis that characterize each species. Due, in part, to morphological constraints imposed by ancestry, members of different phyla often utilize different vitellogenic mechanisms. This vitellogenic diversity has resulted in profound implications for their subsequent life histories by limiting the maximum rate of egg production and the interval between egg-laying events. In its broadest sense, yolk includes a heterogeneous population of ooplasmic inclusions including lipid droplets, glycogen granules, and chemically complex, membrane-bounded organelles containing proteins, carbohydrates, lipids, pigments, free amino acids, free sugars, nucleotides, and nucleic acids. Wourms (1987) outlined the types of carbohydrate, lipid, and protein components of yolk that are encountered in most eggs. Carbohydrate yolk reserves include glycogen, galactogen and various polysaccharide-protein complexes. Lipid reserves include "fatty" yolk globules, phospholipids, and triglycerides. Protein reserves include "protein yolk" consisting of chemically uncharacterized protein reserves, lipoproteins, phosphoproteins (vitellogenins), and protein-polysaccharide complexes. Although individual authors often neglect to define their use of the term "yolk," they are usually referring to characteristic, electron dense organelles (yolk granules) that dominate the ooplasm of the mature egg and distinguish the egg from other cells.

Despite myriad papers on vitellogenesis, yolk is one of the least understood components of the metazoan oocyte. Many biologists assume that yolk functions solely as an energy reserve despite scanty supporting evidence. Yolk (vitellin) is ultimately derived from the products of digestion but yolk precursors can be delivered to the oocyte in several forms including low molecular weight precursors, high molecular weight female-specific yolk proteins (vitellogenin), or both. Schechtman (1955) described three mechanisms of yolk synthesis (Fig. 2): 1) autosynthetic yolk formation occurs when the oocyte synthesizes vitellin using its own proteosynthetic organelles after internalizing low molecular weight, exogenous precursors; 2) heterosynthetic yolk synthesis occurs when yolk proteins are synthesized by other cells and transported to the oocyte for incorporation; and 3) mixed yolk synthesis in which a combination of autosynthetic and heterosynthetic mechanisms are used. In oocytes utilizing heterosynthetic pathways, a specific class of female-specific yolk proteins referred to as vitellogenin, is incorporated into the oocyte (Fig. 2A) and usually comprises 60–90% of the soluble yolk proteins (vitellins) in the cell (Hagedorn & Kunkel 1979). Vitellogenin is a generic term first applied to female-specific proteins in insects but it has been widely used in vertebrates, and more recently in other invertebrates. Thus far, there is little evidence that vertebrate vitellogenins have more than an analagous relationship to in-

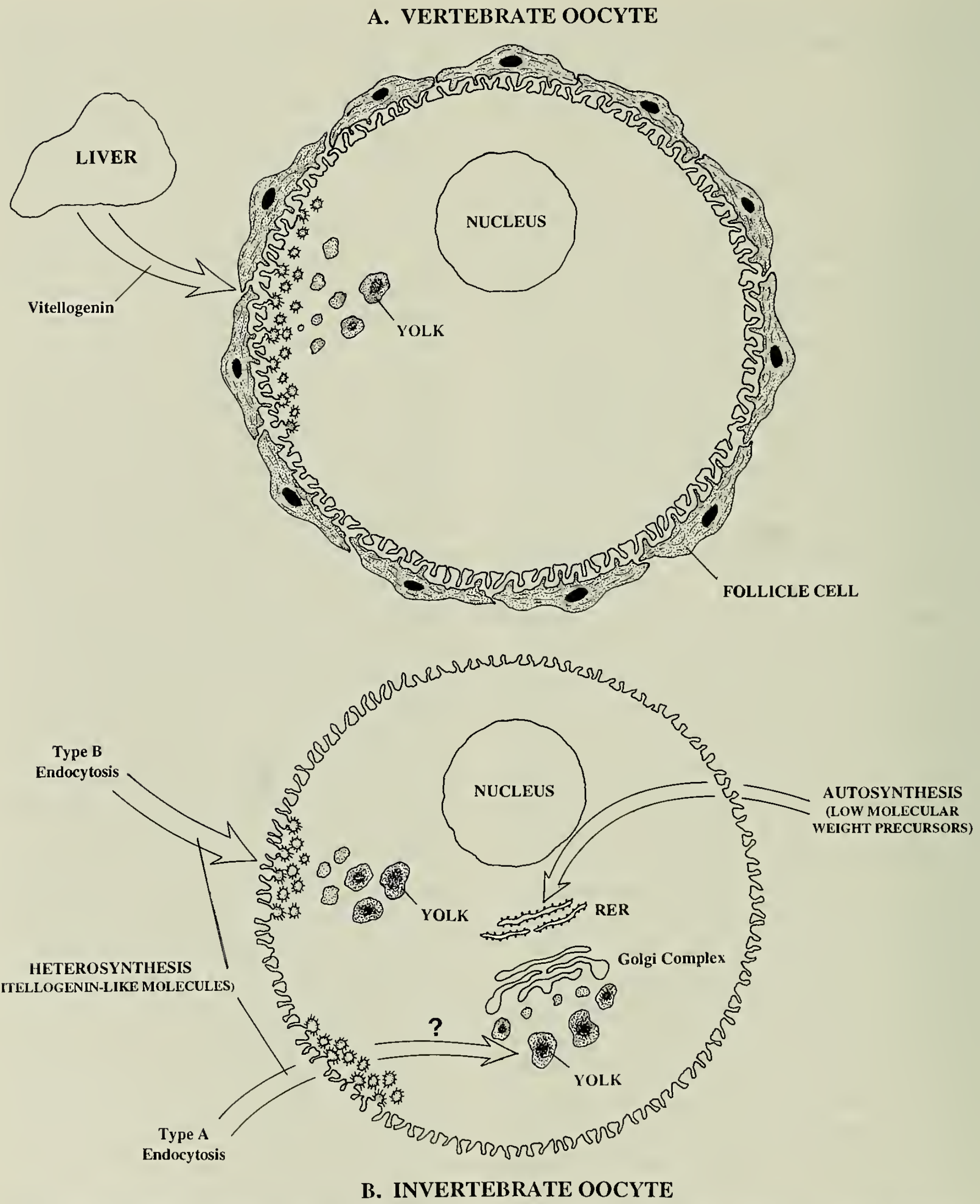

Fig. 2. Diagrammatic representations showing pathways of yolk precursor incorporation by nonmammalian vertebrate (A) and invertebrate (B) oocytes.

vertebrate vitellogenin. Yolk inclusions have not been observed in the eggs of mammals, suggesting that the vitellogenin genes were either lost or silenced in the transition from prototherian to therian mammals (Wallace 1985). In general, one observes a progressive adaption of heterosynthetic mechanisms of yolk synthesis as one moves from the lower to the higher phyla, culminating in the non-mammalian vertebrates which employ heterosynthesis exclusively (Fig. 3).

The most common means for determin-

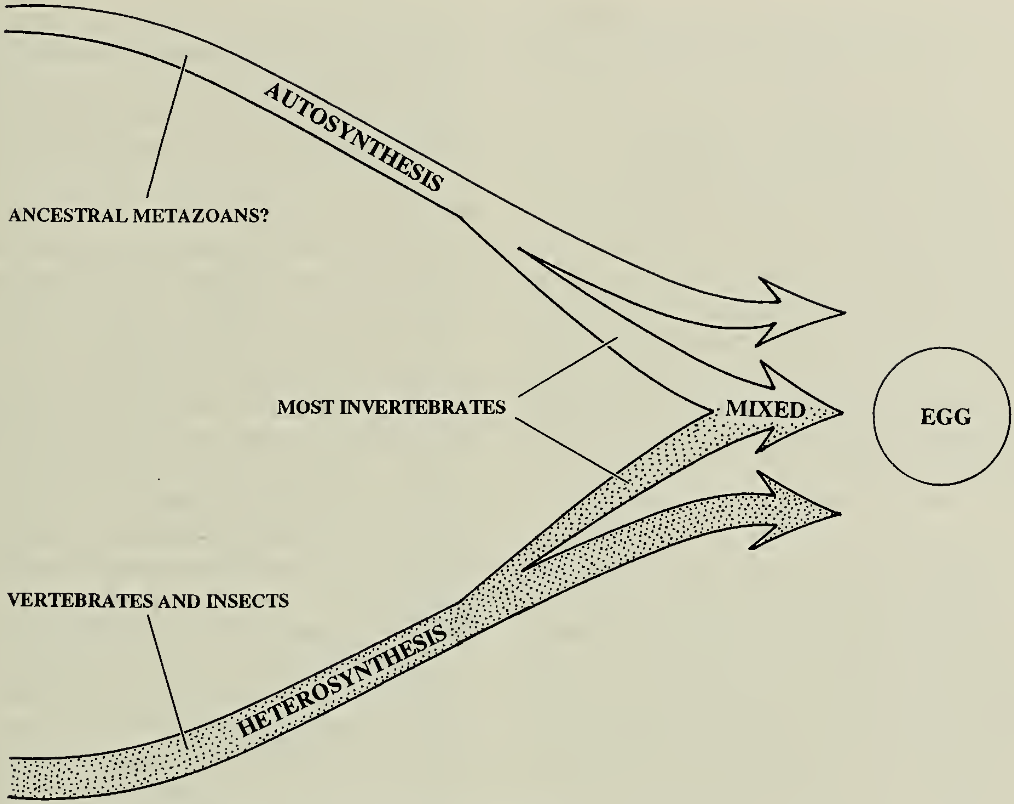

Fig. 3. Hypothetical pathways of metazoan yolk synthesis.

ing the mechanism(s) of vitellogenesis is through inference from ultrastructural observations. Species that utilize autosynthetic mechanisms typically have oocytes containing abundant rough endoplasmic reticulum (RER) and Golgi complexes which appear to collaborate in the biosynthesis of yolk protein(s). In these organisms, there is little or no morphological evidence for the incorporation from extraoocytic sources of large molecular weight yolk precursors by the oocyte and oocyte growth tends to be very slow (Fig. 2B). However, low molecular weight precursors are assumed to be sequestered through the numerous microvilli that typically adorn the oocyte surface. In other species, the uptake of large molecular weight exogenous precursors (vitellogenin?) can be visualized ultrastructurally by the appearance of distinctive coated pits and vesicles (endosomes) along the oocyte surface involving a process of receptor-mediated endocytosis (Fig. 2B) (Wild 1980). High levels of endocytotic activity during vitellogenesis are generally associated with rapidly growing oocytes. In some instances, ultrastructural studies suggest the fusion of endosomes with the products of the RER and Golgi complexes (type A endocytosis). In others, endosomes fuse directly into yolk bodies (type B endocytosis) (Fig. 2B). An assumption is frequently made that ultrastructural evidence of endocytotic activity is sufficient to indicate the incorporation of vitellogenin for yolk assembly. However, the mere presence of coated pits and vesicles does not indicate conclusively that extraoocytic molecules contribute to yolk synthesis unless ultrastructural studies indicate that type B endocytosis results in the direct fusion of endosomes into yolk bodies. Conversely, the absence of endocytotic activity does not necessarily preclude the possibility of incorporation of heterosynthetic precursors if uptake of high molecular weight precursors is a slow process. For example, nereid polychaetes were considered typical examples of autosynthetic eggs due to the presence of abundant RER and Golgi complexes and low levels of endocytotic activity. However, immunological approaches have demonstrated that vitellogenin is actually synthesized by free-floating coelomocytes in *Nereis virens* and *Perinereis cultrifera* and incorporated slowly into the oocytes from the coelomic fluid (reviewed in Fischer & Dhainaut 1985).

Egg Volume and Energy Content

Larval ecologists have drawn attention to the relationship between egg size, energy content (parental investment), and fecundity in marine invertebrates. The reserves deposited in the egg during oogenesis are assumed to be catabolized during embryogenesis prior to the formation of a functional larval digestive system. In fact, little is known about the metabolic fates of yolk proteins during embryogenesis (Yamishita & Indrasith 1988). Generalizations regarding the functional role of yolk in life histories are often unjustified because the organelles designated as "yolk bodies" may not play a nutritive role, and few experimental studies have confirmed the trophic role of yolk (Williams 1967). More importantly, it is not known if the various organelles described as yolk bodies are qualitatively and functionally similar in different species. Teleost (Wallace 1985, Sellman et al. 1988) and crustacean (Blades-Eckelbarger & Marcus 1992) biologists, for example, recently determined that some "yolk granules" are involved in the fertilization reaction and play no trophic role in development.

Echinoderms have played a central role in discussions of the relationship between egg size and energy content (reviewed by Emlet et al. 1987) but the results have often been confusing or contradictory. These collective investigations have shown that there is no simple relationship between egg size and energy content and that broad generalizations within and between taxa are not warranted. Recent studies of *Arbacia* development by Armant and co-workers (1986) demonstrated that there was no evidence of yolk platelet depletion during embryonic development to the pluteus stage (e.g., no decrease in concentration of yolk platelet protein was detected during development) although yolk platelet protein subsequently disappears during later larval development. The authors concluded that yolk might be used in the event the larva was unable to obtain food when feeding begins at the pluteus stage. In a related study of echinoid development, Scott & Lannarz (1989) reported limited proteolytic processing of yolk glycoproteins to lower molecular mass glycoproteins during the course of development but that the glycoproteins remained within the yolk platelet. In a comparative study of yolk proteins in the planktotrophic urchin *Heliocidaris tuberculata* and the direct developing species, *H. erythrogramma,* Scott and her co-workers (1990) found that eggs of the former species contained yolk protein within yolk bodies while the latter did not. Expecting to find a greater increase in yolk proteins in the larger, direct-developing eggs, they found much lower levels of glycoproteins. The authors considered these results consistent with the theory that yolk glycoproteins in sea urchins are not utilized in early development but rather during late larval and premetamorphic stages in planktotrophic species.

Strathmann & Vedder (1977) reported that organic matter per unit volume decreased with egg size in echinoderms with feeding larvae and predicted that such a trend may not be evident in eggs of larger size. Turner & Lawrence (1979) confirmed the Strathmann & Vedder prediction and found no relationship between organic matter concentration and egg size with larger echinoderm eggs. McEdward & Chia (1991) recently reported no interspecific relationship between energy concentration (Joules/ul) and egg size for the pelagic lecithotrophs they examined. Due to compositional similarity of eggs of different sizes and developmental modes, some workers concluded that the significance of larger echinoderm eggs is not to accommodate the differences in the energetic demands of development, but rather to create a larger offspring (Lawrence et al. 1984). McClintock & Pearse (1986), in a study of three Antarctic echinoderms, found no direct correlation between egg size and energy content because no loss of energy was recorded during development from the egg to the juvenile. In some echinoderms, egg volume and energetic content varies within a single spawn of a single female (McEdward & Coulter 1987). In other species, egg size varies among individual females from the same population, and among individuals from different populations (Emlet et al. 1987). In the asteroid, *Solaster,* variation has been observed in egg size and organic content 1) among eggs from a single spawn, 2) among females from a single population, and 3) among populations (McEdward & Carson 1987). The authors point out that accurate estimates of egg volume cannot be obtained by simply measuring egg diameter for invertebrates because many eggs are spheroidal in shape. In the echinoid *Arbacia lixula,* egg size varied between different adult populations having different levels of available food with eggs and larvae significantly larger in the higher food population (George 1990). It is clear that the functional role of yolk deserves further study.

We will next assess the relationship between vitellogenic mechanisms and life history patterns. Specifically, is there a correlation between the mechanism of vitellogenesis and the frequency of egg laying?

Vitellogenic Mechanisms and Breeding Frequency

Invertebrates differ significantly with respect to the timing of sexual maturity and the frequency of reproductive episodes. Species that breed only once are termed "semelparous" or "monotelic" (Cole 1954, Stearns 1976) (Fig. 4A). Among semelparous species, the age of reproduction may range from a few hours to several years. Those that breed several times are termed "iteroparous" or "polytelic" (Wynne-Edwards 1962, Clark & Olive 1973). Iteroparous species may be further subdivided to distinguish those that breed during a series of discrete episodes separated by periods of usually one year (annual iteroparity, e.g., many echinoderms) (Fig. 4B) and those breeding more or less continuously during an extended breeding season (continuous iteroparity), represented by many small-bodied polychaetes (Fig. 4C). Among iteroparous species that undergo repeated reproductive episodes, the period between successive breeding episodes can vary from hours to more than a year. Following the first reproductive episode, reproduction may then be repeated at various intervals ranging from daily to semiannually, annually, or biennially.

Ultrastructural studies of oocyte differentiation during the vitellogenic phase of oogenesis can be useful in determining the possible mechanism(s) of vitellogenesis utilized by a given species. Species utilizing heterosynthetic mechanisms often produce eggs rapidly and have short intervals between reproductive episodes while those utilizing autosynthetic mechanisms generally demonstrate slow rates of egg production and have relatively long periods between reproductive episodes.

The level of endocytotic activity in grow-

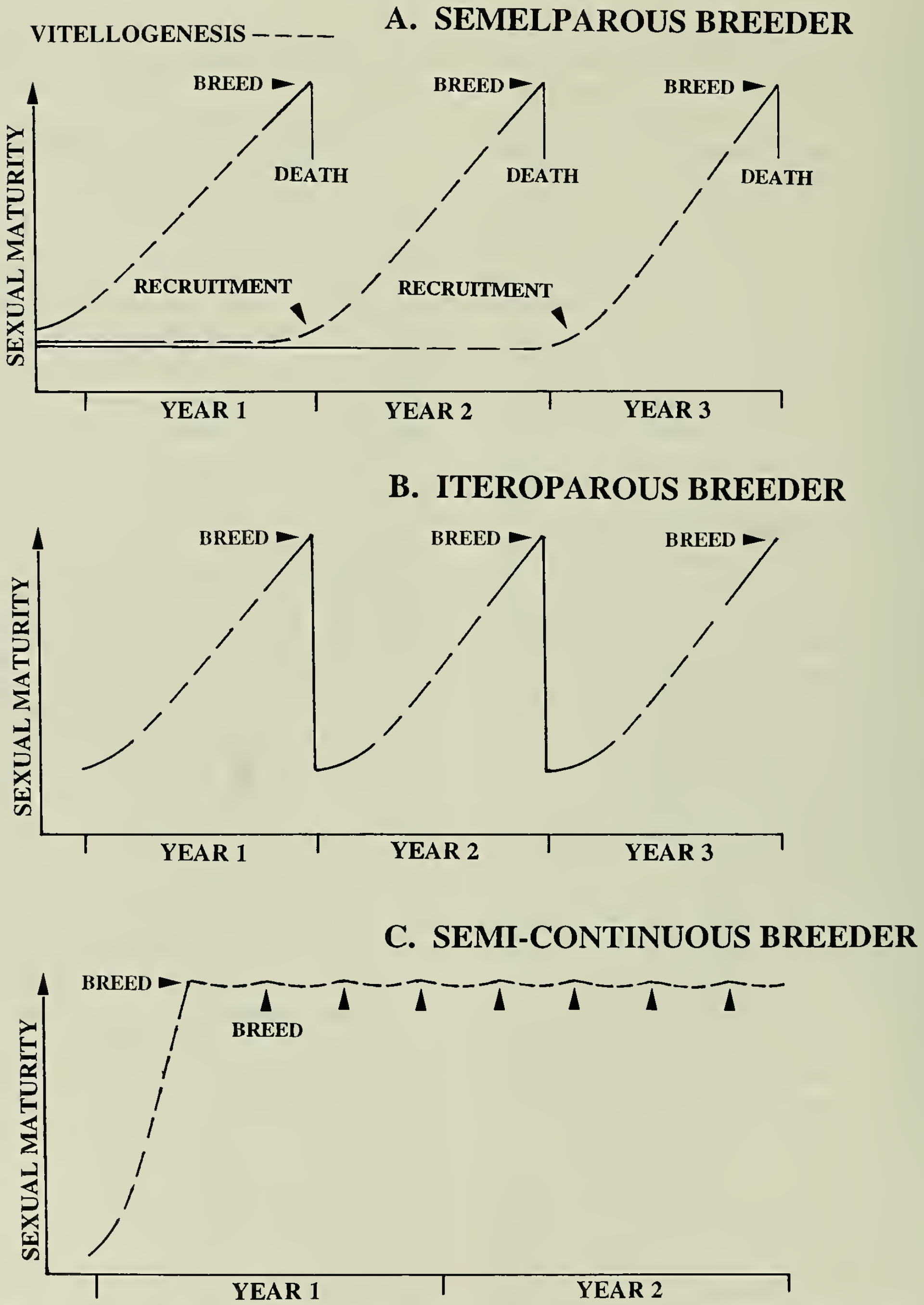

Fig. 4. Metazoan breeding patterns. A) semelparous breeder; B) iteroparous breeder; C) semi-continuous breeder.

ing oocytes is often positively correlated with the rate of oocyte growth. Semelparous and annual iteroparous species generally show low levels of endocytotic activity during vitellogenesis because there is no premium on rapid yolk precursor incorporation and yolk production. For example, endocytotic activity is minimal in most iteroparous echinoderms based on ultrastructural studies of asteroids, echinoids, crinoids, ophiuroids, and holothuroids (see review of Eckelbarger & Young 1992). However, the lack of significant endocytotic activity in growing oocytes does not suggest that exogenous precursors are not being incorporated but rather that they are being incorporated at a slow rate. The oocytes of the asteroid *Asterias rubens* are known to incorporate high molecular weight exogenous molecules despite the absence of ultrastructural documentation of endocytotic activity (Beijnick et al. 1984). Low endocytotic activity in growing oocytes may merely indicate a rate of precursor incorporation that is not easily detectable by ultrastructural methods. Oogenesis extends for a period of more than a year in the semelparous nereid polychaete *Nereis virens* (Brafield & Chapman 1967), and 7–8 mo in *N. grubei* (Schroeder 1968). The oocytes of both species show minimal endocytotic activity even though a female-specific yolk protein is known to be produced by coelomocytes and incorporated slowly over the long growth period (Fischer & Dhainaut 1985). Likewise, other semelparous nereids such as *Nereis diversicolor, N. pelagica, Perinereis cultrifera,* and *Platynereis dumerilii* have long periods of vitellogenesis and have little or no detectable endocytotic activity in the oocytes (reviewed in Fischer & Rabien 1985). Other polychaetes with slowly growing oocytes show a similar pattern of low endocytotic activity during vitellogenesis (Eckelbarger 1983, 1986). In contrast, oogenesis occurs in less than three months in the nereid *Neanthes arenaceodentata* (Davis 1969) and ultrastructural studies of their faster developing oocytes have shown high levels of endocytosis during vitellogenesis. Other polychaetes such as *Phragmatopoma lapidosa, Streblospio benedicti,* and *Polydora ligni* undergo vitellogensis in only a few days and show high levels of endocytotic activity during this period (Eckelbarger 1979, 1980, 1983, 1986). Similarly, oocytes of the semaeostome jellyfish, *Aurelia aurita,* an iteroparous neritic species that undergoes rapid egg production, show intense endocytotic activity during vitellogenesis (Eckelbarger & Larson 1988). In insects, including most of the primitive Apterygota, vitellogenesis is a heterosynthetic process in which the fat body produces yolk protein precursors which are secreted into the hemolymph, and rapidly sequestered by the developing oocytes through a receptor-mediated process (Hagedorn & Kunkel 1979, Raikhel & Dhadialla 1992).

Ovarian nurse cells are frequently associated with rapidly developing oocytes, notably in the insects. Vitellogenesis occurs in only 25 h in the mosquito (Roth & Porter 1964) and about 18 h in the fruit fly, *Drosophila* (Brownes 1982), species having the more complex meroistic ovary containing nurse cell complexes. In contrast, in the more primitive panoistic insect ovary lacking nurse cells, vitellogenesis is relatively long, for instance, 3–6 mo in the cricket (in Davidson 1986). Ovarian nurse cells are also responsible for rapid egg growth in ctenophores, rotifers, annelids, and crustaceans (Davidson 1986). In the Ctenophora, the majority of biosynthetic activity during oogenesis appears to be performed by the large population of nurse cells that establish a syncytium with the oocyte (Pianka 1974). Yolk bodies are formed in the ooplasm by the fusion of pre-yolk bodies originating from the nurse cells. Vitellogenesis in ctenophores is believed to occur in only about two days in *Beroe gracilis* and *Pleurobrachia pileus* (Greve 1970). In the rotifer *Asplanchna* there is a 100-fold increase in oocyte volume within 4–6 h resulting from the abrupt transfer of cytoplasmic materials to the oocyte from the syncytial nurse cells of the vitellarium (Bentfield 1971). Accelerated egg production occurs in the small-bodied polychaete, *Ophryotrocha puerilis* with the assistance of a single polyploid nurse cell (Ruthmann 1964). Among hydrozoans, nurse cells-assisted vitellogenesis reduces oogenesis to about four days in *Hydra carnea* (Honegger 1981) and less than eight days in *Tubularia crocea* (Mackie 1966).

Follicle cells are perhaps the most common accessory cell found in invertebrate ovaries and there are some examples in which their function(s) is directly correlated with rapid egg production. The opportunistic polychaete *Capitella jonesi* (Eckelbarger & Grassle 1982) undergoes frequent and rapid egg production with the aid of hypertrophic follicle cells that contribute to the production of yolk precursors during vitellogenesis. Follicle cells also have been shown to be the source of yolk precursors in the rapidly growing eggs of some bryozoans (Reed 1988, 1991). In chaetognaths, egg production can occur at daily intervals and may be facilitated by the endocytotic incorporation of precursors produced by follicle-like accessory cells (Shinn 1992).

The adaptive significance of semelparity and iteroparity has been debated extensively (see Grahame & Branch 1985); theory suggests that these respective life history patterns have evolved to attune the life style of the organism to its environment (Stearns 1976). Often overlooked is the fact that the duration of vitellogenesis is strikingly different between semelparous and iteroparous species. As reviewed above, different mechanisms of yolk synthesis have evolved in these organisms, including those that have endowed some species with the ability to rapidly accumulate yolk reserves. Rather than categorizing species as semelparous or itereroparous, it is more appropriate to view them on a continuum ranging from relatively fast egg producers characterized by heterosynthetic mechanisms designed to accelerate yolk production, to relatively slow egg producers characterized by slower "mixed" mechanisms of yolk synthesis. As the period of vitellogenesis shortens (and the potential rate of egg production increases), the adoption of heterosynthetic mechanisms assisting the egg in yolk production increases. In the examples presented above, these mechanisms range from the direct transport of vitellogenin to the ovary through the blood, hemolymph or coelomic fluid, to trophic support from the biosynthetic activity of follicle cells and/or nurse cells (Fig. 1). The rapid incorporation of yolk precursors by receptor-mediated endocytosis is a common mechanism observed in species having rapidly growing oocytes. Fast egg producers and accompanying heterosynthetic mechanisms of yolk production are generally not found among annual spawners because selective pressures do not favor accelerated egg growth. In these species, "mixed" vitellogenic mechanisms have been adopted in which endocytotic incorporation of yolk precursors plays a lesser role during oocyte growth. Long-lived species have adopted mechanisms for slow egg production consistent with seasonal, continuous, or predictable food supplies and relatively stable environments that characterize shallow water populations at temperate latitudes. Unstable environments with unpredictable food supplies, on the other hand, favor fast egg producers (e.g., opportunistic species) and the accompanying evolution of accelerated mechanisms of yolk synthesis.

Energy Allocation and Oogenesis Among Slow vs. Fast Egg Producers

The manner in which organisms allocate energy among growth, maintenance and reproduction during each reproductive period is critical to their life history and will differ between species depending upon the vitellogenic mechanism employed. Reproduction and somatic growth are generally considered antagonistic and relatively long-lived semelparous species (e.g., *Nereis virens*) often allocate some energy to both, whereas many species that breed semi-continuously (e.g., *Capitella* and *Streblospio*) appear to convert a large proportion of their energy directly into reproduction. In crustaceans, some species can sustain simultaneous gonadal maturation and somatic growth (including molting) while in others, growth is sacrificed at the expense of reproduction (Harrison 1990). Storage of energy reserves in the somatic tissues for later use during oogenesis is common in semelparous species. Many polychaetes, for example, store glycogen and lipid in the gut, peritoneum and coelomic cells for later transfer to the oocytes (reviewed in Eckelbarger 1983). Lipids are commonly stored by copepods from higher latitudes for later use in reproduction (Sargent & Henderson 1986). In nereid polychaetes and cephalopods, maternal muscle tissue is catabolized during vitellogenesis and is gradually incorporated from the coelomic fluid and the circulatory system, respectively, by the oocytes. Some species show an immediate reproductive response to environmental stress or an interruption of food supply. For example, in some fast-breeding polychaetes, the ovarian accessory cells are involved in the resorption of unspawned eggs presumably as a means of energy recycling and they also abruptly resorb oocytes in response to food deprivation or other environmental stresses which may create an energy deficit (Eckelbarger 1986). Regeneration also may impose energetic demands on the female by altering nutrient allocation during sexual reproduction. In some opportunistic polychaetes (e.g., *Capitella*), regenerating females show a delay in maturation and a marked decline in fecundity as compared to non-regenerating worms (Hill & Grassle 1981, Hill et al. 1982). In semelparous nereid polychaetes, regeneration is progressively inhibited as females approach reproductive maturity, indicating a shift in allocation of nutrient resources toward oogenesis (Hofmann 1976). Energy allocation, therefore, differs significantly between fast and slow egg-producing species due to different physiological priorities (Fig. 5).

Reproductive Responses to Food Levels

Nutrition, vitellogenic mechanisms, and egg production are inextricably linked but species show significantly different responses to spatial and temporal variations in food quality and quantity in the marine environment. For example, some species show abrupt reproductive responses to food levels while others do not. These differences may be related to the type of vitellogenic mechanism employed during oogenesis. Reproductive responses to variations in food levels have been extensively documented in pelagic invertebrates (Checkley 1980) yet are poorly understood in benthic species (Levin & Creed 1986). Pelagic species show variable rates of food conversion into egg production and reproductive effort has been observed to be very sensitive to food level (Tester & Turner 1990, Razouls et al. 1991). The semaeostome scyphozoan, *Aurelia aurita,* maintains a high rate of egg production when fed but quickly resorbs its oocytes when deprived of food for as little as two days (Eckelbarger & Larson 1988 and unpubl.). Oogenesis is very short in this species and oocytes show high levels of endocytotic activity during vitellogenesis. In copepods, egg production for some species follows food ingestion within hours whereas, for others, the response may take days (Tester & Turner 1990). Vitellogenesis in *Calanus pacificus* is very rapid after feeding (Runge 1984) with labeled food appearing in oocytes in less than 8 h after food ingestion (Marshall & Orr 1956). Lower food levels slow the rate of yolk synthesis so that spawning intervals are longer and egg production rates are lower (Runge 1984). This species is adapted for rapidly converting nutrients to yolk and will have a short term advantage over species utilizing slower pathways for

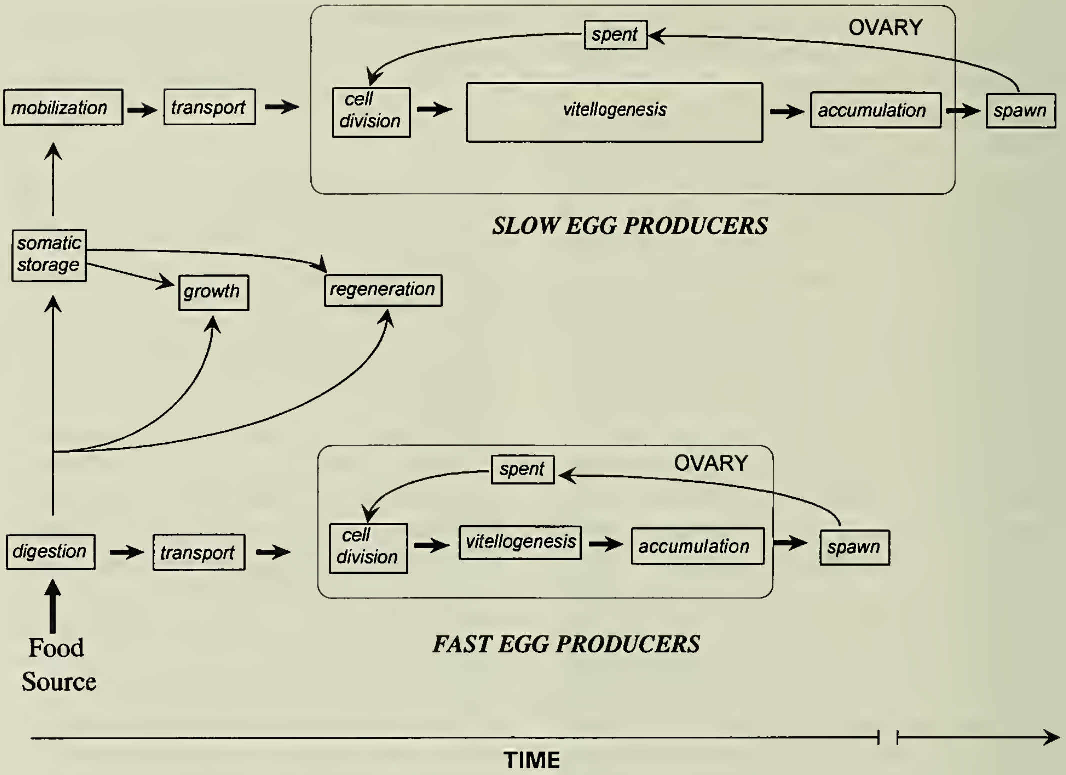

Fig. 5. Energy flow pathways from food source to spawned egg in slow and fast egg producers.

nutrient incorporation. Although the ultrastructural features of oogenesis have not been described in *C. pacificus,* they have been reported in *Labidocera aestiva,* another species that produces eggs rapidly. The oocytes of this species rapidly incorporate exogenous precursors endocytotically from the surrounding hemolymph (Blades-Eckelbarger & Youngbluth 1984). In contrast, the oceanic subantarctic copepod, *Neocalanus tonsa,* exhibits seasonal changes in feeding behavior, egg production response, and organic composition. Winter females dwelling in mesopelagic depths can release eggs in the absence of particulate food due to lipid reserves that allow recruitment to be decoupled from or out of phase with primary production in surface waters. Spring females, on the other hand, have limited lipid reserves and must obtain exogenous sources of nutrition for egg production. They are, therefore, directly coupled to primary production for recruitment (Ohman 1987).

There are many examples of species that respond to feeding or starvation by abruptly switching egg production on or off. For example, while most sea anemones are annual breeders, store food reserves, have extended gametogenic periods, and show little immediate response to food levels (Jennison 1979), the small, estuarine anemone *Nematostella vectensis,* shows dramatic responses to food levels by producing eggs at 8-day intervals as long as feeding continues (Hand & Uhlinger 1992). The remarkable ability of some benthic species to translate increased food supply into accelerated egg production may underlie opportunistic dynamics in shallow water macrobenthos (Levin 1986). Populations of *Capitella* sp. I, for example, are extremely sensitive to changes in food supply and can adjust their reproductive rates accordingly, an important determinant of opportunistic population dynamics (Marsh et al. 1989). The capitellid ovary is capable of rapidly producing yolk precursors in response to food intake with the aid of proteosynthetic follicle cells (Eckelbarger & Grassle 1982). However, even in capitellids, significant variation is observed in the way food is utilized in egg production (Eckelbarger 1986). Sibling species of *Capitella* occupy similar habitats and appear to have similar methods of vitellogenesis, but they show wide variation in egg volume, brood size, and the types of yolk materials deposited in the eggs (Eckelbarger & Grassle 1983). Despite their close genetic relationship and similar habitats, food is utilized differently by the ovary. In organic enrichment studies of *Streblospio benedicti,* a polychaete exhibiting both planktotrophic and lecithotrophic modes of larval development, females exhibiting lecithotrophy showed an increase in egg production while those with the planktotrophic mode showed no increase (Levin & Creed 1986). The eggs of *S. benedicti* contain two kinds of yolk bodies produced by separate autosynthetic and heterosynthetic pathways (Eckelbarger 1980) but the lecithotrophic egg contains a higher proportion of heterosynthetically-derived yolk bodies (Eckelbarger 1986). The circulatory system of *S. benedicti* is capable of rapidly transporting yolk precursors to the ovary following feeding (Eckelbarger 1980). It has been suggested that this increase in egg production by females exhibiting lecithotrophic development could be due to a greater availability of heterosynthetic yolk precursors derived from the enhanced food supply (Levin & Creed 1986).

The fact that reproductive responses to food varies (e.g., the existence of opportunistic and non-opportunistic species) suggests that there are complex interrelationships between trophic dynamics and reproductive biology that are poorly understood. However, recent comparative studies of gut morphology and kinematics of digestive processing indicate that species operate under different digestive constraints related to their respective feeding ecologies (Penry & Jumars 1990). For example in polychaetes, the guts of carnivorous species differ morphologically and functionally from those of deposit feeding species (Penry & Jumars 1990) with carnivorous species having significantly less gut volume than deposit-feeding species. The diet of carnivorous species also contains greater proportions of high quality foods (higher protein, lower in ratios of carbon to nitrogen). Food quality rather than quantity is probably limiting for deposit feeders and the diets of deep-sea deposit feeders are believed to be, on average, of lower quality than nearshore and shelf deposit feeders (Penry & Jumars 1990). Food quality also influences digestion time. For example, diatoms and other labile foods are digested rapidly and absorbed efficiently while "seaweed detritus" requires long residence times. "Lignin" and other refractory organic matter is never appreciably absorbed (Lopez & Levington 1987). Many deposit feeding, opportunistic species such as those in *Capitella, Armandia, Tharyx, Cirratulus, Chaetozone, Paraprionospio, Levinsenia,* and *Streblospio* have simple guts that may be relatively inexpensive to construct and maintain but, due to short throughput times, may limit them to inhabiting areas of organic enrichment in order to exploit higher quality foods to support their high rate of reproduction (Penry & Jumars 1990).

Species apparently differ with respect to their trophic transfer efficiency (net production/food supplied) (Tenore 1983), so it cannot be assumed that similar foods will be energetically processed to support egg production in the same way in different species. In crustaceans, for example, optimal dietary balance and the efficiency of utilization of dietary carbohydrates, lipids, and proteins vary widely among species (Harrison 1990). In polychaetes, food quality and particularly nitrogen content appear to regulate growth and reproduction (Gremare et al. 1988). Juvenile growth has been shown to be especially sensitive to food quality with different growth responses being observed in relation to spring vs. summer detritus (Marsh et al. 1989). When considering population dynamics, interspecific dietary requirements and digestive constraints must be factored because they ultimately influence reproduction and growth. If species show different reproductive responses to nutrients, then nutrient levels in different habitats will present strong selective pressures favoring one species over another. For example, organic enrichment can have a dramatic effect on community structure and population biology of shallow-water organisms by decreasing diversity and increasing the resulting dominance by rapidly-reproducing, opportunistic species (Levin et al. 1993). Individual responses to elevated food quantity and/or quality may include increases in fecundity, early age at first reproduction, and modified egg composition (Levin & Creed 1986, Marsh et al. 1989, Qian & Chia 1991). Notable respondents to these enrichments include *Capitella* spp., *Polydora ligni* and *Streblospio benedicti,* which brood their young, have very high reproductive rates (Levin & Huggett 1990) and utilize heterosynthetic mechanisms of yolk acquisition (Eckelbarger 1983).

Vitellogenic Mechanisms and Habitat Instability

Some species have adopted mechanisms for rapid egg production that appear to be less related to food levels than to a response to inherent habitat instability. For example, life history studies of barnacles have demonstrated that species behave opportunistically to exploit changing conditions in rigorous, unpredictable environments by rapidly increasing yolk accumulation in response to food levels (Hines 1979). The intertidal, reef-building polychaete *Phragmatopoma lapidosa* is an opportinistic species with early age of first reproduction, rapid and continuous egg production (Eckelbarger 1976) and unpredictable mortality due to storms and heavy wave action. Individuals are sexually mature soon after settling and are capable of spawning continuously. Oogenesis occurs in only two days and involves the transport of yolk precursors directly to the ovary via the circulatory system (Eckelbarger 1979) in a manner similar to that reported in the polychaete *Streblospio* (Eckelbarger 1980). Hydrothermal vent communities also represent ephemeral habitats whose age may be as short as 1–10 years (see Scheltema 1994). The fauna associated with these vents is largely unique and must mature and reproduce within a relatively short period of time so new active regions can be colonized. Recent studies of ovarian morphology and oogenesis in the vestimintiferan, *Riftia* sp. indicate that oocytes develop rapidly in close association with blood vessels (Gardiner et al. 1992) in a manner similar to some opportunistic polychaetes (e.g., *Streblospio*). Studies of vent-associated molluscs have shown that many species demonstrate life history traits that appear to be adaptive in this severe environment. Notable among these traits are rapid growth and continuous reproduction, which are probably related to a nutrient source that is relatively constant (Gustafson & Lutz 1994). Iteroparous molluscs that live longer and reproduce either intermittently or continuously throughout their reproductive life, tend to be found in more stable deep-sea environments (Scheltema 1994). Based on comparative studies of vitellogenesis, one would predict that unstable or unpredictable environments would select for species that mature early and reproduce rapidly using heterosynthetic mechanisms of egg production.

Vitellogenic Mechanisms, Food and Habitat Selection

If species convert food into egg production at different rates, one would expect that community structure would be influenced by temporal variation in food levels. Community level responses to variable organic input are much better known for near-shore populations than for the deep sea (Jumars & Wheatfcroft 1989). There has been a resurgent interest in benthic responses to temporal input of organic matter in the deep sea because of the growing realization that deep-sea organisms show a much higher frequency of seasonal reproduction than previously imagined, perhaps in response to environmental cues (Tyler et al. 1994). The relatively recent discovery of episodic inputs of significant organic food falls, plant material, and seasonal deposition of fresh phytodetritus on the deep-sea floor (see Scheltema 1994, for review) has stimulated great interest in determining whether benthic organisms show a reproductive response to these cues (Tyler et al. 1994). The deep-sea, wood-boring bivalve, *Xylophaga* sp., for example, shows an opportunistic life history by undergoing early sexual maturity, rapid egg reproduction, high population densities, and the ability to utilize a highly transient habitat (wood) similar to shallow water opportunistic species (Turner 1973). However, most deep-sea molluscs show no obvious coupling between seasonal periodicity of reproduction and primary productivity occurring at the ocean surface (Scheltema 1994). Scheltema (1994) suggests that seasonal differences in organic particulate flux may be largely irrelevant to many deep-sea molluscs except for filter feeders (e.g., Pectinidae), and possibly deposit-feeders that feed on the surface (e.g., protobranch bivalves). Omnivores, scavengers, and predators (i.e., majority of abyssal gastropods) may show little response to organic fluxes. Scheltema (1994) further suggests that other molluscs would only be secondarily affected. They include *Calyptogena* sp., a hydrothermal vent species harboring chemosynthetic bacteria, predatory or parasitic species affected directly by the relative abundance of their prey or host, and species that can derive much of their nutrition from dissolved organic materials in the pore-water of deep-sea sediments (Southward & Southward 1982). In a study of species pairs of deep-sea organisms, one being a quasi-continuous breeder and the other a seasonal breeder, Tyler and colleagues (1994) studied the effects of seasonal phytodetrital pulses on reproduction. Their results indicated that all the quasi-continuous breeders conformed to the pattern predicted by showing no seasonal variation in their diet while in seasonal breeders, the pattern of reproduction did not vary with the supply of phytodetritus from the surface. Although seasonal reproduction has been widely reported among deep-sea invertebrates, control of these cycles is not necessarily related to these surface-derived fluxes (Tyler et al. 1994).

Do species show different reproductive responses to differing temporal patterns of organic input? Some regions of the deep sea receive a steady rain of organic material while others receive seasonal pulses resulting from surface plankton blooms (reviewed in Gage & Tyler 1991). In a recent study of energy metabolism by deep-sea benthic foraminifera, it was determined that at least two survival strategies have evolved in this group that reflect individual physiological responses to this variable input of food. Based on turnover times of ATP, some suspension feeding species respond to conditions in which they receive a steady rain of organic particles by showing a reduced ATP turnover rate, while some scavenging species respond rapidly to sudden, seasonal nutrient inputs with large seasonal ATP turnover rates (Linke 1992). This study supports the notion that adaptation to nutritional conditions rather than mass properties or physical conditions are the sole controls over foraminiferal distribution. The author suggested that organisms will evolve different survival strategies depending upon whether they live in environments receiving seasonal food input, such as epibenthic species living in temperate and Arctic latitudes, or if they are species exposed to little seasonality in food supply, such as in oligotrophic regions of the ocean (Linke 1992). The downward vertical flux of surface phytodetritus has been viewed as a potential controlling factor in gametogenic cycles and recruitment of seasonally breeding species (Tyler et al. 1994).

It remains an enigma that two or more sympatric species can have different reproductive patterns under the same environmental conditions (Tyler et al. 1994). However, it is relatively common to find congeners in similar habitats with completely different life histories even though the causes are often difficult to determine (Spight 1979). This situation implies that reproductive patterns are attuning the organism to something other than the habitat itself. When viewed from the perspective of vitellogenesis, these differences could be explained by interspecific differences in vitellogenic mechanisms and the manner of nutrient cycling during oogenesis. Since species have very different capacities to respond to organic enrichment it should not be surprising that even closely related species will show different responses to the same food levels. Animals of similar feeding types might exploit different organic components in different ways and at varying rates within the same habitat. Thus organic pulses of surface phytodetritus may be utilized in different ways by individual deposit feeders (or other animals) resulting in different life history responses. Studies of deep sea communities suggest that the strategy of sequestering labile food material by rapid assimilation and population growth is most effective for small organisms with rapid growth rates. This strategy is documented only for bacteria, microfaunal, and meiofaunal populations whereas the evidence for effectively sequestering pulses of raining organic matter for common deposit feeders of intermediate size (between echiurans and meiofauna or the macro-infauna) is very circumstantial (Jumars et al. 1990). Since organic windfalls to the deep sea bottom are often unpredictable, it might explain why so many deep-sea populations contain individuals with only a few mature eggs at any given time (Rokop 1974, Gage & Tyler 1991) and the observation of a few juveniles present on average at any time (Grassle & Sanders 1973). Assuming that juvenile survival is highly variable, it would be useful for the adult to have many reproductive episodes with little energy and offspring invested in each (Jumars et al. 1990). As Jumars and his colleagues point out: "The relevant and unresolved issue for macrofaunal surface deposit feeders is whether these labile pulses are dominant, less important but still significant, or unimportant sources of the matter and energy shunted into production of this group of animals" (Jumars et al. 1990).

Echinoderms are among the most abundant macrofaunal organisms in the deep sea and their reproductive biology is better documented than for most invertebrate groups (Gage & Tyler 1991). Continuous reproduction in deep sea echinoderms is the most common pattern observed in the group but it involves the production of relatively few large eggs (Gage & Tyler 1991). Rapid and frequent egg production is rare in echinoderms, with the notable exception of the shallow water echinoid *Diadema* (Levitan 1988). Specialized heterosynthetic mechanisms for rapid yolk production have not been documented in the phylum and, thus far, vitellogenic mechanisms are highly conserved and of the "mixed" variety (Eckelbarger & Young 1992). Further, most echinoderms do not demonstrate abrupt reproductive responses to food levels. One would predict, therefore, that echinoderms would be well adapted to food conditions in the deep sea due to the prevalence of slow mechanisms of yolk synthesis characterizing the phylum. Seasonal cuing of organic pulses to reproduction are not likely to be strong because most species lack heterosynthetic pathways that would tightly couple nutrient input to egg production.

Table 1.—Some life history correlates of slow vs. fast egg producing species.

Fast egg producers	Intermediate	Slow egg producers
Heterosynthetic yolk production		"Mixed" (auto/heterosynthetic yolk production)
Relatively "r-selected"		Relatively "K-selected"
Small body size		Large body size
High food input		Low or seasonal food input
Low food reserve storage		High food reserve storage
Variable/unpredictable environments		Stable predictable environments
Short-lived		Long-lived
Low fecundity		High fecundity
Early sexual maturity		Late sexual maturity
High brood frequency		Low brood frequency

Conclusion

Efforts to comprehend the evolutionary forces that have shaped metazoan life history patterns must consider the role played by the ovary and the diverse mechanisms of yolk synthesis that have arisen through selection. Species have different capacities for converting food into egg production resulting in wide variation in the interval between reproductive episodes. These varying capacities are strongly influenced by the rate at which developing oocytes can synthesize yolk during oogenesis. Some species living in environments that are inherently unstable or experience sudden, large scale food inputs have evolved specialized mechanisms of yolk synthesis that enable them to respond to sudden nutrient input through rapid egg production. Other species, particularly long-lived iteroparous species, utilize slower methods of egg production and are adapted to stable environments that have seasonal or steady (predictable) inputs of nutrients. Therefore, vitellogenic mechanisms should play a central role in determining optimal species success in any given habitat based on differential reproductive responses to nutrients. In order to avoid simplistic life history models, the complex coupling between habitat, food, feeding strategies, digestive constraints, and vitellogenic mechanisms must be better understood in order to appreciate observed differences in marine community structure. Table 1 lists some life history features that correlate with slow and fast egg-producing species.

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INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

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Applications published in the *Bulletin of Zoological Nomenclature*

The following Applications were published on 30 September 1993 in Vol. 50, Part 3 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.

2854 *Robulina nodosa* Reuss, 1863 (currently *Lenticulina nodosa*; Foraminiferida): proposed retention of neotype despite rediscovery of syntypes.

2855 *Cristellaria humilis* Reuss, 1863 (currently *Astacolus humilis*; Foraminiferida): proposed replacement of neotype by rediscovered lectotype, and *Rotalia schloenbachi* (currently *Notoplanulina*? *schloenbachi*; Foraminiferida): proposed placement on the Official List.

2871 *Helix nitidula* Draparnaud, 1805 and *H. nitens* Michaud, 1831 (currently *Aegopinella nitidula* and *A. nitens*; Mollusca, Gastropoda): proposed conservation of the specific names and designation of a neotype for *H. nitidula.*

2860 *Pleurotoma meneghinii* Mayer, 1868 (currently *Asthenotoma meneghinii*; Mollusca, Gastropoda): proposed replacement of neotype by rediscovered lectotype.

2841 *Platynectes* Régimbart, 1879 (Insecta, Coleoptera): proposed conservation.

2880 *Polycentrus schomburgkii* Müller & Troschel, 1848 (Osteichthyes, Perciformes): proposed conservation of the specific name.

2868 *Hydromantes* Gistel, 1848 (Amphibia, Caudata): proposed designation of *Salamandra genei* Temminck & Schlegel, 1838 as the type species.

2873 *Emys* Duméril, 1806 (Reptilia, Testudines): proposed conservation.

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 30 September 1993 in Vol. 50, Part 3 of the *Bulletin of Zoological Nomenclature.* Copies of these Opinions can be obtained free of charge from the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Opinion No.

1738. *Mopsea* Lamouroux, 1816 (Cnidaria, Anthozoa): *Isis encrinula* Lamarck, 1815 designated as the type species.
1739. *Strombiformis albus* Da Costa, 1778 (currently *Melanella* (*Balcis*) *alba*; Mollusca, Gastropoda): specific name conserved.
1740. *Amicytheridea* Bate, 1975 (Crustacea, Ostracoda): *A. triangulata* Bate, 1975 designated as the type species.
1741. *Gerris paludum* Fabricius, 1794 (currently *Aquarius paludum*; Insecta, Heteroptera): specific name conserved.
1742. *Lincus* Stål, 1867 (Insecta, Heteroptera): conserved; *L. croupius* Rolston, 1983: specific name not conserved.
1743. TACHINIDAE Fleming, 1821 (Insecta, Coleoptera): spelling emended to TACHINUSIDAE to remove homonymy with TACHINIDAE Robineau-Desvoidy, 1830 (Insecta, Diptera), and TACHYPORIDAE MacLeay, 1825 (Insecta, Coleoptera): given precedence over TACHINUSIDAE Fleming, 1821.
1744. *Cheilosia* Meigen, 1822 and *Pyrophaena* Schiner, 1860 (Insecta, Diptera): conserved.
1745. *Copromyza limosa* Fallén, 1820 (currently *Leptocera* (*Rachispoda*) *limosa*; Insecta, Diptera): lectotype replaced, so conserving the usage of the specific name and also that of *Leptocera* (*Rachispoda*) *lutosa* (Stenhammar, 1855).
1746. *Drosophila putrida* Sturtevant, 1916 (Insecta, Diptera): holotype replaced by a neotype.
1747. *Eristalis* Latreille, 1804, *Helophilus* Fabricius, 1805, *Xylota* Meigen, 1822 and *Eumerus* Meigen, 1822 (Insecta; Diptera): conserved.
1748. EPHYDRIDAE Zetterstedt, 1837 (Insecta, Diptera): given precedence over GYMNOMYZIDAE Latreille, 1829.
1749. *Epicrium* Wagler, 1828 and ICHTHYOPHIIDAE Taylor, 1968 (Amphibia, Gymnophiona): conserved, and EPICRIIDAE Berlese, 1885 (Arachnida, Acari): conserved by the emendation of EPICRIIDAE Fitzinger, 1843 (Amphibia, Gymnophiona) to EPICRIUMIDAE.

INFORMATION FOR CONTRIBUTORS

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PROCEEDINGS

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THREE NEW SPECIES OF CILIATE IN THE GENERA *PSEUDOCOHNILEMBUS, PLEURONEMA,* AND *UROTRICHA* (CILIOPHORA)

Gregorio Fernandez-Leborans and Apolonia Novillo

Abstract.—The morphological and biometric characteristics are given for three new species of freshwater ciliates: two of them belonging to the order Scuticociliatida (*Pseudocohnilembus fluviatilis* and *Pleuronema ovata*) and one to the order Prorodontida (*Urotricha rotunda*). *P. fluviatilis* is especially distinguished by the presence of an inner oral membrane consisting of six clearly differentiated kinetosomal segments. *P. ovata* shows a reduced oral infraciliature with an anterior membrane and two posterior membranoid segments, as well as a paroral membrane. In this species, there is an area in "V," located near the posterior pole, where several dorsal kineties converge. *U. rotunda* is characterized by the number and composition of the caudal kinetosomic groups and of the brush kineties. The taxonomic placement of these species is discussed.

A number of species in the genera *Pseudocohnilembus* and *Pleuronema* have been described. Apart from the outstanding work of Evans & Thompson (1964) and Thompson (1966a, 1966b) on *Pseudocohnilembus* further, more recent, descriptions have been made, including those of Foissner & Wilbert (1981), Fernandez-Leborans & Castro de Zaldumbide (1984) and Foissner (1985). Morphogenesis within this genus has been dealt with by Evans & Corliss (1964) and Fernandez-Leborans & Castro de Zaldumbide (1986a). Dragesco (1960, 1968) presented some early descriptions of silver-stained *Pleuronema* material, followed more recently by Dragesco & Dragesco-Kernéis (1986), Agamaliev (1983), Grolière & Detcheva (1974), and Small & Antipa (*Pleurocoptes,* 1978). Dragesco (1960), Foissner (1979, 1983, 1984), Alekperov (1983), Pätsch (1974), Martin-Gonzalez et al. (1985) and Muñoz et al. (1987, 1989) provided descriptions of various species in the genus *Urotricha.*

Throughout these studies the morphological and morphogenetic features of various species in these genera have been described, a noticeable evolution having been observed with respect to the significance of certain structures, such as the infraciliature of *Urotricha* (Muñoz et al. 1989). On the other hand, the number of new species described has been slowly increasing, due to the contributions of Martin-Gonzalez et al. (1985) (*U. vitrea*), Muñoz et al. (1987) (*U. nais*), Muñoz et al. (1989) (*U. ondina*) and Song & Wilbert (1989) (*U. corlissiana* and *U. valida*), and it would be necessary to carry out a comparative analysis of the known species and then determine which characteristics and which order of biometric variability, serve to differentiate the species. In addition, further biometric and statistical studies of each species are necessary, their scarcity contrasting greatly with the large number of morphological descriptions. These aspects, among others, are considered here.

Methods

The samples containing the ciliates studied were collected from three areas from the

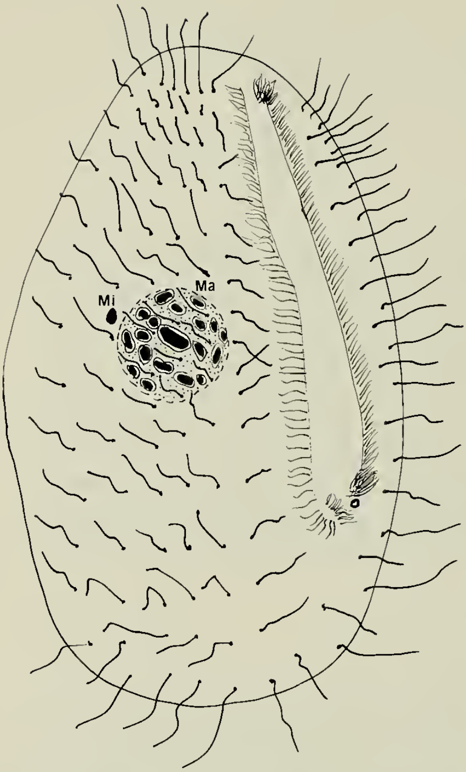


Fig. 1. *Pseudocohnilembus fluviatilis.* General view showing the cilia and the nuclear components.

outskirts of Madrid (Spain). *Pseudocohnilembus* species were found in samples from the Navacerrada reservoir (48 km, NW of Madrid, 4°00′W, 40°45′N); *Pleuronema* species were found in the Guadarrama river at the village of Villalba (4°00′W, 40°35′N, 39 km of Madrid); *Urotricha* species were collected in the reservoir at La Jarosa (60 km of Madrid, 4°10′W, 40°12′N). The ciliates were fixed with 2% OsO4 to preserve them for general biometric measurements. Some of each samples were stained with the silver carbonate impregnation technique (Fernandez-Leborans & Castro de Zaldumbide 1986b) in order to obtain permanent slides and photomicrographs. The statistical treatment of the biometric data was carried out using the Statgraphics program. The terminology used in the different descriptions corresponds to that defined by Lynn (1988).

Results

Pseudocohnilembus species

General morphology.—The ciliates are oval in shape, 33–36.2 μm in length and 24–27 μm in width. They have a spherical or slightly oval macronucleus with a length of 12.6–14.4 μm and a width of 10.8–13.7 μm and a single spherical micronucleus, 3–3.8 μm in diameter (Fig. 1, Table 1).

Somatic infraciliature.—There are 8 ventral kinetics, each one possesses 15–17 pairs of kinetosomes. On the dorsal side there are 8–9 kineties, each with 15–16 pairs of kinetosomes. Each pair of kinetosomes of the somatic kineties show three types of derivatives: 1) an anterior one extends from the right kinetosome of each pair towards the anterior right area of the ciliate (kinetodesmal fibril) and is 1.51–1.61 μm in length; 2) a posterior one extends from the right kinetosome of each pair towards the posterior right area of the ciliate (postciliary microtubules) and is 0.66–0.72 μm in length; and 3) a derivative extends from the left kinetosome of each pair to the anterior left area of the ciliate (transverse microtubules) and is 0.48–0.51 μm in length (Figs. 2, 3 and 4; Table 1).

Oral infraciliature.—The oral area extends from near the anterior pole of the ciliate to ⅔ of the body length. The undulating membrane or paroral formation (PF, Fig. 2) is 16.8–18.5 μm in length; its posterior end is 11.88–13.2 μm from the posterior pole and 24.6–25.8 μm from the anterior pole of the ciliate. It is made up of 54–56 dikinetids that curve round in the posterior area near the cytostome.

On the left side of the oral area is located the inner membrane (IM) consisting of six kinetidal structures that are described in order, from the anterior pole of the ciliate. 1) *a1* is a group of 8–9 kinetosomes, 1.2–1.4 μm long and about 1.6 μm wide. 2) *a2* is a

Table 1.—Biometric characteristics of *Pseudocohnilembus fluviatilis.*

	Arithmetic mean	Standard deviation	Standard error	Coefficient of variation	Pearson coefficient	Minimum	Maximum	Observations
Length	34.80	0.78	0.08	2.24	−0.25	33	36.2	80
Width	25.53	0.83	0.09	3.25	0.63	24	27	80
Length of the macronucleus	13.40	0.59	0.06	4.40	0.67	12.6	14.4	80
Width of the macronucleus	11.89	0.78	0.08	6.56	−0.39	10.8	13.7	80
Diameter of the micronucleus	3.39	0.22	0.02	6.48	−0.44	3	3.78	80
Number of ventral kineties	8.00	0.00	0.00	0.00	0.00	8	8	80
Number of dorsal kineties	8.33	0.49	0.05	5.88	0.67	8	9	80
Length of the paroral formation	17.36	0.51	0.05	2.93	0.31	16.8	18.5	80
Length of a1 (inner membrane)	1.25	0.04	0.00	3.20	0.71	1.2	1.35	80
Width of a1	1.58	0.01	0.00	0.63	0.31	1.56	1.62	80
Length of a2 (inner membrane)	9.84	0.15	0.01	1.52	0.29	9.6	10.1	80
Length of a3 (inner membrane)	1.11	0.03	0.00	2.70	0.66	1.08	1.2	80
Width of a3	0.71	0.04	0.00	5.63	0.25	0.6	0.82	80
Length of a4 (inner membrane)	3.37	0.01	0.00	0.41	−0.69	3.36	3.4	80
Width of a4	1.08	0.01	0.00	0.92	0.33	1.07	1.13	80
Length of a5 (inner membrane)	4.20	0.09	0.01	2.14	0.04	4.14	4.5	80
Width of a5	1.17	0.02	0.00	1.70	0.45	1.13	1.21	80
Length of a6 (inner membrane)	4.28	0.17	0.01	3.97	0.47	4.18	4.82	80
Width of a6	0.82	0.04	0.00	4.87	0.48	0.78	0.92	80
Distance posterior end of paroral–anterior pole	25.03	0.30	0.03	1.19	0.12	24.6	25.8	80
Distance posterior end of paroral–posterior pole	12.18	0.43	0.04	3.53	0.18	11.88	13.2	80
Distance a5–anterior pole	21.00	0.65	0.07	3.09	−0.14	20.1	22.8	80
Distance a5–posterior pole	14.96	0.24	0.02	1.60	0.65	14.7	15.6	80
Number of kinetosomes of the paroral	54.50	0.79	0.08	1.44	0.63	54	56	80
Number of kinetosomes of a1	8.16	0.38	0.04	4.65	0.42	8	9	80
Number of kinetosomes of a2	36.66	0.98	0.10	2.67	0.67	36	38	80
Number of kinetosomes of a3	5.16	0.38	0.04	7.36	0.42	5	6	80
Number of kinetosomes of a4	8.83	0.93	0.10	10.53	0.89	8	10	80
Number of kinetosomes of a5	10.50	0.79	0.08	7.52	0.63	10	12	80
Number of kinetosomes of a6	14.66	0.88	0.09	6.00	0.75	14	16	80
Number of kinetosome pairs of the ventral kineties	15.58	0.79	0.08	5.07	0.73	15	17	80
Number of kinetosome pairs of the dorsal kineties	15.33	0.49	0.05	3.19	0.67	15	16	80
Length of the somatic kinetodesmic fiber	1.58	0.01	0.00	0.63	0.63	1.51	1.61	80
Length of the somatic transverse microtubules	0.48	0.01	0.00	2.08	0.84	0.48	0.51	80
Length of the somatic postciliary microtubules	0.67	0.02	0.00	31.34	0.84	0.66	0.72	80

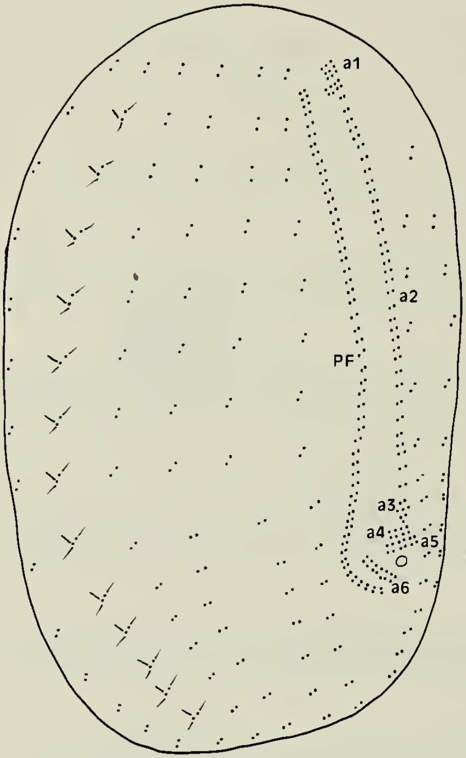
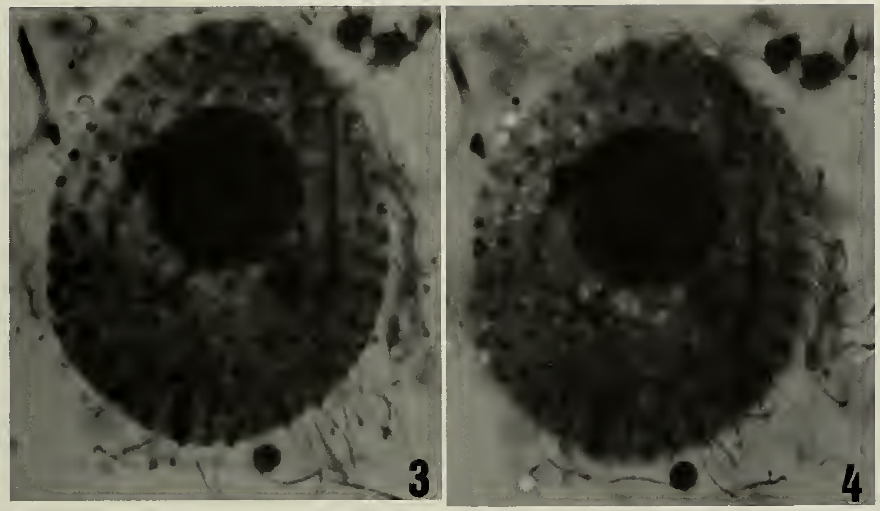


Fig. 2. *Pseudocohnilembus fluviatilis.* Ventral side. PF: paroral formation or outer membrane. a1, a2, a3, a4, a5 and a6: the different elements of the inner membrane.

double row of kinetosomes made up of a linear portion of 30 kinetosomes accompanied in its anterior part by a group of 6–8 kinetosomes. *a2* is about 10 μm long. 3) Slightly separated from *a2, a3* is a triangular group of 5–6 kinetosomes, about 1.1 μm × 0.7 μm in size. Behind *a3,* there are two polykinetids running more or less transversally to the anterio-posterior axis of the ciliate. The more anterior, *a4,* has a length of about 3.4 μm and a width of about 1.1 μm and is made up of 8–10 kinetosomes in two rows. The more posterior, *a5,* is just anterior to the cytosome and is slightly larger than *a4*: about 4.2 μm in length × about 1.2 μm in width. It has 10–12 kinetosomes in two rows. Posterior to the cytostome and parallel to the posterior portion of the paroral, there is a group of 14–16 kinetosomes (*a6*) in two rows, which has a length of 4.2–4.8 μm and a width of about 0.8 μm. In a number of specimens, a pair of kinetosomes were observed posterior to *a6,* and correspond to the scutica (Figs. 2 and 3; Table 1).

Taxonomic position.—These ciliates belong to the class Oligohymenophorea de Puytorac et al. 1974, order Scuticociliatida Small 1967, Family Pseudocohnilembidae Evans & Thompson 1964, genus *Pseudocohnilembus* Evans & Thompson 1964 (Small & Lynn 1985, Corliss 1979, Small 1967, Evans & Thompson 1964). There are 10 species that are most similar to the ciliates studied: *Pseudocohnilembus persalinus* Evans & Thompson 1964; *P. hargisi* Evans & Thompson 1964; *P. longisetus* Evans & Thompson 1964; *P. cantabricus* Fernandez-Leborans & Castro de Zaldumbide 1984; *P. antoniensis* Fernandez-Leborans & Castro de Zaldumbide 1986; *P. portuensis* Fernandez-Leborans & Castro de Zaldumbide 1986; *P. marinus* Thompson 1966 (Foissner & Wilbert 1981); *P. putrinus* Foissner & Wilbert 1981; *P. pusillus* Foissner & Wilbert 1981; *P. caeci* Foissner 1985. These species have been compared with the ciliates studied in the following characteristics: 1, body length; 2, body width; 3, size of macronucleus; 4, number of somatic kineties; 5, number of kinetosomes in each somatic kinety; 6, arrangement of the somatic kinetosomes; 7, derivatives of somatic kinetosomes; 8, size of the oral area; 9, kinetosomal structure of the paroral formation; 10; kinetosomal structure of the inner membrane; and 11, habitat (Table 2). Finding that our specimens (not taking into account the habitat), differ respect *P. persalinus* in 7; *P. hargisi* in 9; *P. longisetus* in 8; *P. cantabricus* in 4; *P. antoniensis* in 7; *P. portuensis* in 7; *P. marinus* in 5; *P. putrinus* in 8; *P. pusillus* in 6; and *P. caeci* in 6 characteristics of the 10 analyzed (Table 2). The size of the body is found in the range of *P. hargisi, P. cantabricus* and *P. marinus.*



Figs. 3–4. 3, *Pseudocohnilembus fluviatilis.* Ventral side, the cilia, nuclear components and infraciliature can be seen (× 1640). 4, Dorsal side (× 1640).

The macronucleus is similar in size to the *P. cantabricus, P. portuensis* and the *P. caeci.* The kinetosomes of the somatic kineties are grouped in pairs as in *P. antoniensis* and *P. portuensis,* while in *P. marinus, P. putrinus, P. pusillus,* the somatic kinetosomes are only in pairs in a part of the total length of the somatic kinety. The oral area takes up ⅔ of the body length of our specimens as in *P. cantabricus,* while in the other species it only takes up ½ or ⅓ of the body length. Regarding the oral infraciliature there are two diplostichomonads, which are only present in *P. antoniensis,* but while this species only shows a small group of 6–8 kinetosomes near the posterior end of the shortest diplostichomonad (IM), in our specimens there are five groups of kinetosomes, two anterior and two posterior of the IM (inner membrane: kinetosomic structures of the left side of the oral area), and a short double row of kinetosomes near the posterior end of the paroral formation. Taking into account these data, and especially, the number of differences from the other species, the ciliates observed could correspond to a new species, which we have named *Pseudocohnilembus fluviatilis.* On the other hand, and taking into account the variability margins and the principal morphological characteristics, various species described could be put into one group. This is the case of *P. persalinus, P. marinus, P. pusillus, P. longisetus* and *P. putrinus* which have no fundamental differences and could be classified together as *P. persalinus,* the first one to be described. They all have a similar size, number of somatic kineties and structure of oral infraciliature (Table 2).

Note.—Foissner (1985) points out that *P. cantabricus* is a synonym for *P. marinus* redescribed by Foissner & Wilbert (1981). However, we differ in this opinion, above all when we analyze in detail both works (Foissner & Wilbert 1981, Fernandez-Leborans & Castro de Zaldumbide 1984): the redescription by Foissner & Wilbert (1981) is very brief and contains very little biometric data or explanations about the somatic and oral infraciliature of *P. marinus.* But, above all, there are two fundamental features that differentiate the two species. First, the somatic kineties of *P. cantabricus* are each made up of a single row of 20 monokinetids, each one of these has a clearly visible kinetodesmal fibril. In contrast,

Table 2.—Comparison between the species of *Pseudocohnilembus*. (P, pairs; s, single; st, stichomonad; sd, stichodyad; dt, diplostichomonad; Th, Thompson 1966; gk, group of kinetosomes; kd, kinetodesmic fiber; mt, transverse microtubules; mp, postciliar microtubules; m, marine; f, freshwater; s, saline; sl, soil; ec, ectoparasite; bl, body length.)

	P. persalinus	*P. hargisi*	*P. longisetus*	*P. cantabricus*
Length (μm)	30	44	26.6	34.8–40.8
Width (μm)	14	18	11.5	22.8–25.8
Size of the macronucleus (μm)	4.5	4.2–6.7	3.7	13.2–20.4 × 12–17.4
Number of somatic kineties	8–9	14	11	10 (12)
Kinetosomes in each somatic kinety	20	27	16	20
Arrangement of somatic kinetosomes	st	st	st	st
Derivatives of somatic kinetosomes	—	—	—	kd
Size of oral area relative to body	½ bl	½ bl	½ bl	⅔ bl
length		21.8	12.8	21–25.2 × 3.6–4.2
Structure of paroral formation (PF)	sd	sd	sd	dt + sd
Structure of the inner membrane	sd (⅘ PF)	sd (=PF)	sd (=PF)	—
Habitat	s	s	m	m

the kineties of *P. marinus* (Foissner & Wilbert 1981) are each made up of dikinetids for the majority of their length. The number of dikinetids in the dorsal kineties, 17–19, makes the total number of kinetosomes in each kinety much greater, 31–35, than in *P. cantabricus*. Second, the oral infraciliature of *P. cantabricus* is composed of one single paroral membrane with two different segments, the anterior one being greater in length, made 39–40 dikinetids, and a posterior segment of 12 dikinetids in zig-zag formation. In *P. marinus* (Foissner & Wilbert 1981), the oral infraciliature is composed of two membranes that show the kinetosomes in zig-zag formation, the shorter (inner membrane) with a posterior kinetosomal group. It is evident taking these differences into account, that we are not dealing with the same species, as Foissner (1985) indicates.

Pseudocohnilembus fluviatilis, new species

Diagnosis.—Rounded, oval in shape, of 33–36 μm in length and 24–27 μm in width. A spherical or oval macronucleus of 12.6–14.4 μm × 10.8–13.7 μm with an adjacent micronucleus of 3–3.8 μm of diameter. Eight ventral kineties and 8–9 somatic dorsal kineties, each with 15–17 dikinetids. The oral area with a paroral formation, which is 16.8–18.5 μm in length with a short polykinetid of two rows near its posterior end and, on the left side, a linear polykinetid (inner membrane) of 14–14.9 μm in length with two small polykinetids anterior and two posterior. Freshwater.

Pleuronema species

General morphology.—Ciliates, oval in appearance, of 70.8–82.8 μm in length and 53.4–60.6 μm in width. A rounded macronucleus is usually located in the anterior half of the body, 15.6–21.2 μm long and 15.9–20.1 μm wide. There are two spherical micronuclei 2.3–2.5 μm in diameter located beside the macronucleus. (Fig. 5; Table 3).

Somatic infraciliature.—There are 29–31 somatic kineties, of which 15–16 are ventral and 14–15 are dorsal. The majority of the kineties are bipolar, except for 6 dorsal kineties and 5–6 ventral kineties. The shortest ventral kineties are found anterior and left of the posterior of the oral area. They have a length of 42–46.8 μm and are made up

Table 2—Extended.

P. antoniensis	*P. portuensis*	*P. marinus*	*P. putrinus*	*P. pusillus*	*P. caeci*	*P. fluviatilis*
12.9–16.5	18.6–24.9	32–36	17–27	25–42	59–105	33–36.2
10–13.5	11.8–17.7	20–22	6.6–14.6	12–26	22–42	24–27
5.8–8.4 × 2.7–4.9	7.2–12.6	10.5–11 × 9.3–10	4–8 × 4–6.6	5–8 × 5–8.1	10–14 × 8–14	12.6–14.4 × 10.8–13.7
10	10	8–9 (10 Th)	10	10–11	10–14	16–17
12–18 p	18–20 p	29–33 p + 5–8 s	14–17 p + s	15–23 p + s	33–46 p + s	15–17 p
sd	sd	sd + st (st Th)	sd + st	sd + st	sd + st	sd
kd	kd, mt, mp	—	—	—	—	kd, mt, mp
½ bl	½ bl	½ bl	½ bl	½ bl	⅓ bl	⅔ bl
9.15–11.4						
dt	st + sd	sd + gk (st Th)	sd	sd	sd + st	dt + dt
dt + 6–8 k	—	sd (st Th)	sd	sd	sd + st	2 gk + dt + 3 gk
m	m	f (m Th)	sl	f	m (ec)	f

of 22–26 dikinetids. The shortest dorsal kineties are found between the anterior pole and an area in the left posterior region where various kineties converge in a "V" shaped suture. In the center of this area, there are two parallel kineties (4 and 5) (somatic kinety 1 is situated on the right of the oral infraciliature) of 53.1–54 μm in length and 38–40 dikinetids each. Lateral to these two kineties another two are found (3 and 6) that converge beneath the posterior end of the previous two; they have 42–44 dikinetids each. Lateral to these last two kineties (3 and 6) are another two (7 and 2) that also converge posteriorly and have 46–48 dikinetids each. The remaining somatic kineties have 50–54 dikinetids each. In each pair of somatic kinetosomes, the one on the right has a thick derivative that runs from the kinetosome to the right anterior area of the ciliate (kinetodesmal fiber) and is 1.8–3 μm long. There is a fibrillar net that circles and accompanies the pairs of somatic kinetosomes (Figs. 6–9; Table 3).

The oral infraciliature.—The oral area takes up a large part (51–57 μm) of the total length of the individual and is composed of three kinetosomal structures: 1) the paroral formation (PF); 2) membrane 1 (M1) and 3) the pericytostomal structures (oral formation, OF).

The paroral formation (PF) has a length of 39.6–45 μm and is longitudinally located on the left side of the oral area. The anterior end of this structure is 21.3–23.2 μm from he anterior pole and is 60.6–62.8 μm from the posterior pole. The posterior end of the paroral is found near the anterior area of the oral formation (OF). This structure is made up of 140–144 dikinetids. Accompanying the paroral formation there is a fiber that runs parallel to this structure for its whole length and extends posteriorly, having a length of 45–50.4 μm (subparoral fiber, SPF). Paroral dikinetids connect by means of fine prolongations (a) with the subparoral fiber.

M1 is found near the anterior end of the paroral formation with its posterior end slightly separated from this structure. It is 5.94–8.4 μm and is made up of 24–38 kinetosomes grouped in pairs (12–19 dikinetids).

The oral formation (OF) is in the posterior oral area, encircling the cytostome. This structure is divided into two parts: one longer one made up of a single row of 60–70 kinetosomes (stichomonad), M2, and an-

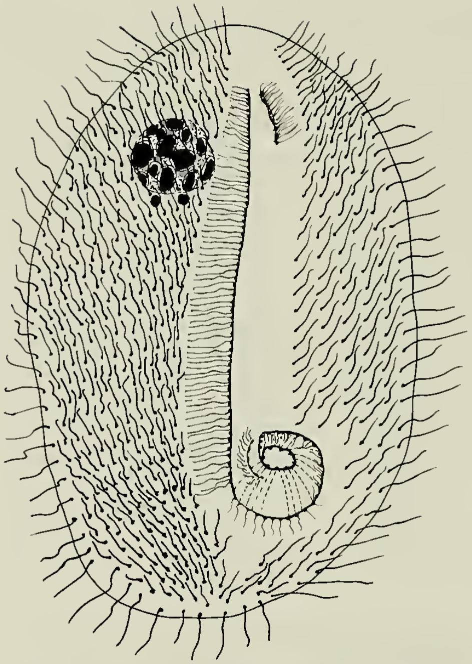


Fig. 5. General view of *Pleuronema ovata* showing the cilia and nuclear components.

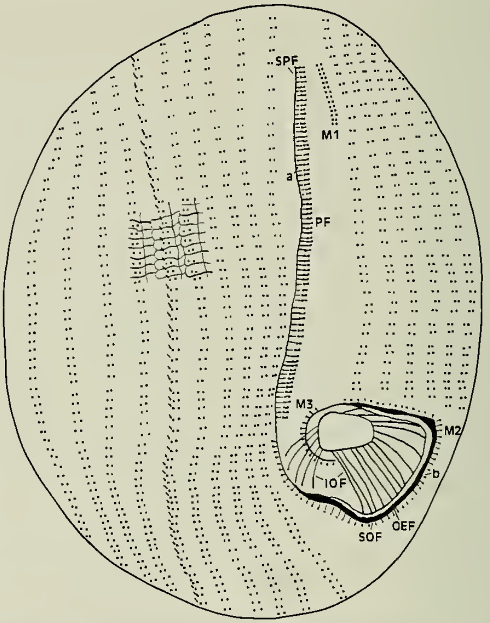


Fig. 6. *Pleuronema ovata.* Ventral side. SPF: subparoral fiber; a: fibrillar connections between the paroral formation (PF) and the SPF; IOF: intermediate oral fibers; OEF: oral external fiber; b: fibrillar connections between the OEF and the M2; SOF: suboral fiber.

other shorter one separated of the anterior for a zone without kinetosomes, found on top of the corresponding cytostome area, and made up of a single row (stichomonad) of 12–16 kinetosomes (M3). Parallel to the oral formation is a thick fibrous structure called the *suboral fiber* (SOF), which forms fine connections (b) with each of the kinetosomes of the oral formation. The suboral fiber is 45–48.6 μm long and connects up with the subparoral fiber.

The oral formation circles a fibrous group (ribbed field, Small, 1967) that is constituted of various structures. First, a closed fibrillar structure, more or less circular, immediately defines the entrance to the cytostome, and is called oral inner fiber (OIF). It is 3.4–5.2 μm in length. Second, an open fibrillar structure, the external oral fiber (OEF), runs parallel to and accompanies the suboral fiber along part of its length. It is 36.8–38.5 μm long. Third, between the oral inner fiber and the external oral fiber there is a group of fibers called intermediate oral fibers (IOF). Some of these fibers (4–6) are connected to an oral inner fiber by one end while the other end remains free in the oral cavity; these fibers measure 1.8–3.6 μm. The remaining fibers (10–14) have as much connection with the oral internal fiber as with the external oral fiber, and are 9–12 μm long (Figs. 6 and 8; Table 3).

Taxonomic position. —The specimens studied belong to class Oligohymenophorea De Puytorac et al. 1974, order Scuticociliatida Small 1967, suborder Pleuronematina Fauré-Fremiet in Corliss 1956, family Pleuronematidae Kent 1881, genus *Pleuronema* Dujardin 1836 (Small & Lynn 1985; Corliss 1979; Small 1967; Grolière & Detcheva 1974; Small & Antipa 1978; Dragesco 1960, 1968; Dragesco & Dragesco-Kernéis 1986; Agamaliev 1983). The structural simplicity of the oral infraciliature of these individuals

Table 3.—Biometric data of *Pleuronema ovata.*

	Arithmetic mean	Standard deviation	Standard error	Coefficient of variation	Pearson coefficient	Minimum	Maximum	Observations
Length	77.3	3.05	0.34	3.94	−0.22	70.8	82.8	80
Width	56.26	1.93	0.21	3.43	0.65	53.4	60.6	80
Length of the macronucleus	18.46	1.56	0.17	8.45	0.29	15.6	21.24	80
Width of the macronucleus	18.18	1.15	0.12	6.32	0.67	15.9	20.16	80
Diameter of the micronuclei	2.41	0.05	0.00	2.07	0.20	2.34	2.52	80
Length of paroral formation	43.15	1.27	0.14	2.94	0.11	39.6	45	80
Length of the M1	7.09	0.61	0.06	8.60	−0.50	5.94	8.4	80
Length of the oral internal fiber zone	4.55	0.60	0.06	13.18	−0.41	3.4	5.2	80
Width of the oral internal fiber zone	5.19	0.82	0.09	12.90	−1.02	4.1	6.3	80
Length of the oral external fiber	37.68	0.57	0.06	1.51	−0.21	36.8	38.5	80
Number of kinetosomes of M1	29.87	4.51	0.50	15.09	0.85	24	38	80
Number of kinetosomes of paroral formation	142	1.34	0.14	0.94	0.00	140	144	80
Number of kinetosomes of the oral formation	78.91	1.62	0.18	2.05	−0.05	76	82	80
Length of subparoral fiber	47.06	1.29	0.14	2.74	0.04	45	50.4	80
Numer of somatic kineties	30	0.60	0.06	2	0	29	31	80
Length of suboral fiber	46.96	1.12	0.12	2.38	0.85	45	48.6	80
Number of kinetosome pairs of each ventral kinety	55.16	1.69	0.18	3.06	0.09	52	58	80
Kinetosome pairs of dorsal kineties 4 and 5	38.91	0.66	0.07	1.69	−0.13	38	40	80
Length of dorsal kineties 4 and 5	53.67	0.31	0.03	0.57	0.87	53.1	54	80
Kinetosome pairs of dorsal kineties 3 and 6	43	0.73	0.08	1.69	0.00	42	44	80
Kinetosome pairs of dorsal kineties 2 and 7	46.83	0.71	0.07	1.51	−0.23	46	48	80
Kinetosome pairs of the rest of dorsal kineties	52.33	1.15	0.12	2.19	0.28	50	54	80
Distance anterior end of paroral formation–anterior pole	22.42	0.53	0.05	2.36	0.03	21.3	23.2	80
Distance anterior end of paroral formation–posterior pole	61.59	0.63	0.07	1.02	−0.33	60.6	62.8	80
Distance anterior end of oral internal fiber–anterior pole	49.38	1.14	0.12	2.30	0.15	47.6	52.2	80
Distance posterior end of oral internal fiber–anterior pole	30.44	0.93	0.10	3.05	−0.17	28.6	32.1	80
Distance anterior end of oral formation–anterior pole	48.85	1.13	0.12	2.31	0.22	46.8	51	80
Distance posterior end of oral formation–posterior pole	16.78	0.93	0.10	5.54	0.62	15.1	18.3	80

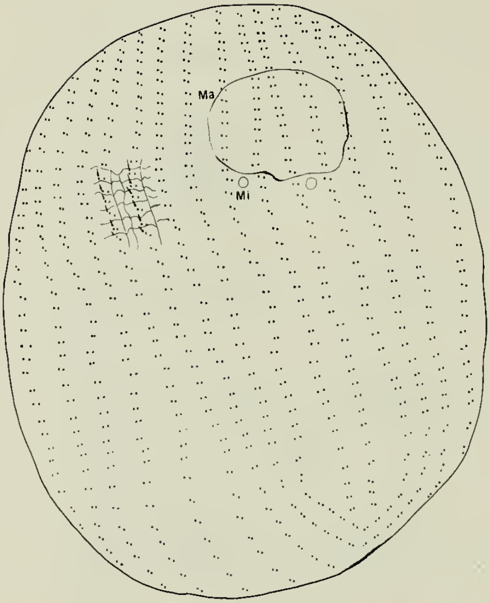
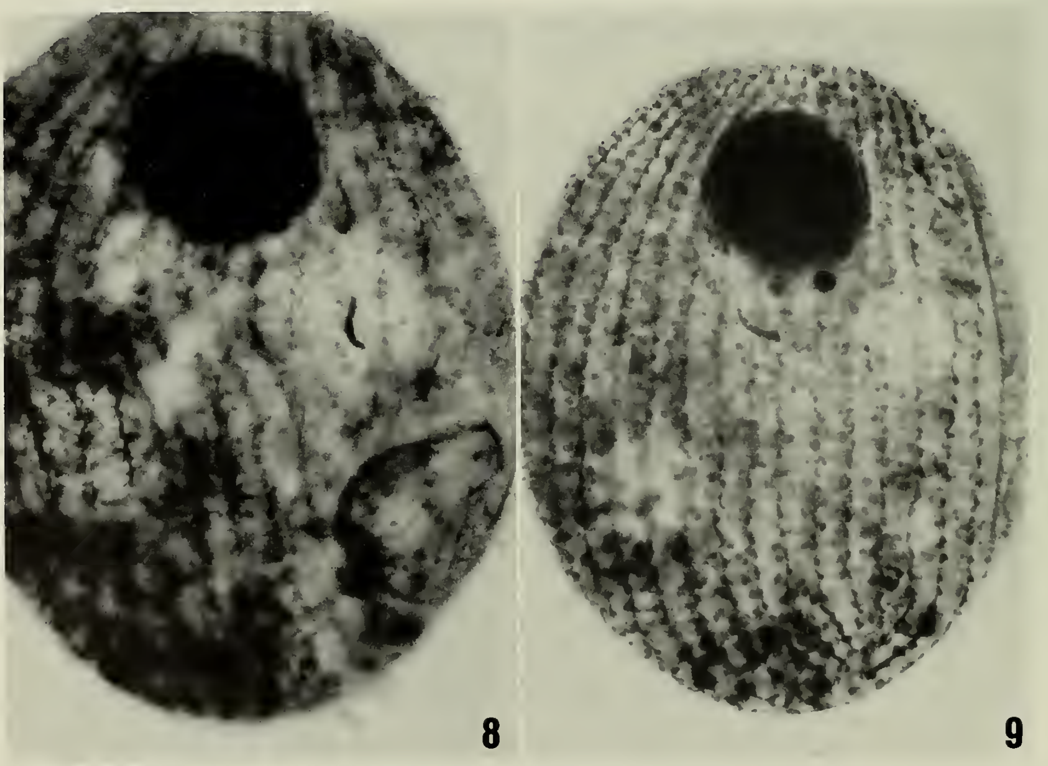


Fig. 7. *Pleuronema ovata.* Dorsal side showing the nuclear arrangement and the "V" area near the posterior end of the ciliate.

makes it unnecessary to compare, from biometric point of view, this *Pleuronema* species with those previously described, which undoubtedly have a greater kinetosomal complexity, particularly in the posterior zone of the oral area. Taking into account the published data (indicated above), these ciliates can be placed in the *Pleuronema simplex* species (Dragesco 1960), which is the one that shows a greater reduction of the oral infraciliature. However, our specimens lack the posterior segment of M2 (Dragesco & Dragesco-Kernéis 1986), although it is somewhat reduced in *Pleuronema simplex.* Furthermore, this species is from a marine habitat, while the Spanish population is from freshwater. Thus, a new species is proposed, *Pleuronema ovata.*

Pleuronema ovata, new species

Diagnosis.—Oval-shaped ciliates, 70.8–82.8 μm long and 53.4–60.6 μm wide.



Figs. 8–9. *Pleuronema ovata.* 8, Ventral side of a stained specimen (× 1510). 9, Dorsal side (× 1360).

Spherical macronucleus of 15.6–21.2 μm × 15.9–20.1 μm in size, with two adjacent micronuclei of 2.3–2.5 μm in diameter. The oral area is of 51–57 μm in length with a infraciliature reduced to a paroral, an anterior membrane M1, and two membranoid segments M2 and M3 (stichomonads). Fifteen–16 ventral kineties, 6 of which converge in a "V" zone located anterior to the posterior pole. Freshwater.

Although the oral region of *Pleuronema* is situated laterally, we call the zone that includes the oral region "ventral" and the opposite "dorsal" to make this description correspond to those of other scuticociliates. The pericytostomal structures have traditionally been included in the paroral formation, but their kinetosomic composition is different from that of the latter, and they include two zones, M2 and M3 (stichomonads), separated by an area without kinetosomes. The fibrillar components of the pericytostomal structures are also different from those of the paroral formation.

Urotricha species

General morphology.—Ciliates, rounded oval in appearance, 48–55.2 μm in length, and 45–48 μm in width. They have an oral opening located in the anterior pole of the individual, which is 2.9–3.6 μm long and 2.2–3.2 μm wide. The oval macronucleus is 19.2–22.2 μm long and 13.2–15.4 μm wide. The micronucleus, is located beside the macronucleus, and is spherical with a diameter of 4.8–6 μm. The contractile vacuole pore is located half-way along the body between the kineties 12 and 13, and is 31.2–32.4 μm from the anterior pole and 21.6–22.4 μm from the posterior pole of the ciliate (Fig. 10; Table 4).

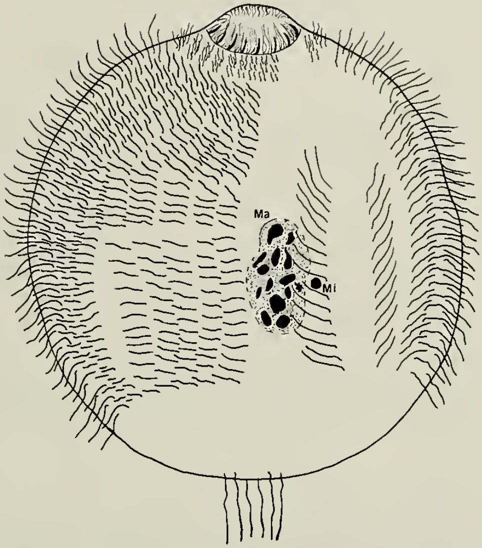


Fig. 10. General view of *Urotricha rotunda* showing the cilia and the nuclear components.

Somatic infraciliature.—There are 45–48 somatic kineties that run between the area near the oral opening and a posterior zone without kinetosomes. Three of these kineties are shorter than the rest as they abut on the brush. The posterior end, where the somatic kineties are broken off, is 40.8–42 μm from the anterior pole and 14.6–15.2 μm from the posterior pole. Each somatic kinety has 30–36 pairs of kinetosomes. The number of pairs of kinetosomes is slightly less on the dorsal side than on the ventral: 30–32 vs. 33–36. The 3–4 most anterior pairs of each kinety are more closely grouped forming a border 1.8–2.4 μm wide. Each pair of somatic kinetosomes has three derivatives: the two associated with the right kinetosome are kinetodesmal fibril and postciliary microtubules, and those associated with the left kinetosome are transverse microtubules.

In the posterior area of the ciliate there are 6–8 groups of 2–4 kinetosomes each. The kinetosomes of each group appear connected to each other by means of a fibrous structures, in such a way that each group as a whole, has a circular appearance. These caudal kinetosomal groups (CKG) give use to the caudal cilia (Figs. 11–13; Table 4).

Oral infraciliature.—This is made up of two structures: the perioral formation (PF) and the adoral organellar complexes (brush).

The perioral formation (PFO) consists of

Table 4.—Biometric data of *Urotricha rotunda.*

	Arithmetic mean	Standard deviation	Standard error	Coefficient of variation	Pearson coefficient	Minimum	Maximum	Observations
Length	51.84	1.76	0.19	3.39	0.48	48.00	55.20	80
Width	46.87	0.82	0.09	1.74	0.45	45.00	48.00	80
Length of the oral opening	3.18	0.22	0.02	6.91	0.36	2.94	3.60	80
Width of the oral opening	2.71	0.24	0.02	8.85	0.45	2.16	3.20	80
Length of the perioral formation zone	11.05	0.15	0.01	1.35	0.33	10.80	11.40	80
Width of the perioral formation zone	7.30	0.31	0.03	4.40	0.09	6.60	7.80	80
Length of the fibrillar bundles of the perioral formation	1.36	0.08	0.00	6.17	0.75	1.26	1.50	80
Length of the macronucleus	20.49	0.83	0.09	4.05	0.59	19.20	22.20	80
Width of the macronucleus	14.35	0.62	0.06	4.32	0.56	13.20	15.40	80
Diameter of the micronucleus	5.31	0.35	0.03	6.59	0.31	4.80	6.00	80
Length of B1	3.05	0.19	0.02	6.22	−0.26	2.64	3.30	80
Length of B2	1.99	0.18	0.02	9.04	−0.05	1.68	2.26	80
Length of B3	1.65	0.18	0.02	10.90	0.27	1.20	1.90	80
Number of kinetosomes of B1	8.37	1.02	0.11	12.18	0.36	7.00	10.00	80
Number of kinetosomes of B2	6.25	0.45	0.05	7.20	0.55	6.00	7.00	80
Number of kinetosomes of B3	3.41	0.51	0.05	14.95	0.80	3.00	4.00	80
Number of fibrillar bundles of perioral formation	23.00	0.60	0.06	2.60	0.00	22.00	24.00	80
Number of caudal kinetosomal groups	6.91	0.66	0.07	9.55	−0.13	6.00	8.00	80
No. kinetosomes of each caudal kinetosomal group	3.00	0.60	0.06	20.00	0.00	2.00	4.00	80
Number of ventral kineties	23.83	0.83	0.09	3.48	0.99	23.00	25.00	80
Number of dorsal kineties	22.25	0.45	0.05	2.02	0.55	22.00	23.00	80
No. kinetosome pairs of anterior segment of somatic kineties	3.16	0.38	0.04	12.02	0.42	3.00	4.00	80
Length of the anterior segment of the somatic kineties	2.00	0.17	0.01	8.50	0.58	1.80	2.40	80
Number of kinetosome pairs in each ventral kinety	34.08	0.99	0.11	2.90	0.08	33.00	36.00	80
Number of kinetosome pairs in each dorsal kinety	31.41	0.79	0.08	2.51	−0.74	30.00	32.00	80
Distance posterior end of somatic kineties–anterior pole	41.21	0.29	0.03	0.70	0.03	40.80	42.00	80
Distance posterior end of somatic kineties–posterior pole	14.82	0.19	0.02	1.28	0.10	14.60	15.20	80
Distance B1–anterior pole	11.15	0.29	0.03	2.60	0.51	10.80	11.90	80
Distance B1–posterior pole	49.30	0.64	0.07	1.29	0.15	48.10	50.80	80
Distance B2–anterior pole	13.43	0.40	0.04	2.97	0.57	13.00	14.40	80
Distance B2–posterior pole	47.92	0.59	0.06	1.23	−0.13	47.00	49.00	80
Distance B3–anterior pole	15.75	0.69	0.07	4.38	0.79	15.00	17.10	80
Distance B3–posterior pole	47.20	0.33	0.03	0.69	0.00	46.80	47.90	80
Length of each caudal kinetosomal group	1.60	0.03	0.00	1.87	0.66	1.56	1.68	80
Width of each caudal kinetosomal group	1.20	0.01	0.00	0.83	0.08	1.16	1.23	80
Distance pore of contractile vacuole–anterior pole	31.92	0.28	0.03	0.87	0.42	31.20	32.40	80
Distance pore of contractile vacuole–posterior pole	22.02	0.22	0.02	0.99	0.11	21.60	22.40	80

a crown of 22–24 pairs of kinetosomes that circle the oral opening. From each of these pairs of kinetosomes and towards the buccal opening, there is a fibrous bundle of 1.3–1.5 μm long. The perioral formation as a whole is 10.8–11.4 μm long and 6.6–7.8 μm wide.

There are three adoral organellar complexes (brush kineties) (B1, B2 and B3) running more or less meridionally from the anterior part of the ciliate to its equatorial zone. B1 is the most anterior, 10.8–11.9 μm from the anterior pole and 48.1–50.8 μm from the posterior pole of the ciliate; it is 2.6–3.3 μm long and is made up of two rows that have a total of 7–10 kinetosomes. B2 is 13–14.4 μm from the anterior pole, and 47–49 μm from the posterior pole of the individual; it is 1.7–2.3 μm long and is made up of 6–7 kinetosomes grouped in two rows. B3, the most posterior, is 15–17.1 μm from the anterior pole and 46.8–47.9 μm from the posterior pole of the ciliate; it is 1.2–1.9 μm long and has 3–4 kinetosomes (Figs. 11 and 12; Table 4).

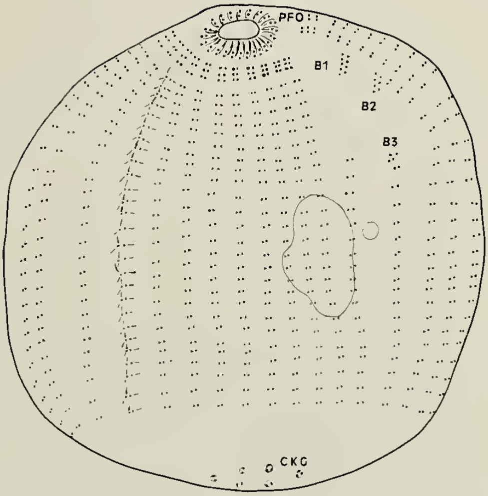


Fig. 11. *Urotricha rotunda.* PFO: perioral formation; B1, B2 and B3: brush kineties; CKG: caudal kinetosomic groups.

Taxonomic position.—The specimens studied belong to the class Prostomatea Schewiakoff 1896, order Prorodontida Corliss 1974, Family Urotrichidae Small &

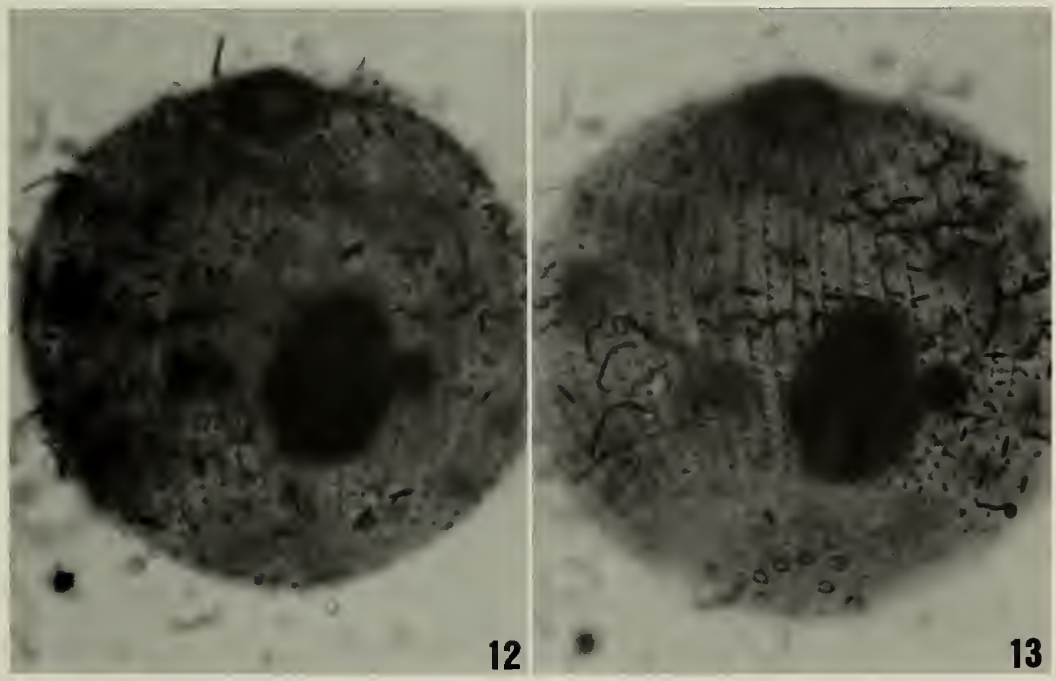


Fig. 12–13. 12, *Urotricha rotunda.* The ventral side of a stained specimen (× 1800). 13, *Urotricha rotunda.* Dorsal surface. The caudal kinetosomic groups can be observed (× 1800).

Table 5.—Comparison between species of *Urotricha* genus. (ov, oval; el, elongated; sr, spheric; p, pairs; Kh, Kahl 1935; s, single; cd, double corone).

	U. castalia	*U. puytoraci*	*U. sphaerica*	*U. apsheronica*	*U. pelagica*	*U. armata*	*U. ovata*	*U. macrostoma*	*U. agilis*	*U. ondina*	*U. armata*(*)
Length	44–67	50–60	48–55	75	50–65	47–55 Kh 31–42	25–45 Kh 25–40	30–40	10–20	19–40	80
Width	39–65	—	46–51	55–60	38–50	24–32	20–38	—	—	16–35	—
Length and shape of the macronucleus	11–19sr	el	10–15 ov	18 ov	sr	7–11 sr 17 el Kh	sr	sr			
Width of the macronucleus	—	—	—	—	—	7.5–11	—	—	sr	9 sr	sr
Distance posterior end of adoral organellar zone–anterior pole	—	—	—	—	—	8–15	—	—	—	—	—
Distance posterior end of adoral organellar zone–posterior pole	—	—	—	—	—	25–36	—	—	—	—	—
B1: length/number of rows/number of kinetosomes	–/2/10–18	—	—	—	—	2.8–3/3/–	1.5–2/–/–	—	—	—	—
B2: length/number of rows/number of kinetosomes	–/2/8–12	—	—	—	—	2.8–3/3/–	1.5–2/–/–	—	—	–/2/6–8	—
B3: length/number of rows/number of kinetosomes	–/2/6–12	—	—	—	—	2.8–3/3/–	1.5–2/–/–	—	—	–/2/5–6	—
Number of somatic kineties	45–50	48–51	59–61	60	45–50	35–41 60–67 Kh	19–24	—	—	–/2/3–4	—
Number of kinetosomes of each somatic kinety	16–18	—	—	—	—	20–30	—	24–26	12–14	23–26	—
Number of caudal cilia	5–7	s	1	18	10	1 Kh	1	—	—	9–16	—
Number of caudal kinetosomic group (number of kinetosomes in each group)	1	—	1(1)	18(1)	—	1(1)	1(1)	2	1	1	5–7
Number of kinetosomes in the perioral formation	23–25 p	26–27 p	26 p	30–35 p	cd	15–20 p 27–30 p Kh	10 p 30 p Kh	—	—	1	—
Number of short somatic kineties	5–7	5	2	5	3	3(6 Kh)	2	13 p	—	12–16 p	—
Number of adoral organelles (brush)	3	3	3	3	3	3(6 Kh)	3	3	—	3	—

Table 5.—Continued.

	U. satrophila	*U. vitrea*	*U. nais*	*U. venatrix*	*U. farcta*	*U. faurei*	*U. baltica*	*U. rotunda*	*U. corlissiana*	*U. valida*
Length	20	27–47	16–34	66	19–32	35–46	65–80	48–55.2	25–33	52–63
Width	45	26–44	12–32	—	—	—	—	45–48	17–22	43–55
Length and shape of the macronucleus	ov	sr	8–11 ov	17 el	sr	14–22 sr	—	19–22 ov	7–10 ov	26–33 ov
Width of the macronucleus	—	—	—	—	—	—	—	13.2–15.4	6–8	12–16
Distance posterior end of adoral organellar zone–anterior pole	—	—		—	—	—	—	15–17.1	—	—
Distance posterior end of adoral organellar zone–posterior pole	—	—	—	—	—	—	—	40.8–42		
B1: length/number of rows/number of kinetosomes	–/2/6	–/2/8	–/2/8	—	—	—	—	2.6–3.3/3/7–10	—	–/2/–
B2: length/number of rows/number of kinetosomes	–/2/6	–/2/6	–/2/4	—	—	—	—	1.6–2.2/2/6–7	—	–/2/–
B3: length/number of rows/number of kinetosomes	–/2/6(13)	–/2/4	—	—	—	—	—	1.2–1.9/2/3–4	—	–/2/–
Number of somatic kineties	23–25	20–23	18–21	65–70	28–30	55–60	32–36	45–48	42–51	76–87
Number of kinetosomes of each somatic kinety	11–16	15–20	5–11	—	—	—	—	30–36	—	—
Number of caudal cilia	3	1	1	10–15	1	12–15	—	12–32	1	10–14
Number of caudal kinetosomic group (number of kinetosomes in each group)	1	1(2)	1(2)	—	—	—	—	6–8(2–4)	1	—
Number of kinetosomes in the perioral formation	23–25 p	13–16 p	9–10 p	—	13–14 s, p	12 p	25 p	22–24 p	16 p	50 p
Number of short somatic kineties	0	3	1	4	—	4	—	3	—	—
Number of adoral organelles (brush)	13	3	2	3	3–4	4	3	3	3	3

Lynn 1985, and genus *Urotricha* Claparède & Lachmann 1895. The best-known species of this genus are: *Urotricha castalia* Muñoz et al. 1987; *U. puytoraci* Dragesco et al. 1974; *U. sphaerica* Grolière 1977; *U. apsheronica* Alekperov 1983; *U. pelagica* Wilbert 1986; *U. armata* Kahl 1927 (Foissner 1984); *U. ovata* Kahl 1926 (Foissner 1979); *U. macrostoma* Foissner 1983; *U. agilis* Stokes 1886 (Foissner 1979); *U. ondina* Muñoz et al. 1989; *U. armata* Kahl 1927 (Dragesco 1960); *U. satrophila* Kahl 1935 (Pätsch 1974); *U. vitrea* Martin-Gonzalez et al. 1985; *U. nais* Muñoz et al. 1987; *U. venatrix* Kahl 1935; *U. farcta* Dragesco et al. 1974; *U. faurei* Dragesco et al. 1974; *U. baltica* Czapik & Jordan 1976; *U. corlissiana* Song & Wilbert 1989, and *U. valida* Song & Wilbert 1989. The species that permit a more detailed comparison, due to the fact that there is more biometric data available, are A, *U. castalia,* F, *U. armata,* G, *U. ovata,* J, *U. ondina,* L, *U. satrophila,* M, *U. vitrea,* N, *U. nais.* With respect to these 7 species, our specimens differ from *U. castalia* in 10; *U. armata* in 15; *U. ovata* in 10; *U. ondina* in 11; *U. satrophila* in 10; *U. vitrea* in 10 and from *U. nais* in 13 of the 16 characteristics it has been possible to consider: 1, body length; 2, body width; 3, length of the macronucleus; 4, width of the macronucleus; 5, distance between the posterior end of the adoral organelles (brush) and the anterior pole; 6, distance between the posterior end of the adoral organelles (brush) and the posterior pole; 7, B1 length/number of kineties/number of kinetosomes; 8, B2 length/number of kineties/number of kinetosomes; 9, B3 length/number of kineties/number of kinetosomes; 10, number of somatic kineties; 11, number of kinetosomes of the somatic kineties; 12, number of caudal cilia; 13, number of caudal kinetosomal groups (CKG); 14, number of kinetosomes of the perioral formation (circumoral corone); 15, number of short somatic kineties; and 16, number of adoral organelles (brush). With regard to the ciliates studied, the length of the body is greater in *U. apsheronica, U. armata* (Dragesco 1960), *U. venatrix* and *U. baltica.* The body is shorter in *U. ovata, U. macrostoma, U. agilis, U. ondina, U. satrophila, U. vitrea, U. nais, U. farcta, U. faurei* and *U. corlissiana,* being similar in the rest of the species. The number of somatic kineties is higher in *U. sphaerica, U. apsheronica, U. venatrix, U. faurei* and *U. valida,* and lower in *U. armata, U. ovata, U. macrostoma, U. agilis, U. ondina, U. satrophila, U. vitrea, U. nais, U. farcta* and *U. baltica.* The number of caudal cilia is similar in *U. apsheronica, U. venatrix, U. faurei* and *U. valida,* being lower in the rest of the species. The number of kinetosomes in the perioral formation is higher in *U. puytoraci, U. sphaerica, U. apsheronica* and *U. valida,* and lower in *U. armata, U. ovata, U. macrostoma, U. ondina, U. vitrea, U. nais, U. farcta, U. faurei* and *U. corlissiana.* Due to these various differences, we conclude that our specimens represent a new species, *Urotricha rotunda* (Table 5).

Urotricha rotunda, new species

Diagnosis.—Ciliates, round or oval in appearance, 48–55.2 μm long and 45–48 μm wide. Oval macronucleus (19.2–22.2 μm × 13.2–15.4 μm in size) with an adjacent spherical micronucleus 4.8–6 μm in diameter. 45–48 somatic kineties broken off in the posterior zone of the body, with 30–36 pairs of kinetosomes each. 6–8 caudal kinetosomal groups. Perioral formation of 22–24 pairs of kinetosomes.

Type specimens: permanent slides stained with silver carbonate technique, deposited in the Laboratorio de Biología General, Departamento de Biología Animal I (Zoología), Facultad de Biología, Universidad Complutense, ref. n. 2314 a–f (*Pseudocohnilembus fluviatilis*), ref. no. 3126 a–g (*Pleuronema ovata*), ref. no. 2788 a–l (*Urotricha rotunda*).

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MORPHOLOGICAL VARIABILITY IN WARM-TEMPERATE AND SUBTROPICAL POPULATIONS OF *MACRODASYS* (GASTROTRICHA: MACRODASYIDA: MACRODASYIDAE) WITH THE DESCRIPTION OF SEVEN NEW SPECIES

Wayne A. Evans

Abstract.—Seven new species of *Macrodasys, M. ancocytalis, M. achradocytalis, M. deltocytalis, M. meristocytalis, M. dolichocytalis, M. blysocytalis* and *M. stenocytalis* (Gastrotricha: Macrodasyida: Macrodasyidae) are described from warm temperate and subtropical marine sediments along the Atlantic and Gulf coasts of Florida, U.S.A. Multivariate analyses of morphometric characters reveal that the shape and size of the reproductive organs are the most useful characters for discriminating among species. The numerically abundant species *M. achradocytalis* and *M. meristocytalis* displayed the widest geographic range. High morphological variability within *Macrodasys* populations at certain locations can be attributed to the presence of two or more species.

During previous investigations of the marine gastrotrich fauna of warm temperate and subtropical sandy sediments along the Atlantic and Gulf coasts of Florida, U.S.A (Evans 1992), several populations belonging to the genus *Macrodasys* were observed that exhibited differences in both internal and external morphology. Subsequently, I sampled nine locations in southern Florida (Fig. 1): Honeymoon Island (three locations), Crandon Park on Key Biscayne (two locations), Sombrero Beach on Vaca Key (one location), Bahia Honda Key (two locations), and Key West (one location). Variability of morphology of the forms within *Macrodasys* populations at each location was quantified and overall variability within populations was used to discriminate among forms, to identify critical taxonomic characters, and to assess the taxonomic status of each form. Particular attention was paid to the size and shape of the reproductive organs.

Members of the genus *Macrodasys* are simultaneous hermaphrodites with a reproductive system that consists of paired testes with vasa deferentia, a single ovary, a frontal organ which receives and stores allosperm, and a caudal organ which gathers autosperm and passes them to the partner during copulation. The frontal organ consists of an anterior seminal receptacle and a posterior spermatheca. The caudal organ comprises an anterior glandulomuscular structure and a posterior glandular sac ("antrum feminum" of Remane 1924). Ruppert (1978) provides a histological account of the functional anatomy of the reproductive system in two undescribed species of *Macrodasys.*

Materials and Methods

Littoral and sublittoral sediments were collected at each location in January, 1992 with a hand-held piston corer. The gastrotrichs were extracted by means of serial decantation with isosmotic $MgCl_2$ (see Evans & Hummon 1991). Specimens were located at 30× under a stereomicroscope, mounted on glass slides, and observed under Nomarski differential interference contrast op-

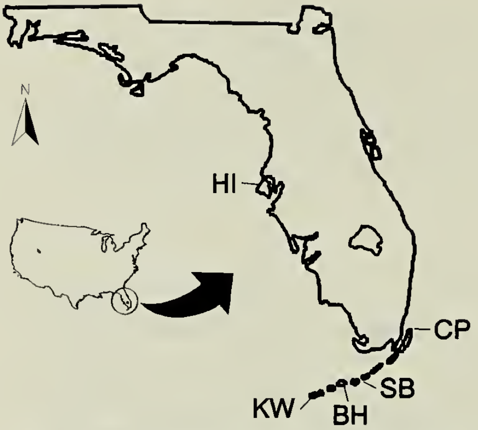

Fig. 1. Study locations in southern Florida. BH—Bahia Honda (two sites), CP—Crandon Park on Key Biscayne (two sites), HI—Honeymoon Island (three sites), KW—Key West (one site), and SB—Sombrero Beach on Vaca Key (one site). Littoral and sublittoral samples were taken at each site.

tics. During observation, high resolution Super-VHS video recordings were made of the living, narcotized animals. Recorded individuals were later measured using a video frame-grabber and a microcomputer-based measurement system. A minimum of five and a maximum of 40 specimens were measured for each form (putative species) according to their availability at the time of extraction. All measurements are reported in μm. Univariate statistics and canonical variates analysis were performed using the SAS-PC Statistical Analysis System. All type specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). High resolution videotapes (Super-VHS format) of each type specimen are deposited in the Ohio University Invertebrate Museum, Athens, Ohio.

Statistical Analyses and Results

After observation and measurement, each specimen was preliminarily assigned to one of seven forms based on overall morphological similarity. Morphometric data were then submitted to analysis of variance and to canonical variates analysis. The mean and standard deviation of each metric and meristic character used in the analysis are presented in Fig. 2. All morphometric and meristic parameters were found to different significantly ($P < 0.01$) among forms. No individuals needed to be reassigned to another form based on the results of the canonical variates (CV) analysis.

Arraying individuals in two-dimensional canonical space (Fig. 3) results in seven tightly grouped, well-separated clusters. These morphologically coherent clusters can contain individuals from two or more geographic locations (depending on the number of locations at which a particular form was found), that is, individual forms are morphologically redundant regardless of their geographic population allegiances. The first two canonical variates (CV1, CV2) explained 91.8% of the total morphological variation among individuals ($R^2 > 0.6$). Character loadings based on standardized-canonical-variate scores are interpreted as follows: CV1—shape of the middle portion of the glandulomuscular structure of the caudal organ, CV2—relative lengths of the anterior and middle portions of the glandulomuscular structure and the presence of an auxiliary chamber on the seminal receptacle of the frontal organ. A 3rd canonical variate (not plotted) explained an additional 3.9% of the variation and is interpreted as the size and shape of the seminal receptacle. The seven forms are given species status and formally described below.

Taxonomy

Order Macrodasyida Rao & Clausen, 1970

Family Macrodasyidae Remane, 1924

Macrodasys Remane, 1924

Macrodasys ancocytalis, new species

Fig. 4

Holotype.—Adult specimen 650 μm in length, mounted on glass slide. Honeymoon Island, Florida, U.S.A., sand spit facing the

Measurement	Macrodasys						
	ancocytalis (n = 5)	achradocytalis (n = 40)	deltocytalis (n = 5)	meristocytalis (n = 40)	dolichocytalis (n = 5)	blysocytalis (n = 5)	stenocytalis (n = 5)
Total Length of Adult	621.4 ± 27.3	838.9 ± 86.1	669.9 ± 59.1	634.4 ± 75.6	690.2 ± 14.6	731.3 ± 75.2	669.6 ± 51.1
Head Width at Piston Pits	63.1 ± 9.2	73.5 ± 11.3	59.7 ± 6.4	58.4 ± 10.3	45.2 ± 6.0	54.4 ± 1.7	71.3 ± 7.2
Seminal Receptacle Length	62.3 ± 4.8	34.9 ± 3.4	23.7 ± 3.6	58.6 ± 7.4	64.9 ± 4.3	70.2 ± 9.6	64.4 ± 8.1
Seminal Receptacle Width	22.2 ± 0.9	24.5 ± 3.9	18.3 ± 2.7	21.8 ± 4.4	11.3 ± 1.4	32.6 ± 10.0	24.6 ± 2.7
SR Accessory Chamber Length	0	0	0	16.7 ± 3.1	0	28.2 ± 3.4	0
GMS Anterior Portion Length	83.5 ± 3.4	50.6 ± 8.4	38.4 ± 5.9	45.3 ± 11.4	61.8 ± 4.1	53.1 ± 17.5	55.4 ± 7.4
GMS Anterior Portion Width	19.1 ± 0.7	13.0 ± 2.1	11.9 ± 1.6	14.4 ± 3.1	17.4 ± 1.8	16.3 ± 2.6	14.9 ± 3.5
GMS Middle Portion Length	53.1 ± 0.6	98.3 ± 12.9	57.6 ± 4.4	58.0 ± 9.9	49.4 ± 8.7	69.8 ± 14.3	58.5 ± 11.8
GMS Middle Portion Width	30.6 ± 0.4	32.1 ± 3.7	21.6 ± 3.5	23.2 ± 4.7	19.8 ± 3.0	27.5 ± 6.8	27.6 ± 7.3
Anterior Adhesive Tubes F1	5 - 7	5 - 8	6 - 8	4 - 9	6 - 7	7 - 8	12 - 14
Anterior Adhesive Tubes F2	0	2 - 4	0	0	1 - 2	2 - 3	0
Anterior Ashesive Tubes F3	0	1 - 2	0	0	0	0	0
Ventral Adhesive Tube Rows	2	0	2	2	0	2	0
Dorsal Adhesive Tube Rows	0	2	0	0	0	0	0

Fig. 2. Metric and merisitic characters of seven species of *Macrodasys*. Metric characters are given as the mean ± standard deviation; meristic characters as the range. Abbreviations: GMS—glandulomuscular structure of caudal organ; SR—seminal receptacle of frontal organ; F1, F2, F3—Fields 1–3 of anterior adhesive tubes.

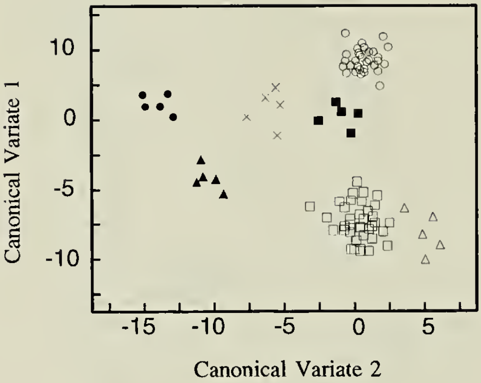

Fig. 3. Canonical variate (CV) plots of *Macrodasys* species, based on 14 characters. CV1 and CV2 are interpreted as the size and shape of the glandulomuscular structure of the caudal organ and the presence of an accessory chamber on the seminal receptacle of the frontal organ. Solid circles—*M. ancocytalis*, open circles—*M. achradocytalis*, solid squares—*M. deltocytalis*, open squares—*M. meristocytalis*, solid triangles—*M. dolichocytalis*, open triangles—*M. blysocytalis*, and X—*M. stenocytalis*.

Gulf of Mexico [28°05'N, 82°50'W]. USNM 168056.

Etymology.—anco (L.) meaning curved, after the shape of the seminal receptacle; *cyto* (L.) meaning chamber or receptacle; *alis* meaning possession.

Diagnosis.—Macrodasys with trunk much longer than pharyngeal region. Lateral and ventral adhesive tubes present on trunk; dorsal tubes lacking. Anterior adhesive tubes ventral, a single row of from five to seven tubes on each side of body, near anterior margin of head. Frontal organ a small spermatheca and elongate seminal receptacle with small nozzle; accessory chamber absent. Glandulomuscular structure of caudal organ with anterior glandular portion longer than middle portion bearing circular musculature; posterior portion a small, curved "neck" with terminal pore; copulatory tube without branches. Glandular sac of caudal organ a rounded, triangular shape.

Description.—Elongate, strap-shaped body; adults 602–685 μm long, 49–65 μm wide. Caudum tapers into long, narrow "tail" (Fig. 4a). Dorsal and lateral body surfaces covered with long sensory bristles. Piston pits ("stempelgrube" of Remane 1924) on each side of head. Ventral surface entirely covered with locomotor cilia except small, bare area around female pore (Fig. 4b). Dorsal ciliary band present on head. Anterior adhesive tubes a ventral, single row, an arc of from five to seven tubes on each side of body, adjacent to mouth (Fig. 4c); most medial tube shortest, most lateral longest. About 16 lateral adhesive tubes on each side of trunk; an additional 10–12 tubes on each side of tail. Two ventral rows of adhesive tubes near lateral margins of trunk, about 16 per row. Adhesive tubes on trunk begin just anterior to pharyngeal-intestinal junction; lateral and ventral rows merge where trunk narrows into tail.

Mouth leads into buccal cavity, which opens into pharynx. Pharyngeal-intestinal junction at U40 (U0, anterior-most tip; U100, posterior-most tip; in the terminology of Schoepfer-Sterrer 1969); pharyngeal pores (U24) small. Intestine narrows continuously from pharyngeal-intestinal junction to terminus; anus ventral.

Small, paired lateral testes at pharyngeal-intestinal junction taper into vasa deferentia; male pores separate and ventral, adjacent to frontal organ (Fig. 4a). Frontal organ an anterior seminal receptacle and posterior spermatheca (Fig. 4d). Seminal receptacle with weak circular musculature and small, lightly cuticularized anterior pore (nozzle); length about three times width. Spermatheca hollow with few secretory droplets. Ovary adjacent to spermatheca; ova increase in size anteriorly. Ovum adjacent to nozzle of spermatheca receives sperm. Large caudal organ a spindle-shaped glandulomuscular structure and a glandular sac with opening to ventral surface (Fig. 4e); anterior tip of glandulomuscular structure adjacent to spermatheca.

Anterior portion of glandulomuscular structure longer than middle portion and sheathed in longitudinal muscles. Middle

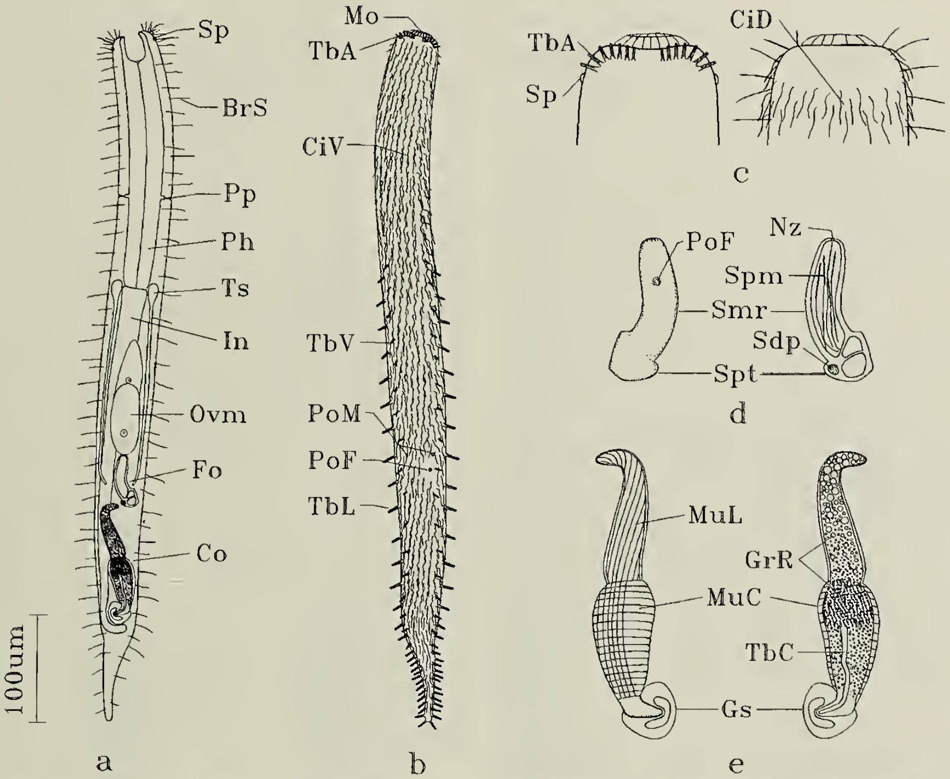

Fig. 4. *M. ancocytalis,* new species. Single row of anterior adhesive tubes. Ventral tubes present. Curved seminal receptacle of frontal organ lacks an auxiliary chamber. Anterior portion of glandulomuscular structure of caudal organ longer than middle portion. a) internal organs, b) ventral surface, c) ventral and dorsal head, d) frontal organ, and e) caudal organ. c–e not to scale. Abbreviations: BrS—sensory bristle, CiD—dorsal ciliary band, CiV—ventral locomotor cilia, Co—caudal organ, Eg—egg, Fo—frontal organ, GrR—refractile granules, Gs—glandular sac, MuC—circular muscles, MuL—longitudinal muscles, Nz—nozzle, Ov—ovum, Ph—pharynx, PoF—female reproductive pore, PoM—male reproductive pore, Pp—pharyngeal pore, PtP—piston pit, Sdp—secretory droplet, Smr—seminal receptacle, Spm—spermatozoa, SpT—spermatheca, TbA—anterior adhesive tube, TbD—dorsal adhesive tube, TbL—lateral adhesive tube, TbV—ventral adhesive tube, Ts—testis.

portion with longitudinal muscles on ventral side only, but entirely sheathed in robust circular muscles. Posterior portion of glandulomuscular structure an angled neck that extends into center of glandular sac. Glandulomuscular structure filled with refractile granules of various diameters; unbranched copulatory tube in middle portion of glandulomuscular structure leads to opening in neck. Glandular sac of caudal organ a rounded, triangular shape.

Distribution and habitat.—Uncommon species, found in littoral and sublittoral zones in coarse, poorly-sorted sediments with both siliceous and carbonate fractions. Honeymoon Island (two locations).

Macrodasys achradocytalis, new species
Fig. 5

Holotype.—Adult specimen 825 μm in length, mounted on glass slide. Bahia Honda Key, Florida, U.S.A., sandy beach facing the Atlantic Ocean [24°38′N, 81°35′W]. USNM 168055.

Etymology.—*achrado* (L.) meaning wild pear, after the shape of the seminal receptacle; *cyto* (L.) meaning chamber or receptacle; *alis* (L.) meaning possession.

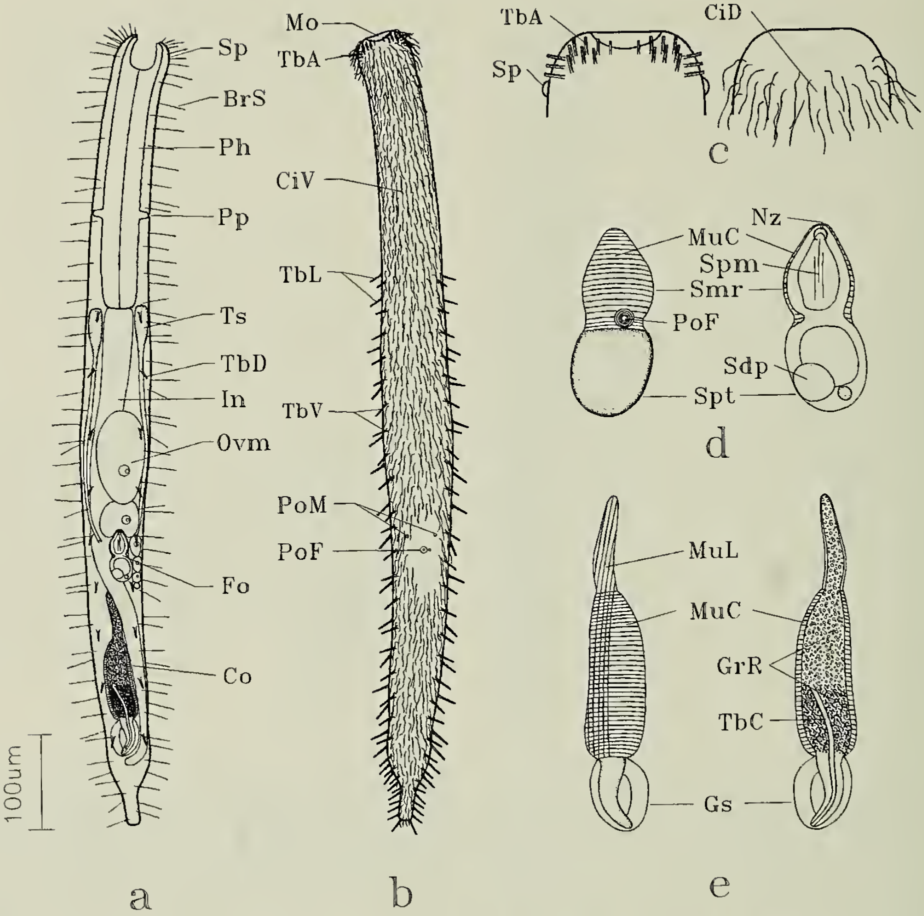

Fig. 5. *M. achradocytalis*, new species. Dorsal adhesive tubes in two rows of 10 tubes each. Anterior adhesive tubes in three fields. Seminal receptacle and spermatheca of frontal organ of similar size. Anterior portion of glandulomuscular structure of caudal organ much shorter than middle portion; neck long and narrow. Abbreviations and a–e as in Fig. 4; c–e not to scale.

Diagnosis.—*Macrodasys* with trunk much longer than pharyngeal region. Lateral and dorsal adhesive tubes present on trunk; ventral tubes lacking. Anterior adhesive tubes ventral in three fields on each side of body, near anterior margin of head. Anterior field a row of from five to eight tubes arranged in two distinct groups at 95° angle to each other; middle field a row with from two to four tubes; posterior-most field with one or two tubes. Frontal organ a rounded spermatheca and pear-shaped seminal receptacle; nearly equal in size. Seminal receptacle sheathed in circular muscles; nozzle large and cuticularized; accessory chamber absent. Anterior, glandular portion of glandulomuscular structure of caudal organ short and narrow, about one-half length of middle portion; neck long and slightly curved; copulatory tube without branches. Glandular sac of caudal organ oval.

Description.—Very long strap-shaped body; adults 661–1033 μm long and 54–97 μm wide. Caudum narrows abruptly into short tail (Fig. 5a). Dorsal and lateral body surfaces covered with long sensory bristles. Ventral surface entirely covered with locomotor cilia except large, bare area around female pore (Fig. 5b). Sparse dorsal ciliary band on head. Anterior adhesive tubes ventral, in three fields on each side of body just posterior to mouth (Fig. 5c). Anterior field with row of seven tubes in two distinct groups at about 95° angle to each other; tubes increase in length from medial to lateral. Middle field a transverse row with from two to four tubes. Posterior-most field with one or two tubes. About 40 lateral adhesive tubes on each side of trunk; tubes longest where trunk narrows into tail. An additional five or six tubes on each side of tail. Two dorsal rows of about 10 small tubes each (Fig. 5a). Ventral adhesive tubes lacking. Adhesive tubes on trunk begin just anterior to pharyngeal-intestinal junction. Lateral tubes continue onto tail; dorsal tube rows end just anterior to tail.

Mouth leads into large buccal cavity, which opens into pharynx. Pharyngeal-intestinal junction at U35; pharyngeal pores at U23. Intestine narrows toward caudal end of trunk; anus ventral.

Paired lateral testes at pharyngeal-intestinal junction taper into vasa deferentia; male pores separate and ventral, adjacent to seminal receptacle. Spermatheca of frontal organ rounded with internal cavity and large secretory droplets. Seminal receptacle of frontal organ pear-shaped, anterior end with large, heavily cuticularized D-shaped nozzle; accessory chamber lacking. Seminal receptacle sheathed in circular muscles (Fig. 5d). Small tube leads from posterior ventral portion of seminal receptacle to ventral female pore. Spermatheca and seminal receptacle approximately the same size; secretory droplets often large. Ovary lies to right of frontal organ; ova increase in size anteriorly. Glandulomuscular structure of caudal organ with anterior portion short (one-third the length of middle portion) and narrow. Long, narrow neck of glandulomuscular structure extends to posterior end of glandular sac; copulatory tube unbranched. Refractile granules densest and smallest in posterior end of glandulomuscular structure (Fig. 5e). Glandular sac of frontal organ oval.

Distribution and habitat.—Common species, found in littoral and sublittoral zones in both coarse, poorly-sorted carbonate sediments and medium-fine siliceous sediments. Abundant where found. Crandon Park (two locations), Bahia Honda (two locations), and Sombrero Beach.

Macrodasys deltocytalis, new species

Fig. 6

Holotype.—Adult specimen 670 μm in length, mounted on glass slide. Crandon Park, Florida, U.S.A., small, sandy beach facing harbor on Biscayne Bay [25°44'N, 80°10'W]. USNM 168058.

Etymology.—*delto* (L.) meaning in the shape of a triangle, after the shape of the seminal receptacle; *cyto* (L.) meaning chamber or receptacle; *alis* (L.) meaning possession.

Diagnosis.—*Macrodasys* with pharynx and trunk of about equal length. Lateral and ventral adhesive tubes present on trunk; dorsal tubes lacking. Anterior adhesive tubes ventral, in one row of from six to eight tubes on each side of body, near anterior margin of head. Tubes arranged in arc with shortest tubes medially and longest tubes laterally. Spermatheca of frontal organ simple, round; seminal receptacle triangular-shaped, twice as long as diameter of spermatheca and without visible circular musculature; accessory chamber absent. Anterior portion of glandulomuscular structure of caudal organ wide and about two-thirds length of middle portion; neck strongly curved; copulatory tube without branches. Glandular sac of caudal organ small.

Description.—Strap-shaped body; adults 602–685 μm long, 49–65 μm wide. Caudum tapers quickly into medium-length tail (Fig. 6a). Dorsal and lateral body surfaces sparsely covered with long sensory bristles. Ventral surface entirely covered with locomotor cilia except small, bare area around female

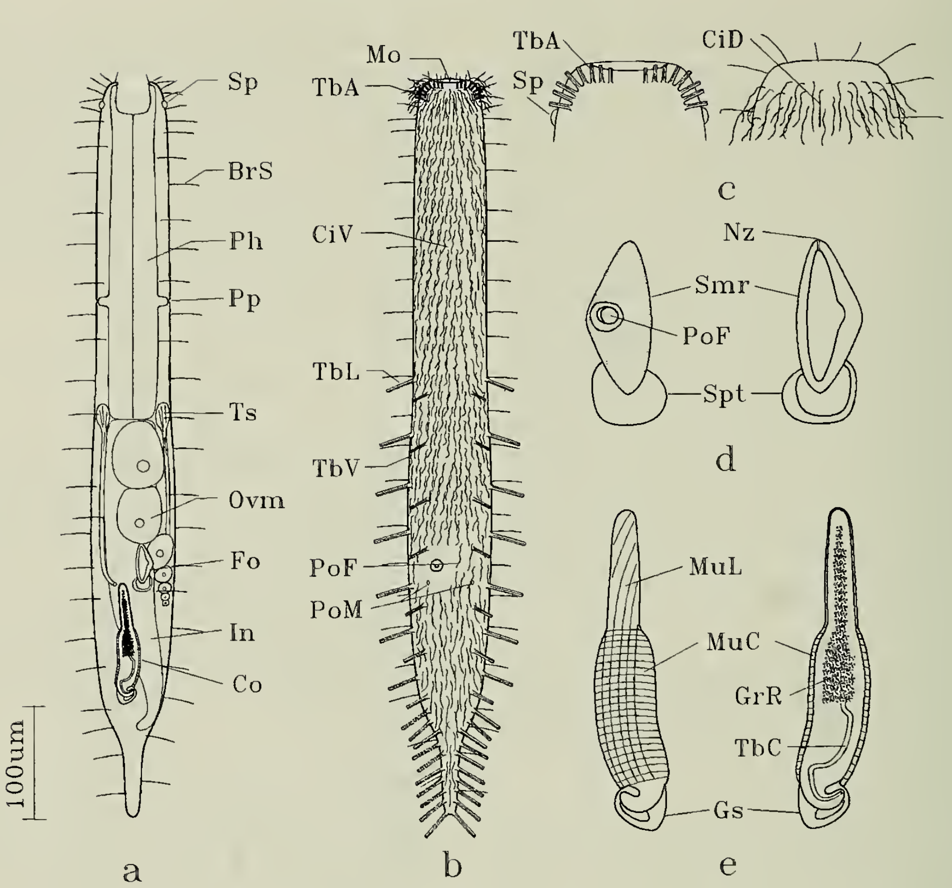

Fig. 6. *M. deltocytalis,* new species. Pharyngeal region and trunk equal in length. Anterior adhesive tubes in a single row of eight tubes. Ventral adhesive tubes present. Seminal receptacle of frontal organ triangular in shape. Abbreviations and a–e as in Fig. 4; c–e not to scale.

pore (Fig. 6b). Sparse dorsal ciliary band on head near anterior margin. Anterior adhesive tubes a single ventral row of from six to eight tubes on each side of body near anterior margin of head and arranged in an arc with tubes increasing in length from medial to lateral (Fig. 6c). About 10 lateral adhesive tubes on each side of trunk; additional seven or eight tubes on each side of tail. Lateral tubes longest in mid-trunk region. Two ventral rows of about seven tubes each. Adhesive tubes on trunk begin just anterior to pharyngeal-intestinal junction. Lateral and ventral rows converge where trunk narrows into tail.

Mouth leads into shallow buccal cavity, which opens into long pharynx. Pharyngeal-intestinal junction at U50; pharyngeal pores at U30. Intestine narrows at caudal end of trunk; anus ventral.

Small, paired lateral testes at pharyngeal-intestinal junction taper into vasa deferentia; male pores separate and ventral, adjacent to posterior edge of spermatheca. Spermatheca of frontal organ rounded, with large internal cavity; secretory droplets not observed. Seminal receptacle of frontal organ triangular-shaped with small nozzle at anterior apex; thick-walled tubular chamber leads to ventral female pore from lateral apex. Ventral pore surround by epidermal sculpturing. Right wall of seminal recepta-

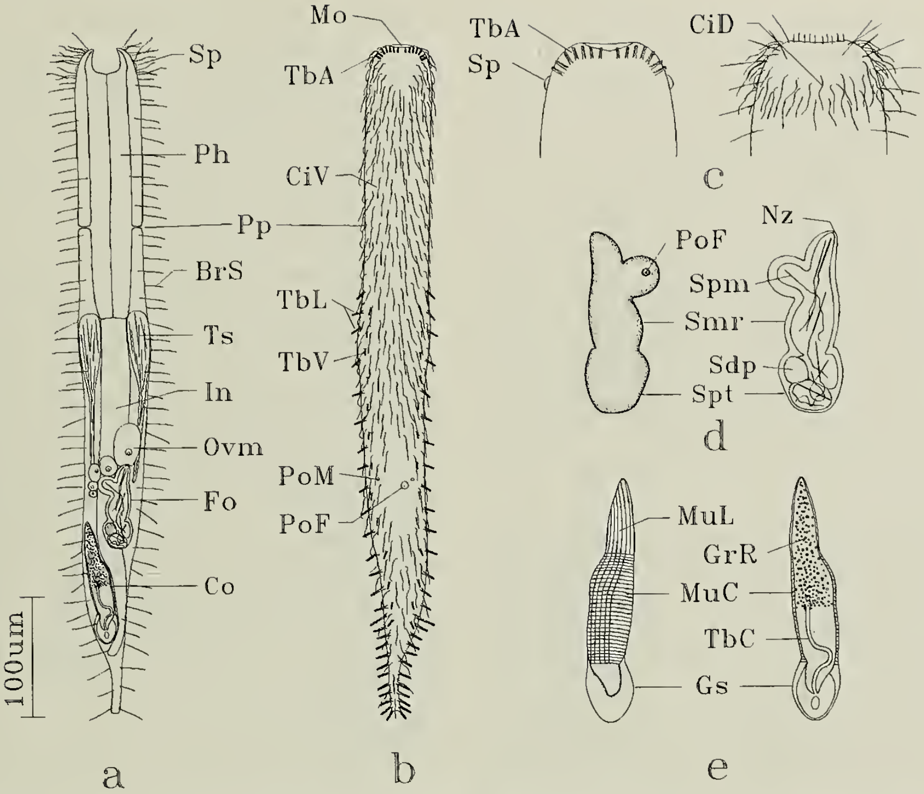

Fig. 7. *M. meristocytalis*, new species. Ventral adhesive tubes present. Seminal receptacle of frontal organ with a small accessory chamber containing female pore. Testes large. Anterior portion of glandulomuscular structure of caudal organ about one-half as long as middle portion. Abbreviations and a–e as in Fig. 4; c–e not to scale.

cle thickened; circular muscles not evident. Accessory chamber lacking. Seminal receptacle approximately 2.5 times as long as diameter of spermatheca. Ovary lies posterior and right of frontal organ; ova increase in size anteriorly. Glandulomuscular structure of caudal organ with anterior portion broad and about two-thirds as long as middle portion (Fig. 6e). Short, severely curved neck of glandulomuscular structure extends to left margin of glandular sac; copulatory tube unbranched. Refractile granules present from anterior end of copulatory tube to anterior tip of glandulomuscular structure. Glandular sac of caudal organ small.

Distribution and habitat.—Uncommon species, found only in littoral zone of small beach facing harbor on Biscayne Bay. Well-sorted, medium-fine siliceous sediments. Crandon Park (one location).

Macrodasys meristocytalis, new species
Fig. 7

Holotype.—Adult specimen 670 μm in length, mounted on glass slide. Key West, Florida, U.S.A., small sandy beach facing Atlantic Ocean [24°35′N, 81°50′W]. USNM 168060.

Etymology.—*meristo* (L.) meaning divided, after the division of the seminal receptacle into two chambers; *cyto* (L.) meaning chamber or receptacle; *alis* (L.) meaning possession.

Diagnosis.—*Macrodasys* with trunk slightly longer than pharyngeal region. Lateral and ventral adhesive tubes present on trunk; dorsal tubes lacking. Anterior adhesive tubes ventral, a single row of from four to nine tubes on each side of body, near anterior margin of head. Testes very large. Frontal organ a simple, round spermatheca and elongate seminal receptacle. Seminal receptacle 2.5 times as long as diameter of spermatheca and without visible circular musculature; accessory chamber present. Anterior portion of glandulomuscular structure of caudal organ broad and short, about two-thirds length of middle portion; neck very short; copulatory tube unbranched. Glandular sac of caudal organ oval.

Description.—Strap-shaped body; adults 495–797 μm long, 38–89 μm wide. Caudum tapers gradually into narrow tail (Fig. 6a). Dorsal and lateral body surfaces covered with numerous sensory bristles. Ventral surface entirely covered with locomotor cilia except a V-shaped, bare area posterior to anterior series of adhesive tubes and a large, bare area surrounding female pore (Fig. 7b). Sparse dorsal ciliary band on head at level of sensory pits. Anterior adhesive tubes ventral, a single row of from four to nine tubes on each side of body near anterior margin of head, arranged in an arc with tubes increasing in length from medial to lateral (Fig. 7c). About 20 lateral adhesive tubes on each side of trunk; an additional eight or nine tubes on each side of tail. Lateral tubes longest where trunk narrows into tail. Two ventral rows of about 13 small tubes each. Adhesive tubes on trunk begin just anterior to pharyngeal-intestinal junction. Lateral and ventral rows converge where trunk narrows into tail.

Mouth leads into shallow buccal cavity, which opens into long pharynx. Pharyngeal-intestinal junction at U41; well-developed pharyngeal pores at U26. Intestine narrows at caudal end of trunk; anus ventral.

Very large, paired lateral testes at pharyngeal-intestinal junction taper into vasa deferentia; male pores separate and ventral, adjacent to seminal receptacle of frontal organ. Spermatheca of frontal organ rounded with dual internal cavities; secretory droplets present. Seminal receptacle of frontal organ a rounded cone, with bulbous accessory chamber on right side; small nozzle present at anterior apex (Fig. 7d). Thin-walled, cylindrical tube leads from accessory chamber to simple ventral female pore. Seminal receptacle approximately 2.5 as long as the diameter of spermatheca; circular muscles not visible. Ovary lies posterior to and left of frontal organ; ova increase in size anteriorly with largest ovum in front of seminal receptacle. Glandulomuscular structure of caudal organ with broad anterior portion that tapers to rounded point anteriorly, about three-quarters as long as middle portion. Stubby, slightly-curved neck of glandulomuscular structure extends to center of glandular sac; refractile granules sparse; copulatory tube unbranched. Glandular sac of caudal organ oval.

Distribution and habitat.—Common species, found in littoral and sublittoral zones in coarse, poorly-sorted carbonate sediments and in medium-fine, siliceous sediments. Abundant where found. Honeymoon Island (one location), Crandon Park (two locations), Bahia Honda (one location), and Key West.

Macrodasys dolichocytalis, new species

Fig. 8

Holotype.—Adult specimen 690 μm in length, mounted on glass slide. Honeymoon Island, Florida, U.S.A., beach facing the Gulf of Mexico near causeway [28°05′N, 82°50′W]. USNM 168059.

Etymology.—*dolicho* (L.) meaning elongate, after the shape of the seminal receptacle; *cyto* (L.) meaning chamber or receptacle; *alis* (L.) meaning possession.

Diagnosis.—*Macrodasys* with trunk longer than pharyngeal region. Lateral adhesive tubes present on trunk; ventral and dorsal tubes lacking. Anterior adhesive tubes ven-

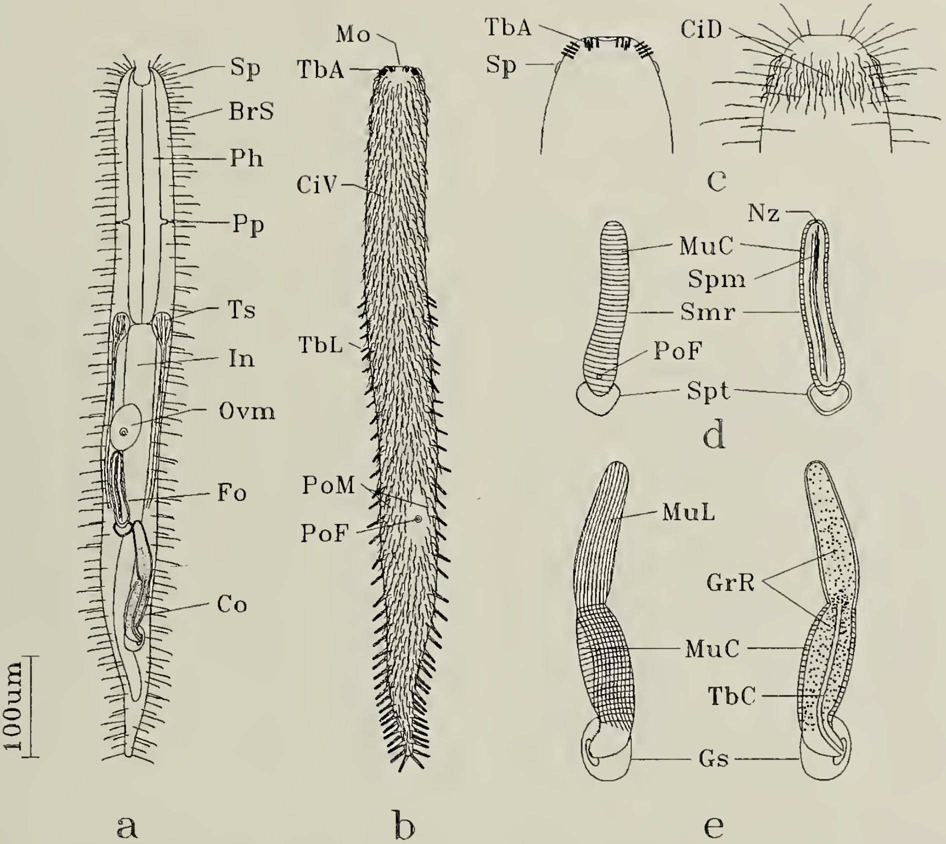

Fig. 8. *M. dolichocytalis,* new species. Lateral adhesive tubes abundant, especially in tail region. Anterior adhesive tubes in two fields. Seminal receptacle of frontal organ about six times as long as wide. Sperm with very long tails. Anterior portion of glandulomuscular structure of caudal organ slightly longer than middle portion. Abbreviations and a–e as in Fig. 4; c–e not to scale.

tral, in two fields on each side of body, near anterior margin of head. Anterior field a row of six or seven tubes of equal size in two distinct groups of three or four tubes each, at about 130° angle to each other. Second field with one or two tubes. Seminal receptacle of frontal organ long and narrow, about six times as long as wide, with strong circular musculature; accessory chamber lacking. Spermatheca of frontal organ small. Anterior portion of glandulomuscular structure of caudal organ nearly as wide as, and slightly longer than, middle portion; neck wide; copulatory tube without branches. Glandular sac of caudal organ ovoid.

Description.—Strap-shaped body; adults 680–701 μm long, 41–49 μm wide. Caudum tapers gradually into wide tail. Dorsal and lateral body surfaces densely covered with long sensory bristles (Fig. 8a). Ventral surface entirely covered with locomotor cilia except small, bare area posterior to anterior series of adhesive tubes and bare, diamond-shaped area surrounding female pore (Fig. 8b). Dorsal ciliary band on head at level of sensory pits. Anterior adhesive tubes ventral in two fields, on each side of body, near anterior margin of head (Fig. 8c). Anterior field a row of six or seven tubes of equal size in two distinct groups of three or four each, at about 130° angle to each other. Second field with one or two tubes. No anterior tubes reach level of sensory pits. About 26 lateral adhesive tubes on each side of trunk; an additional 10 tubes on each side of tail. Lateral tubes slightly longer near caudum. Adhesive tubes on trunk begin just anterior to pharyngeal-intestinal junction.

Mouth leads into small buccal cavity, which opens into pharynx. Pharyngeal-intestinal junction at U35; pharyngeal pores at U23. Intestine narrows in mid-trunk region; anus ventral.

Round, paired lateral testes at pharyngeal-intestinal junction taper into vasa deferentia; male pores separate and ventral, adjacent to seminal receptacle of frontal organ. Spermatheca of frontal organ small and irregular in shape, without secretory droplets. Seminal receptacle long and narrow, six times longer than wide with rounded apex; very small nozzle present at apex (Fig. 8d). Thin-walled tube leads from posterior end of seminal receptacle to simple ventral female pore. Seminal receptacle approximately five times as long as the diameter of spermatheca; circular muscle bands present. Ovary not observed, large ovum in front of seminal receptacle. Glandulomuscular structure of caudal organ with anterior portion long and broad with broadly rounded apex, about same length as middle portion; refractile granules sparse; copulatory tube unbranched. Stubby, curved neck of glandulomuscular structure extends to left side of glandular sac of caudal organ. Glandular sac ovoid.

Distribution and habitat.—Uncommon species, found only in sublittoral zone of small beach facing Gulf of Mexico. Coarse, poorly-sorted siliceous/carbonate mixed sediments. Honeymoon Island (one location).

Macrodasys blysocytalis, new species
Fig. 9

Holotype.—Adult specimen 780 μm in length, mounted on glass slide. Honeymoon Island, Florida, U.S.A., inside of sand spit beach facing St. Joseph Sound [28°05'N, 82°50'W]. USNM 168057.

Etymology.—*blyso* (L.) meaning bubble, after the bubble-like accessory chamber on the seminal receptacle; *cyto* (L.) meaning chamber or receptacle; *alis* (L.) meaning possession.

Diagnosis.—*Macrodasys* with trunk much longer than pharyngeal region. Lateral and ventral adhesive tubes present; dorsal tubes lacking. Anterior adhesive tubes ventral, in two fields on each side of body, near anterior margin of head. Anterior field a row of seven or eight tubes of equal size in two distinct groups of three or four tubes each, at about 100° angle to each other. Second field a row of two or three tubes. Additional, single lateral adhesive tube on each side of head separate from anterior series. Frontal organ a large, cone-shaped seminal receptacle with large, ovoid dorsal accessory chamber and a thick-walled spermatheca, about same size as seminal receptacle. Anterior portion of glandulomuscular structure of caudal organ broad with rounded tip, about half as long as middle portion; neck short; copulatory tube T-shaped. Glandular sac of caudal organ small.

Description.—Strap-shaped body; adults 678–784 μm long and 53–56 μm wide. Caudum tapers gradually into indistinct tail (Fig. 9a). Dorsal and lateral body surfaces covered with sensory bristles. Ventral surface entirely covered with locomotor cilia except small, bare area surrounding female pore (Fig. 9b). Sparse dorsal ciliary band on head at level of sensory pits. Anterior adhesive tubes ventral, in two fields on each side of body, near anterior margin of head (Fig. 9c). Anterior field a row of seven or eight tubes in two distinct groups of three or four tube each, at about 100° angle to each other; tubes in medial group one-half as long as tubes in lateral group. Posterior field a row of two or three tubes about 1.5 times as long as tubes in anterior field. Additional, single ventrolateral adhesive tube on each side of head separate from usual

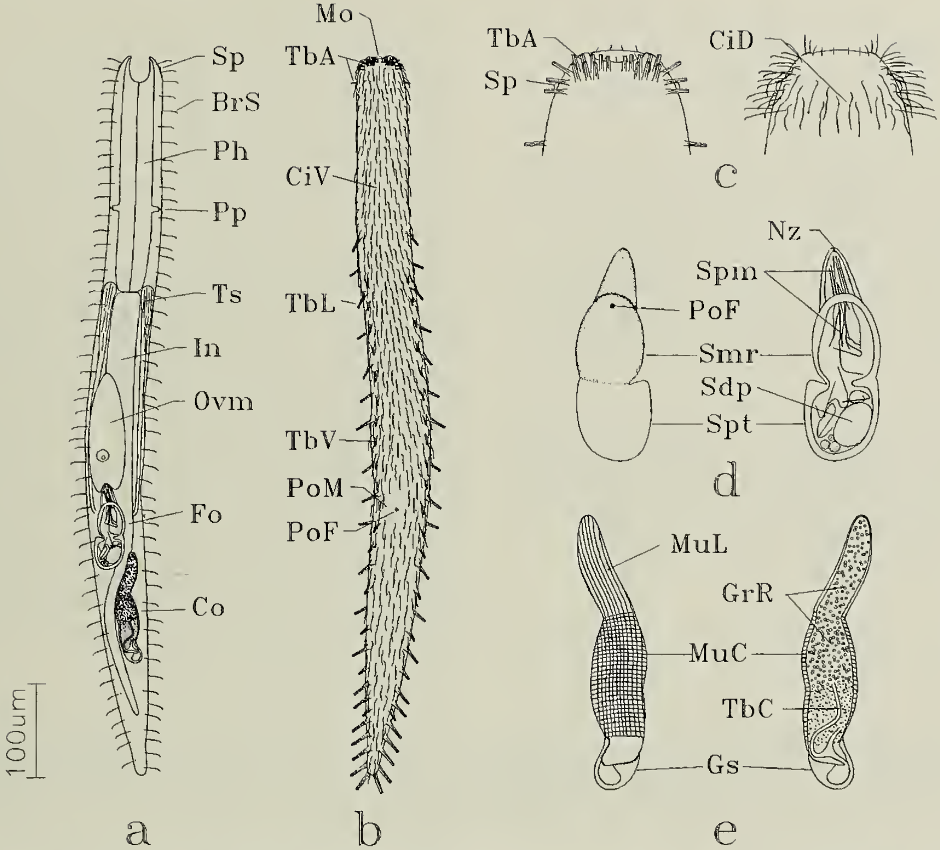

Fig. 9. *M. blysocytalis,* new species. Caudum tapers gradually into indistinct tail. Anterior adhesive tubes in three fields; additional pair of tubes laterally in head region. Seminal receptacle of frontal organ with accessory chamber in the form of a large, ventral blister. Copulatory tube of glandulomuscular structure of caudal organ branched. Abbreviations and a–e as in Fig. 4; c–e not to scale.

anterior series. About 15 lateral adhesive tubes on each side of trunk; additional six or seven tubes on each side of tail. Aside from single pair of tubes near anterior series, lateral tubes begin nearly at level of pharyngeal pores and are of uniform size. Two ventral rows of adhesive tubes begin posterior to second pair of lateral tubes and are much smaller than lateral tubes; about 10 ventral tubes per row. Lateral and ventral rows begin to converge on posterior third of trunk; ventral rows stop where tail begins.

Anterior mouth leads into buccal cavity, which opens into pharynx. Pharyngeal-intestinal junction at U30; pharyngeal pores at U21. Intestine narrows abruptly in mid-trunk region; anus ventral.

Elongate, paired lateral testes at pharyngeal-intestinal junction taper gradually into vasa deferentia; male pores separate and ventral, adjacent to anterior end of seminal receptacle of frontal organ. Spermatheca of frontal organ small and irregular in shape, with thick wall and large secretory droplets. Seminal receptacle cone-shaped with large, ovoid dorsal accessory chamber, about same size as spermatheca (Fig. 9d). Small nozzle present in anterior end of seminal receptacle; circular muscles not evident. Female pore exits from anterior end of accessory chamber of seminal receptacle. Ovary not observed; large ovum lies in front of seminal receptacle. Anterior portion of glandulomuscular structure of caudal organ wide with rounded apex, about half as long as middle portion. Copulatory tube T-shaped, branching as it enters middle portion of glandulomuscular structure (Fig. 9e); refractile granules larger anteriorly. Stubby, curved neck of glandulomuscular structure extends to left side of glandular sac of caudal organ.

Distribution and habitat.—Uncommon species, found only in littoral zone on inside of sand spit facing St. Joseph Sound. Medium-fine, well-sorted siliceous sediments. Honeymoon Island (one location).

Macrodasys stenocytalis, new species
Fig. 10

Holotype.—Adult specimen 670 μm in length, mounted on glass slide. Sombrero Beach, Vaca Key, Florida, U.S.A., small beach facing Atlantic Ocean [24°41'N, 81°05'W]. USNM 168061.

Etymology.—*steno* (L.) meaning narrow or constricted, after the constriction of the seminal receptacle; *cyto* (L.) meaning chamber or receptacle; *alis* (L.) meaning possession.

Diagnosis.—*Macrodasys* with trunk about same length as pharyngeal region. Lateral adhesive tubes present; ventral and dorsal tubes lacking. Anterior adhesive tubes ventral, in single row of from 12 to 14 tubes on each side of body, near anterior margin of head. Tubes arranged in arc with shortest medial and longest lateral. Frontal organ a seminal receptacle with muscularized bulb anterior to narrow constriction and an ovoid spermatheca about one-half as long as seminal receptacle. Anterior portion of glandulomuscular structure of caudal organ broad, both with narrow extension to tip, slightly more than one-half as long as middle portion; copulatory tube without branches; refractile granules sparse. Glandular sac of caudal organ small.

Description.—Broad, strap-shaped body; adults 661–680 μm long, 67–74 μm wide. Caudum tapers abruptly into short tail (Fig. 10a). Dorsal and lateral body surfaces covered with long sensory bristles. Ventral surface entirely covered with locomotor cilia except small, bare area surrounding female pore (Fig 10b). Sparse dorsal ciliary band on head at level of sensory pits. Anterior adhesive tubes ventral, in single row of from 12 to 14 tubes on each side of body, near anterior margin of head (Fig. 10c). Medial tubes shortest, lateral tubes longest. About 24 lateral adhesive tubes on each side of trunk; an additional six to eight tubes on each side of tail. Lateral tubes begin just anterior to pharyngeal-intestinal junction and are longest and most numerous where trunk constricts to form tail.

Mouth leads into buccal cavity, which opens into the pharynx. Pharyngeal-intestinal junction at U45; pharyngeal pores at U30. Intestine gradually narrows toward tail; anus ventral.

Paired lateral testes at pharyngeal-intestinal junction taper into vasa deferentia; male pores separate and ventral, adjacent to seminal receptacle of frontal organ. Spermatheca of frontal organ large and ovoid, with various-size secretory droplets. Seminal receptacle with ovoid posterior section which narrows before forming a bulbous, muscularized, anterior portion; small nozzle present (Fig. 10d). Seminal receptacle about twice as long as spermatheca. Female pore exits from posterior portion of seminal receptacle. Ovary not observed; large ovum lies in front of seminal receptacle. Anterior portion of glandulomuscular structure of caudal organ broad, but with narrow tip; slightly more than one-half as long as middle portion (Fig. 10e). Middle portion broad at midsection, narrow at ends; copulatory tube straight; refractile granules present. Short, curved neck of glandulomuscular structure extends to left side of glandular

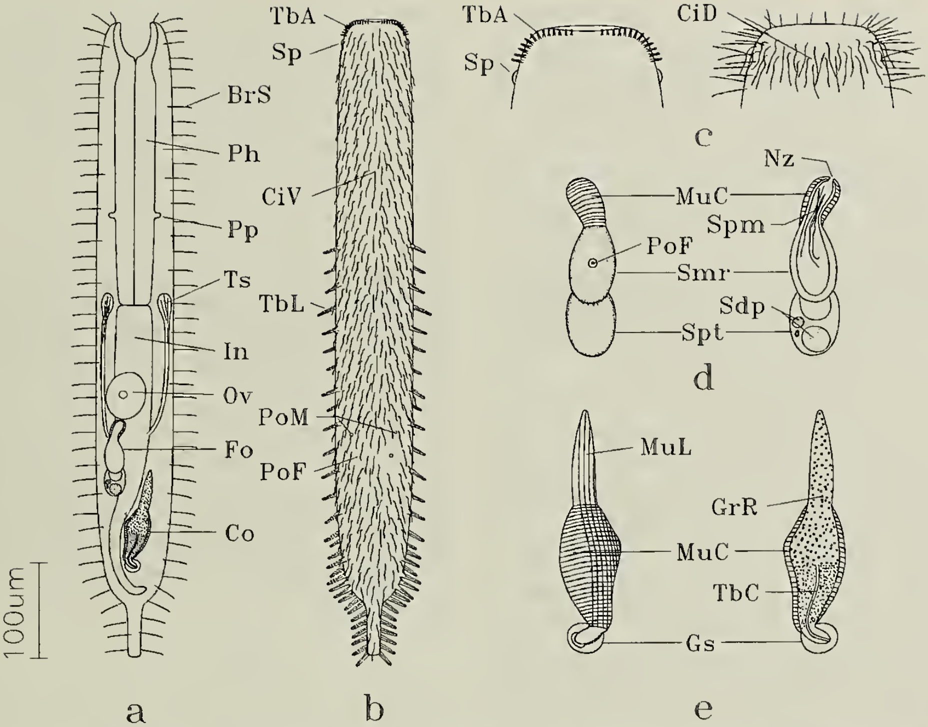

Fig. 10. *M. stenocytalis,* new species. Numerous small anterior adhesive tubes in single row. Seminal receptacle of frontal organ constricted in the middle; portion anterior to constriction sheathed in circular muscles. Glandular sac of caudal organ very small. Abbreviations and a–e as in Fig. 4; c–e not to scale.

sac of caudal organ. Glandular sac very small.

Distribution and habitat.—Uncommon species, found only in sublittoral zone on small beach facing the Atlantic Ocean. Coarse, poorly-sorted carbonate sediments. Sombrero Beach.

Discussion

Comparing the species described above to previously described species on the basis of reproductive morphology is difficult because descriptions of the reproductive system have been either omitted or described in insufficient detail by previous workers (e.g., Boaden 1963, Ganapati & Rao 1967, Roszczak 1939, Thane-Fenchel 1970). Where details of the reproductive system are given (e.g., Remane 1936, Schmidt 1974, Valbonesi & Luporini 1984, Wieser 1957) they do not match any of the species described herein; however, *M. meristocytalis* does closely resemble the *Macrodasys* sp. II of Ruppert 1978, fig. 1c, p. 210 from Florida. The reproductive morphologies of the seven Florida species described here are unique and provide an excellent basis for discriminating among species. Schoepfer-Sterrer (1974) found this to be the case with the only other genus, *Urodasys,* in the family Macrodasyidae.

It is also possible to make correct species assignments, at least in south Florida populations of *Macrodasys,* on the basis of external features such as length, the number of rows of lateral adhesive tubes, and the arrangement of the anterior tubes, when these features are used in combination. However, adhesive tubes, especially of the anterior, dorsal, and ventral series can be difficult to see without differential interference contrast optics. The number of tubes in each series is hard to determine and varies with the age of the individual, making them an unreliable character (Luporini et al. 1973). Conversely, the reproductive organs, once formed, are stable in size and shape, large, and easily observed in adult specimens, even with transmitted-light microscopy. They are often visible even when the specimen otherwise is in poor condition and would be the preferred characters for identifying species in this genus.

What might appear to be a considerable amount of morphological variability in *Macrodasys* populations at particular geographic locations is, in the Florida case, largely caused by species that are superficially similar and whose ecological distributions overlap. For example, the Crandon Park inside-location had three species occurring together in the littoral zone that contributed to the overall variability of the *Macrodasys* population as a whole. Morphometric analyses based on reproductive characters can help to resolve such variability into species-specific components.

The two most abundant species (*M. achradocytalis* and *M. meristocytalis*) had much wider geographic distributions than the rarer species. Each of the two occurred at five locations, in both littoral and sublittoral zones, and in a wide variety of sediment types. When found in the same beach, these two species exhibited non-overlapping horizontal distributions in steep, tidal beaches, but were mixed in narrow, atidal beaches. Less abundant species were found only at one, or at most two, sampling locations and were always restricted to either the littoral or sublittoral zone. Vertical overlap of species within beaches and seasonal changes in geographic and ecological distributions were not investigated.

The large number of species found in a limited (on a global scale) geographical area in this and similar studies (Schmidt 1974, Valbonesi & Luporini 1984), suggests that *Macrodasys* is a very speciose genus. This requires that claims of global distributions for members of this genus, particularly the frequently reported *M. caudatus,* be supported by detailed morphological analyses on local and regional bases.

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This work was completed while a Postdoctoral Fellow at Ohio University under National Science Foundation Grant BSR-9006798 to William D. Hummon, and was supported, in part, by Ohio University Research Committee Grant 2335 to the author and by the Ohio University Meiofaunal Research Support Fund. W. D. Hummon and M. A. Todaro helped collect material for preliminary analyses and critically reviewed the manuscript.

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A NEW SPECIES OF *ELAPHOIDELLA* (CRUSTACEA: HARPACTICOIDA) CLOSELY RELATED TO *E. BIDENS* (SCHMEIL) AND THE GENUS *ATTHEYELLA* FROM NEPAL

Teruo Ishida

Abstract.—*Elaphoidella nepalensis,* n. sp., from a small stream in Kathmandu, Nepal, is described. The new species is closely related to *Elaphoidella bidens,* and the genus *Attheyella* since the species has two setae on the basoendopodite of the male fifth leg.

In a sediment sample from a small stream in the Botanical Garden of Kathmandu, the herein described new species, *Elaphoidella nepalensis* was found. Dr. Tomiko Ito (Hokkaido Fish Hatchery, Japan) collected the sample by scraping the bottom with a fine mesh hand net.

E. nepalensis, n. sp. is in many aspects very similar with *Elaphoidella bidens* (Schmeil) but differs from the latter by its caudal rami and by the peculiar ornamentation of the male fifth leg, bearing two elements.

Specimens were mounted in gum-chloral medium; drawings and measurements were made from the mounted specimens. Specimens were deposited in the U.S. National Museum of Natural History, Smithsonian Institution (USNM).

Order Harpacticoida Sars, 1903
Family Canthocamptidae Brady, 1880
Genus *Elaphoidella* Chappuis, 1929
Elaphoidella nepalensis, new species
Figs. 1–19

Material.—Holotype: female, dissected on 1 slide (USNM 259575). Allotype: male, dissected on 5 slides (USNM 259576). Paratypes: 1♂, (leg 4 and abdomen only), dissected on 2 slides (USNM 259577); 1♂, dissected on 1 slide (USNM 259578); 5♀♀, habitus, on 1 slide (USNM 259579); 20♀♀, in 70% ethanol (USNM 259580). All from a small stream in the Botanical Garden (alt. ca 1400 m), Godavari, Kathmandu, 11 May 1983.

Female.—Length of holotype excluding caudal setae 0.52 mm: range of lengths of 5 paratypes 0.52–0.67 mm. Cephalothorax (Fig. 1) with elongate planarian-shaped nuchal organ. All somites except anal somite with posterior margins serrated. All somites except cephalothorax with transverse rows of minute spinules (Fig. 13). Genital double somite with remnant of division beneath integument; genital field as in Fig. 2, reaching midlength of double somite. Two urosomites posterior to genital double somite (Figs. 1, 2) each with one row of long spines on ventral and lateral margin; 3rd urosomite also with grouped fine spines in middle of ventral surface. Anal somite (Fig. 2) without spines near the posteroventral margin; anal operculum (Fig. 3) with 18 spines, slightly convex. Caudal ramus (Figs. 1, 2, 4) about 1.7 times longer than broad, subrectangular, with dorsal, terminally hooked longitudinal keel extending over ⅔ of the length of ramus. Ramus with basally biarticulate dorsal seta inserted near end of keel, two lateral setae, a transverse row of three spines ventrolaterally, group of slender spines distal to medial lobe, and three terminal setae. Median terminal seta inserted a little above outer and inner terminal setae, lacking proximal breaking plane, basally expanded, and about 1.3 times longer than urosome. Outer distal seta (Fig. 2) slender, with bulbous base. Inner terminal seta naked, slightly longer than half the outer one.

Rostrum very small, with two sensilla. Antennule (Fig. 5) of eight articles, article 4 with long esthetasc reaching past end of antennule, article 8 with short and slender esthetasc. Antenna (Fig. 6) biarticulate. Exopodite uniarticulate bearing four setae. Palp of mandible (Fig. 7) biarticulate. Proximal article with a single seta. Distal article with four terminal setae and one lateral seta.

Legs 1–4 (Figs. 8-11) with triarticulate exopodites; endopodite of leg 1 triarticulate, longer than exopodite; endopodites of legs 2–4 biarticulate. Setal formula as follows:

Leg 1	basis 1-1	exp 0-1; 1-1; 0,2,2
		enp 1-0; 1-0; 0,2,1
Leg 2	basis 0-1	exp 0-1; 1-1; 1,2,2
		enp 1-0; 2,2,1
Leg 3	basis 0-1	exp 0-1; 1-1; 2,2,2
		enp 1-0; 3,2,1
Leg 4	basis 0-1	exp 0-1; 1-1; 2,2,2
		enp 1-0; 2,1,1

Couplers of legs 1 and 2 with row of spines on each side; those of legs 3 and 4 with smooth surfaces.

Leg 5 (Fig. 12), inner expansion of basoendopodite reaching ⅓ length of exopodite, with four setae; edge of inner expansion produced into denticles between first and second and second and third setae (commencing at medial margin). Exopodite with five setae of which outer lateral two setae are short and next to innermost seta longest. Leg 6 (Fig. 2) consisting of protrusion bearing two plumose setae.

Male.—Length of allotype 0.47mm, of paratypes 0.42 and 0.43 mm. Body form similar to female. Second to 4th urosomal somites (Fig. 13) with one row of long spines on ventral and lateral margin. Anal somite (Fig. 13) with one or two spines near posteroventral margin above each caudal ramus. Caudal ramus (Fig. 13) narrower posteriorly. Lateralmost terminal seta with slightly bulbous base.

Legs 1, 2, and leg 4 exopodites similar to those of female. Leg 3 (Fig. 16) exopodite, major lateral spines of article 1, 2, thick; endopodite triarticulate, modified, spiniform process of article 2 slender to tip, seeming to lack hook, reaching only midlength of exopodite article 3, article 3 with two long apical plumose setae. Leg 4 endopodite (Fig. 17) article 2 shorter than that of female.

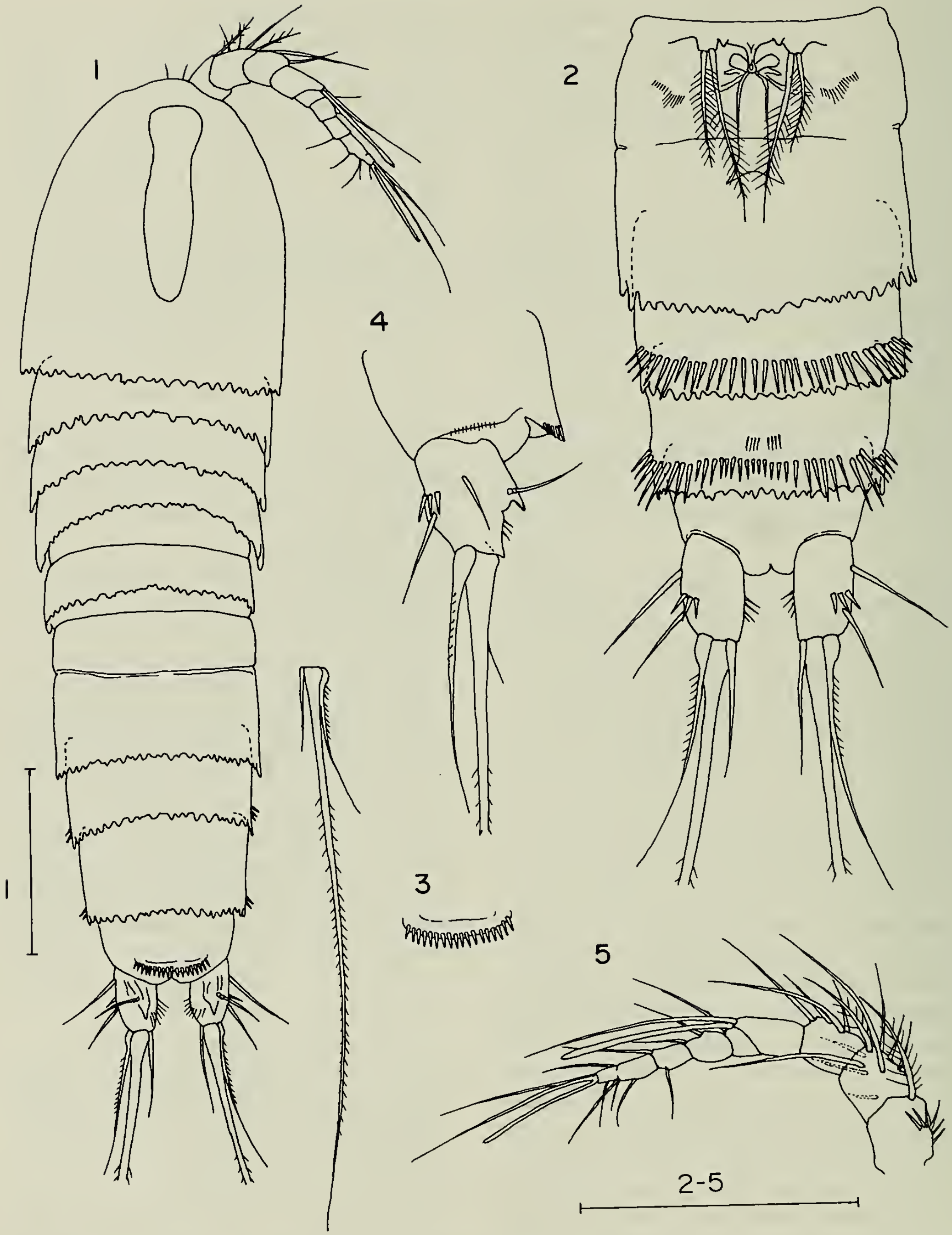
Leg 5 (Fig. 18) basoendopodite reduced, with two setae, inner one longer than outer one. Exopodite slightly longer than broad and bearing five setae. Leg 6 (Fig. 19) rudimentary forming posterior margin of somite, only one seta on each side, setae of different lengths.

No variation was observed among specimens of either sex.

Etymology.—Specific name refers to its distribution in Nepal.

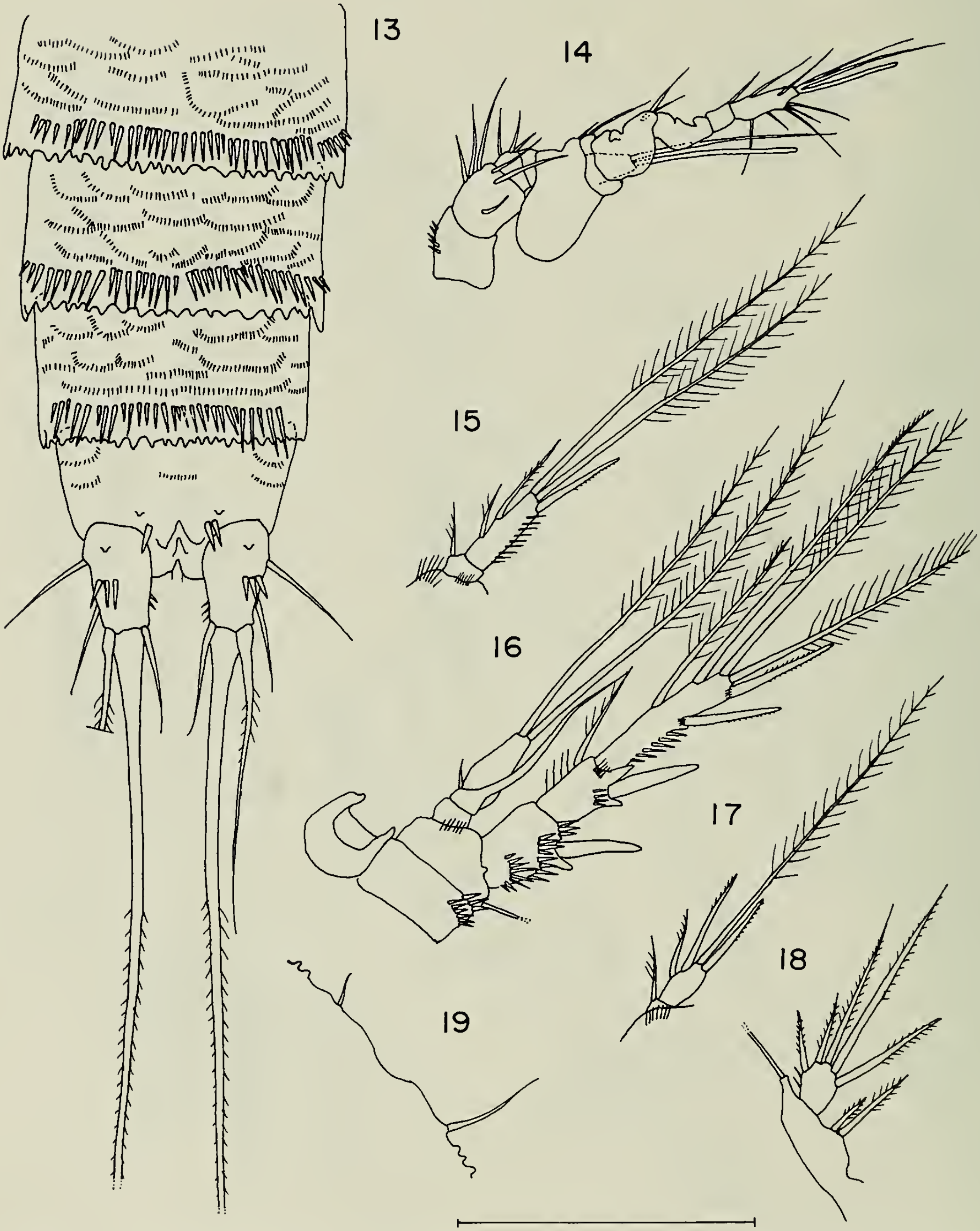
Affinities.—*Elaphoidella nepalensis,* n. sp. is most closely related to *E. bidens.* The morphological characteristics of the female specimens are the same as those of *E. bidens* s. s. and *E. bidens coronata* (Sars), except the leg 4 endopodite and the shape of the caudal rami (Chappuis 1931, Gurney 1932, Coker 1934, Lang 1948, Carter & Bradford 1972, Tai & Song 1979, Hamond 1987), and similar to *E. bidens decorata* (Daday), including the leg 4 and caudal rami (Chappuis 1931, Tai & Song 1979).

Differences between the two species exist in the male. Important diagnostic features of the male of the new species, in contrast to the male of *E. bidens* s. l. are the armament of the biarticulate endopodite of leg 4 which bears an inner seta on the proximal article and four setae or spines on the distal article (versus uniarticulate in *E. b. coronata* or biarticulate in *E. bidens* s. s. and *E. b. decorata* with two setae on the distal article, except *E. bidens* s. s. with four setae or spines on the distal article). Also, leg 5 basoendopodite bears two setae and the exopodite



Figs. 1–5. *Elaphoidella nepalensis*, n. sp., female, holotype: 1, Habitus, dorsal; 2, Abdomen, ventral; 3, Anal operculum; 4, Anal somite and caudal ramus, lateral; 5, Antennule. Scales = 100 μm.

Figs. 6–12. *Elaphoidella nepalensis*, n. sp., female, holotype: 6, Antenna; 7, Mandible; 8, Leg 1 and coupler; 9, Leg 2 and coupler; 10, Leg 3 and coupler; 11, Leg 4 and coupler; 12, Leg 5. Scale = 100 μm.



Figs. 13–19. *Elaphoidella nepalensis,* n. sp., male, allotype: 13, Abdomen except 1st urosomite, ventral; 14, Antennule; 15, Leg 2 endopodite; 16, Leg 3 and coupler; 17, Leg 4 endopodite; 18, Leg 5; 19, Leg 6. Scale = 100 μm.

bears five setae (versus naked basoendopodite and exopodite bearing four setae in *Elaphoidella bidens* s. l.) (Chappuis 1931, Dussart 1967, Carter & Bradford 1972, Tai & Song 1979, Reid & Ishida 1992). Among the already known *Elaphoidella* species, as far as I know, only *Elaphoidella caeca* Miura is equipped with two or three setae on the basoendopodite of leg 5 of the male (Miura 1964). However, this species is quite different from *E. nepalensis* in the formula for major armament of legs 2–4 and the rudimentary leg 5.

The genus *Elaphoidella* is closely related to *Attheyella,* and in particular *E. bidens* is close to *Attheyella crassa* (Sars) (Lowndes 1950). Leg 5 of the male of *E. nepalensis* is closer to that of *A. crassa* than to *E. bidens.* It can be said that the new species occupies a transitional position between the *Elaphoidella* and the *Attheyella.* The discovery of this species further confuses the generic distinctions within the Canthocamptidae, providing support for Hamond's (1987) statement that the family is in need of revision. Hamond returned several generic and subgeneric taxa including *Elaphoidella* to the synonymy of the genus *Canthocamptus* Westwood, 1836 s. l. pending eventual revision of the family Canthocamptidae. The revision must be comprehensive, and until then, I employ the more familiar genus name.

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I wish to pay most cordial thanks to Dr. T. Ito, Hokkaido Fish Hatchery, for her stimulating sampling in Nepal. Sincere thanks are also due to Dr. J. W. Reid for reading the manuscript. Several anonymous reviewers made valuable suggestions for improvement of the manuscript.

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MONSTRILLA ELONGATA, A NEW MONSTRILLOID COPEPOD (CRUSTACEA: COPEPODA: MONSTRILLOIDA) FROM A REEF LAGOON OF THE CARIBBEAN COAST OF MEXICO

E. Suárez-Morales

Abstract.—A new species of a monstrilloid, *Monstrilla elongata,* is described from plankton samples collected in a reef lagoon along the northern portion of the eastern coast of the Yucatan Peninsula. The new species is described from a single female and can be distinguished from the other species of *Monstrilla* by the combination of the body proportions, a single-lobed fifth leg bearing only two setae, furcal rami with five setae, and the unusual annulated structure of the ovigerous spines.

Monstrilloid copepods are occasional elements in plankton samples, since only the reproductive adult stage is free-living (Davis 1984). Naupliar and juvenile stages of these copepods are parasites of polychaetes and gastropod molluscs (Hartmann 1961, Huys & Boxshall 1991). This group is one of the least known within the Copepoda. The number of known species is relatively small (around 90 nominal species) and several have been described from a single specimen (Davis 1947, 1949; Suárez-Morales & Gasca-Serrano 1992). Valuable, but not comprehensive revisions of the group have been made by Davis (1949) and by Isaac (1975). Only three genera are now recognized, *Monstrilla, Monstrillopsis* and *Thaumaleus* (Huys & Boxshall 1991).

Some previous records of *Monstrilla* in the western tropical Atlantic include: *M. floridana* Davis, 1947, *M. rugosa* Davis, 1947, *M. reticulata* Davis, 1949, *M. helgolandica* Giesbrecht, 1892 and *M. grandis* Giesbrecht, 1891 (Davis 1947, 1949; Isaac 1975, Fish 1962, Reid 1990). Additional records of monstrillids have been stated from material obtained on the northern and central portions of the eastern coast of the Yucatan Peninsula. In these areas, several new species of *Monstrilla* (*M. barbata* Suárez-Moralez & Gasca-Serrano, 1992; *M. reidae* Suárez-Morales, 1993a; *M. rebis* Suárez-Morales, 1993b; *M. mariaeugeniae* Suárez-Morales & Islas-Landeros, 1993) as well as the new species *Monstrillopsis ciqroi* Suárez-Morales, 1993b and *Thaumaleus boxshalli* Suárez-Morales, 1993c have been reported.

During plankton surveys carried out by CIQRO in a reef lagoon located off Puerto Morelos along the northern portion of the Yucatan Peninsula's eastern coast (Suárez & Gasca 1990), one undescribed species of monstrilloid copepod belonging to the genus *Monstrilla* was collected. This species was previously misidentified by Suárez & Gasca (1990) as *Monstrilla leucopis* Sars, 1921.

Monstrilla elongata, new species

Type locality.—Reef lagoon off Puerto Morelos, northern portion of the eastern coast of the Yucatan Peninsula (20°51.40′N; 86°54.15′W). Date of collection 1988 Jan 16. Water column. Over *Thalassia testudinum* beds.

Material examined.—Holotype; female, undissected, deposited in the U. S. National Museum of Natural History, Smithsonian Institution, under number USNM-259488. Paratype; female, undissected, deposited in

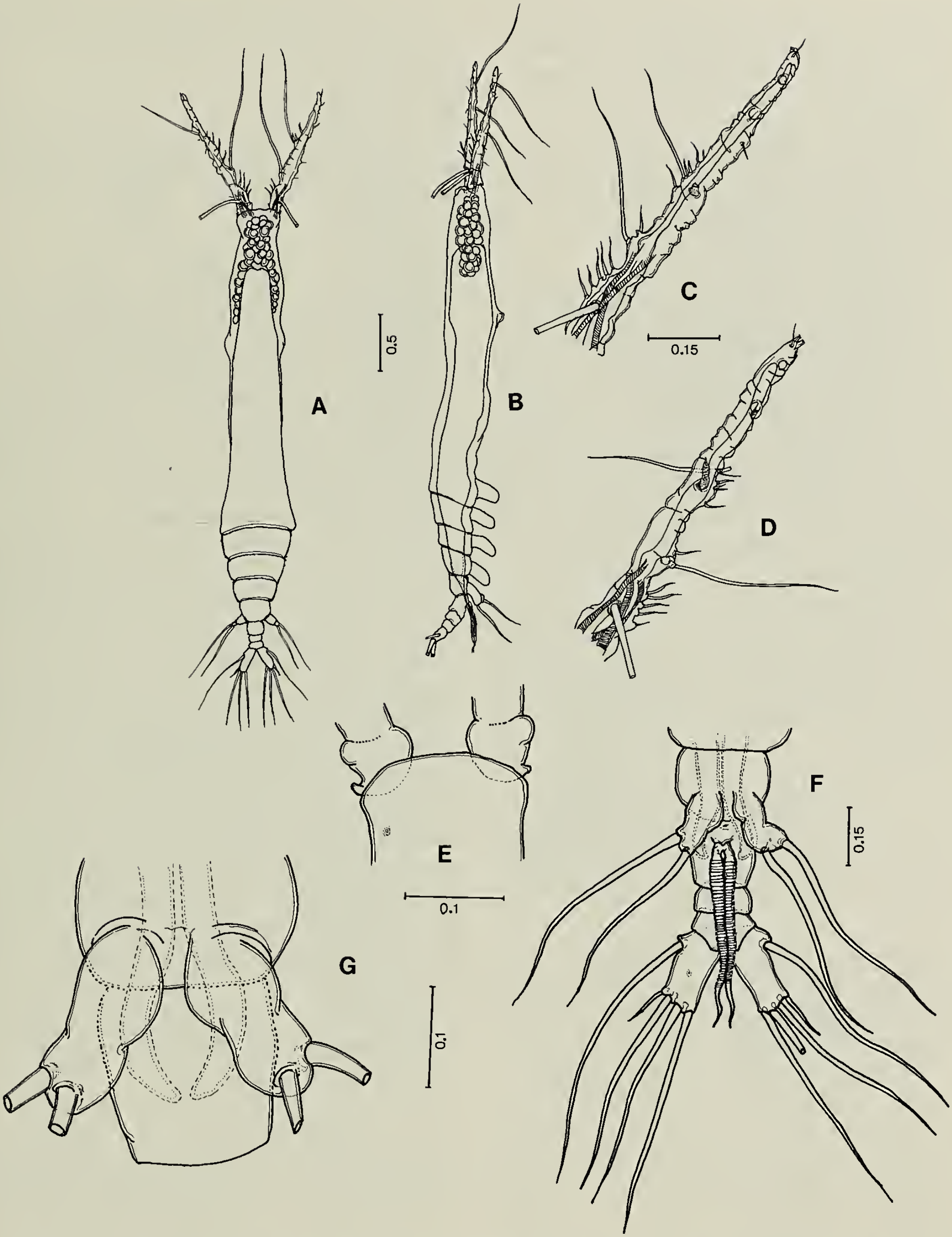

Fig. 1. A. *Monstrilla elongata* n. sp. habitus, dorsal. B. habitus, lateral. C. right antennule, dorsal view. D. left antennule, dorsal view. E. head and first antennular segments. F. urosome, ventral view. G. fifth legs, ventral view.

the same institution under number USNM-259665. Specimens preserved in 70% ethanol. Paratype; female, dissected, author's collection at CIQRO.

Female.—Length 4.2 mm. Cephalic segment long and slender, almost 0.65 of total body length. Oral papilla located 0.43 of way back along cephalic segment. Eyes absent (Figs. 1A, B).

Antennulae 5-segmented, with segments 2–5 partially fused. Antennulae armed with three spines on first segment, and ten spines and six setae on remaining four segments. Three of these setae ripped away, sockets remaining. Large aesthetasc at midlength. Ratio of length of first segment and remainder being: 14:86 = 100 (Figs. 1C, D). Antennulae 0.24 of total body length. First segment with small lateral protuberance on basis, visible in dorsal view (Fig. 1E).

Incorporated first thoracic somite and succeeding three thoracic segments bearing well developed, biramous swimming legs with triarticulated rami (Figs. 2J, K, L). Swimming legs equal in length and armed as follows:

	basis	endopodite	exopodite
leg 1	1-0	0-1; 0-1; 0-1, 1, 3	I-0; 0-1; I, 1, 3
leg 2	0-0	0-1; 0-1; 0-1, 1, 3	I-0; 0-1; I, 1, 4
leg 3	0-0	0-1; 0-1; 0-1, 1, 3	I-0; 0-0; I, 1, 3
leg 4	0-0	0-1; 0-1; 0-1, 1, 3	I-0; 0-1; I, 1, 3

Fifth leg 1-segmented with broad single lobe bearing two setae (Fig. 1G); outer seta slightly longer than inner but both reaching beyond distal end of furcal rami (Fig. 1F).

Urosome consisting of fifth pedigerous somite, genital double and two free abdominal somites (Fig. 2H), length ratio of these 4 segments being: 39.6:33.3:14.6:12.5 = 100. Genital complex with two thick, annulated ovigerous structures, as shown in Fig. 1I. Distal ends of ovigerous structures reaching slightly beyond distal end of furcal rami.

Furcal rami 2.3 times longer than wide, bearing five setae, four of them strongly developed, remaining one being thinner and ⅙ as long as others. One of large setae borne on proximal outer margin, small seta on distal outer margin, remaining three setae terminal.

Male.—unknown.

Etymology.—The specific name makes reference to the unusual proportional length of the cephalic segment.

Discussion

The new species has been assigned to the genus *Monstrilla* on the basis of the presence of two free abdominal somites posterior to the genital double somite, the absence of eyes, and the location of the oral papilla more than 0.25 of the way back along the cephalic segment (Isaac 1975).

Monstrilla elongata differs from all other species of the genus *Monstrilla* in some relevant features. The presence of a single lobe with two setae on the fifth leg is a feature shared with *M. conjunctiva* Giesbrecht, 1902, *M. helgolandica* Claus, 1863, *M. longipes* A. Scott, 1909 and *M. ghardagensis* Al-Kholy, 1963. The structure of the lobe is different in each case; in *M. helgolandica,* it is narrow and bent in the middle (Park 1967, Isaac 1975), but in *M. conjunctiva,* the same structure is broad at base and narrows abruptly (Isaac 1975). *Monstrilla longipes* exhibits a very long and slender fifth leg lobe (Davis 1949, Scott 1909), and in *M. ghardagensis* is short and slender (Al-Kholy 1963). In *M. elongata,* this lobe is broad both at the base and at distal portion, with a slight medial constriction, as shown in Fig. 1G.

The relative length of the antennulae differs in the five species; in *M. conjunctiva,* the antennulae constitute 0.35 of the total body length, this proportion is 0.28 in *M. helgolandica,* 0.19 in *M. ghardagensis,* 0.22 in *M. longipes* and 0.24 in *M. elongata.* Moreover, neither of these species have fused antennular segments, a condition clearly present in *M. elongata.* This feature, however, is not uncommon throughout the genus; in *M. longiremis* Giesbrecht, 1892,

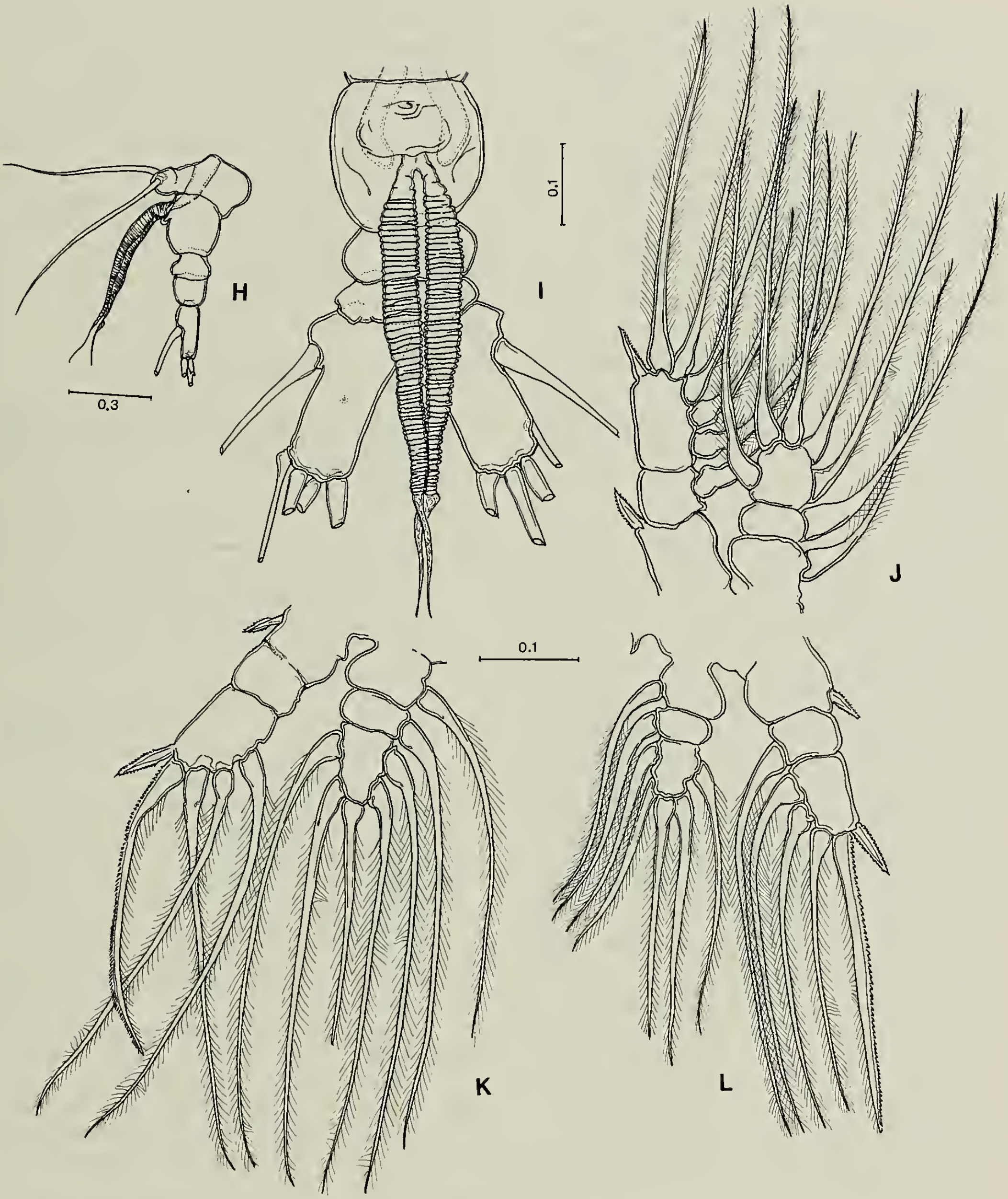

Fig. 2. H. urosome, lateral view. I. genital segment with ovigerous structures, and furcal rami. J. second leg. K. third leg. L. first leg.

only the proximal segment is clearly defined, and in *M. grandis* Giesbrecht, 1891, only the first two segments are separated.

The presence of a spine on the medial side of the basis of the first legs is another distinctive feature of *M. elongata* when comparing it with *M. helgolandica, M. longipes* and *M. ghardagensis.* It is only present in a few other monstrilloids (Grygier, pers. comm.). Furthermore, *M. elongata* differs from *M. helgolandica, M. longipes* and *M. ghardagensis* in the number of furcal setae, six in *M. helgolandica* and *M. longipes,* and four in *M. ghardagensis,* but only five in the new species. *Monstrilla conjunctiva* also has five furcal seta, with the same arrangement found in *M. elongata* (Sewell 1949).

In both *M. helgolandica* and *M. conjunctiva,* the genital double somite is at least 1.5 times longer than the free abdomen (Sewell 1949, Isaac 1975). It is shorter in *M. longipes.* In *M. elongata* and in *M. ghardagensis,* the genital somite is almost the same length as the free abdomen. The structure of the genital complex is also different in these species. In *M. helgolandica, M. ghardagensis* and in *M. conjunctiva,* the ovigerous spines are long and slender, reaching beyond the distal end of the furcal rami (Sewell 1949). The structure of the genital complex or of the ovigerous spines are not described in the original description of *M. longipes* (Scott 1909). In *M. elongata,* the ovigerous structure is broader and shorter, and is not slender, but exhibits a thick, annulated aspect. The same type of structure has also been found for *M. mariaeugeniae* from the same locality (Suárez-Morales & Islas-Landeros 1993). These kind of apparently undeveloped genital structures can not be related to copepodids or other immature stages since the development of monstrilloids takes place up to the fully mature adult within the host, and the adult burrows out of the host as a planktic form (Davis 1984).

Finally, measuring 4.2 mm, the new species is clearly larger than *M. conjunctiva* (3.3–3.8 mm), *M. longipes* (1.83 mm), *M. ghardagensis* (1.35 mm) and *M. helgolandica* (1.4–2.3 mm). It is also is one of the largest species of the genus, after *M. mariaeugeniae* (4.4 mm) and *M. clavata* (4.5 mm).

Acknowledgments

Thanks to Dr. Thomas E. Bowman for his comments on the drawings. This work was carried out with the logistic and financial support of the Centro de Investigaciones de Quintana Roo (CIQRO) (Proj. 01-02-009) and of CONACYT (Proj. 1118-N9023). Additional material of this species was sorted by Ma. Eugenia Islas-Landeros. Ms. Janice Clark, of the National Museum of Natural History, Smithsonian Institution, kindly made the deposition and catalogation of the type specimens. Mark J. Grygier granted relevant literature.

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ANNINA MANNAI, A NEW ISOPOD FROM THE GANGES RIVER, WEST BENGAL (CRUSTACEA: ISOPODA: CIROLANIDAE)

Marilyn Schotte

Abstract.—*Annina mannai,* n. sp., the fifth known species of *Annina,* is described from fresh water of the Ganges River in West Bengal, India. It is distinguished from its congeners by a single, crescent-shaped dorsal projection in the male on pereonite 2.

The genus *Annina* was erected in 1908 by Budde-Lund to accommodate *A. lacustris,* taken from a salt-water pool in Zanzibar off the East Africa coast. Three others have since been described from mangrove swamps, estuaries and streams (*A. kumari* [Bowman 1971] from Malaysia; *A. fustis* Bowman & Iliffe 1991 from Thailand; and *A. mesopotamica* [Ahmed 1971] from Iraq). Jones (1983) provided a revised diagnosis of *Annina,* declaring it distinct from the closely-related *Excirolana* due to the presence of dorsal projections on the male cephalon and/or pereonites 1 and/or 2, a transverse non-facetted band in the eye, and other characters.

Herein is described a fifth species, collected by Dr. A. K. Manna in fresh water of the Ganges River along with atyid shrimp. All known species of *Annina* have been described from near the northern perimeter of the Indian Ocean region (see Fig. 4). Non-type localities include Singapore (*A. fustis*) and Kenya and Comoros Islands, where *A. lacustris* has been found (Bowman & Iliffe 1991).

Genus *Annina* Budde-Lund, 1908
Annina mannai, new species
Figs. 1–3

Material.—USNM 252750 Holotype ♂, TL 7.0 mm; USNM 252751 Allotype ♀, TL 8.9 mm; USNM 252752 Paratypes, 1♂, 18 ♀, 11 juvs., shore of Ganges River in District Murshidabad, West Bengal, India, coll. A. K. Manna, 1992.

Description.—Length up to 8.9 mm. Body widest at pereonite 6; pleon narrower than pereon. Marked sexual dimorphism; adult male with dense patch of setae between eyes and crescent-shaped middorsal process on pereonite 2; blunt, raised "shoulders" at anterolateral parts of pereonite 2; pereonite 1 with middorsal depression. Female cephalon without setae or processes; no processes on pereon.

Cephalon produced anteriorly into rounded rostrum projecting between antennal bases. Lateral incision posterior to each eye, reaching medially ⅓ width of cephalon. Clypeus triangular, pointed, directed antero-ventrally. Eyes large, with transverse, unfacetted gap dividing dorsal and ventral halves. Coxae of pereonites 1–3 rounded posteriorly; coxae 4–7 progressively more sharply pointed. Lateral margins of pleonites 1–2 straight; those of 3–5 increasingly more extended. Telson triangular, posterior ⅔ finely scalloped, bearing plumose setae, without spines. Uropodal endopod similarly scalloped on both margins, bearing plumose setae, endopod barely extending beyond apex of telson. Uropodal exopod lanceolate, faintly notched on medial margin, acuminate at apex, reaching distal ⅔ length of endopod. Pigment densest near posterior margins of cephalon, pereonites,

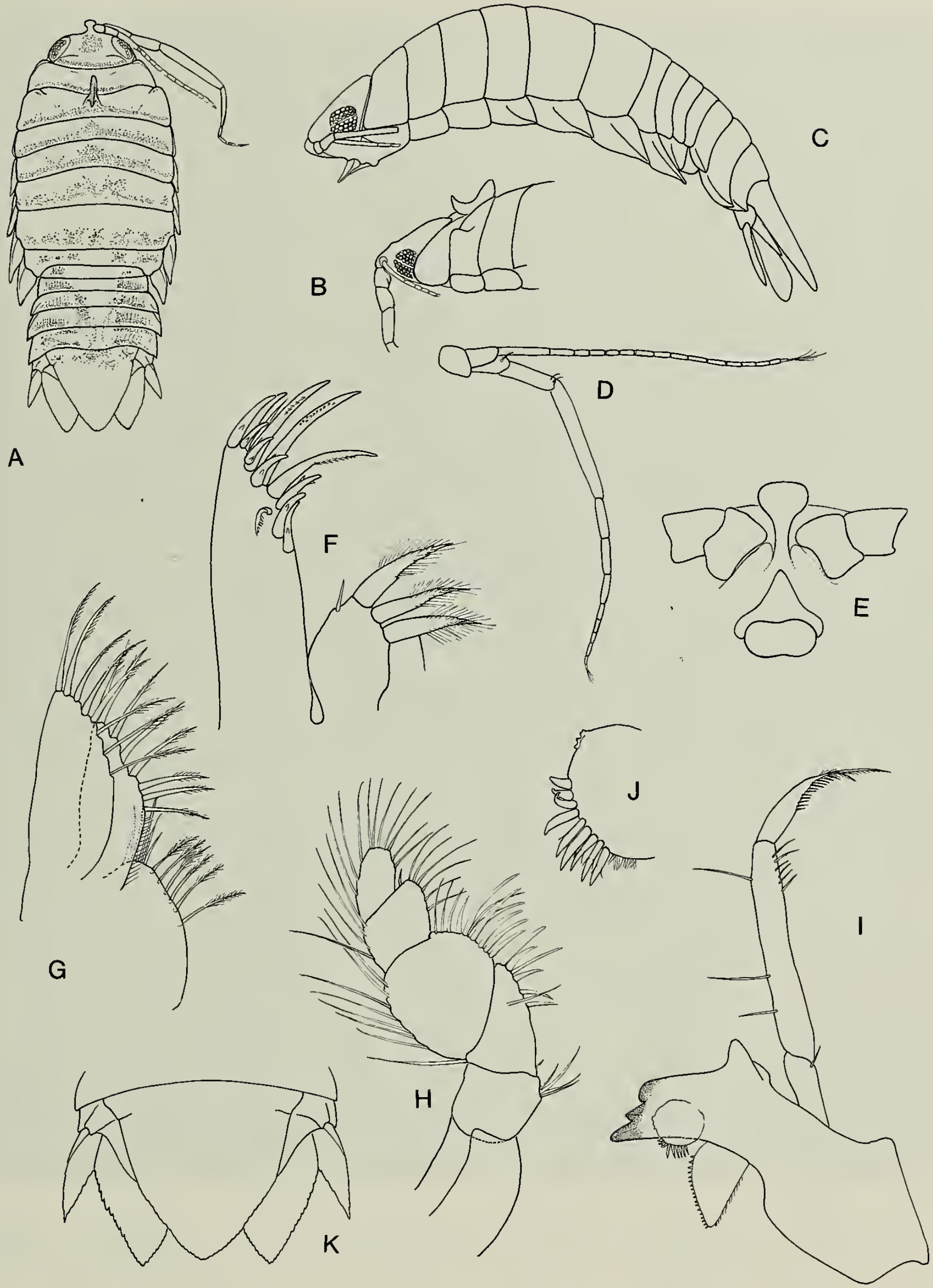

Fig. 1. *Annina mannai,* new species. A, ♂ habitus. B, ♂, lateral view of anterior. C, lateral view of ♀. D, antennae 1 and 2. E, frontal lamina and clypeus. F, maxilla 1. G, maxilla 2. H, maxilliped. I, right mandible. J, spine row and lacinia mobilis, detail. K, telson and uropods.

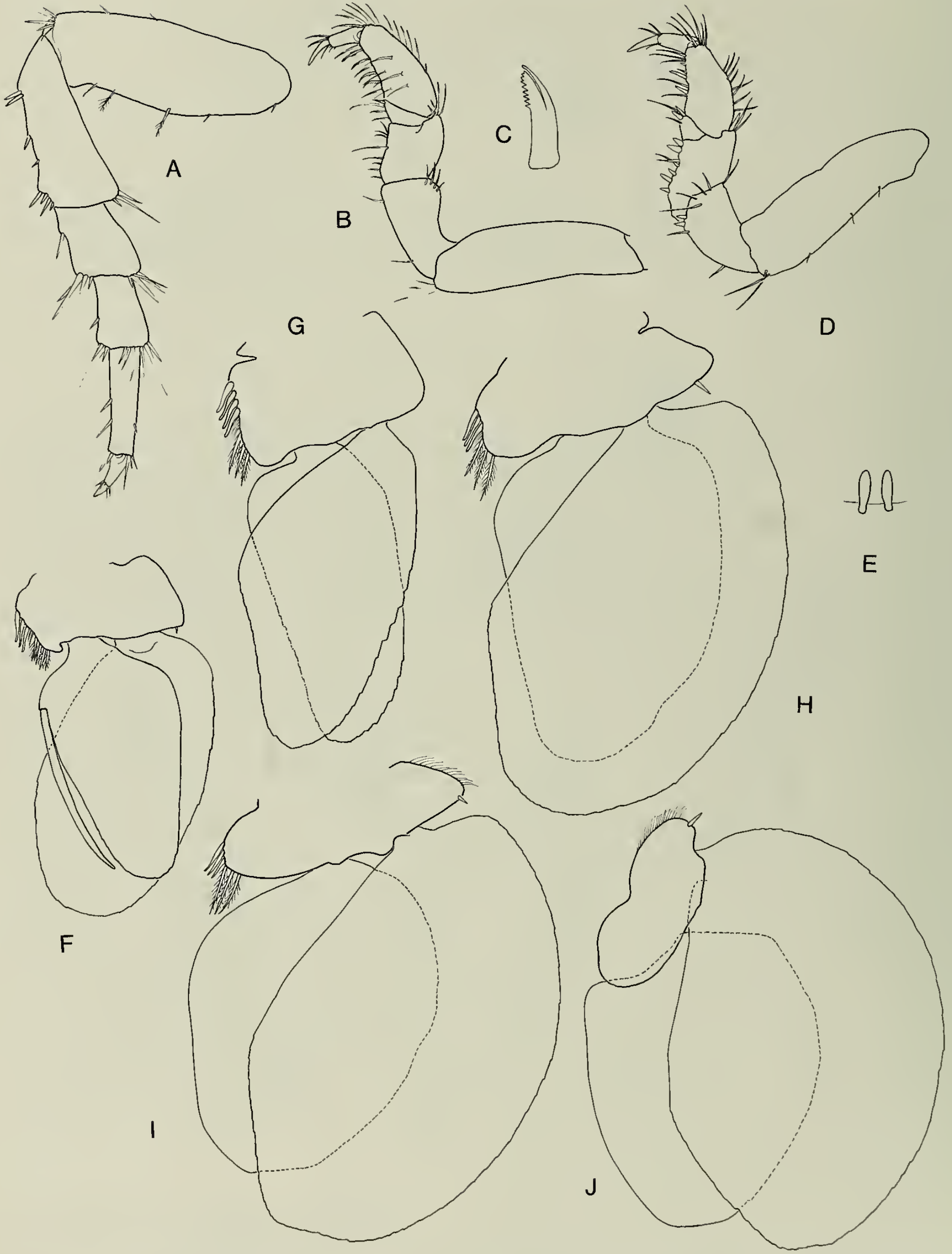

Fig. 2. *Annina mannai,* new species. A, pereopod 7. B, pereopod 1. C, cleft spine on pereopod 1. D, pereopod 2. E, penes. F, pleopod 2, ♂. G, pleopod 1. H, pleopod 3. I, pleopod 4. J, pleopod 5.

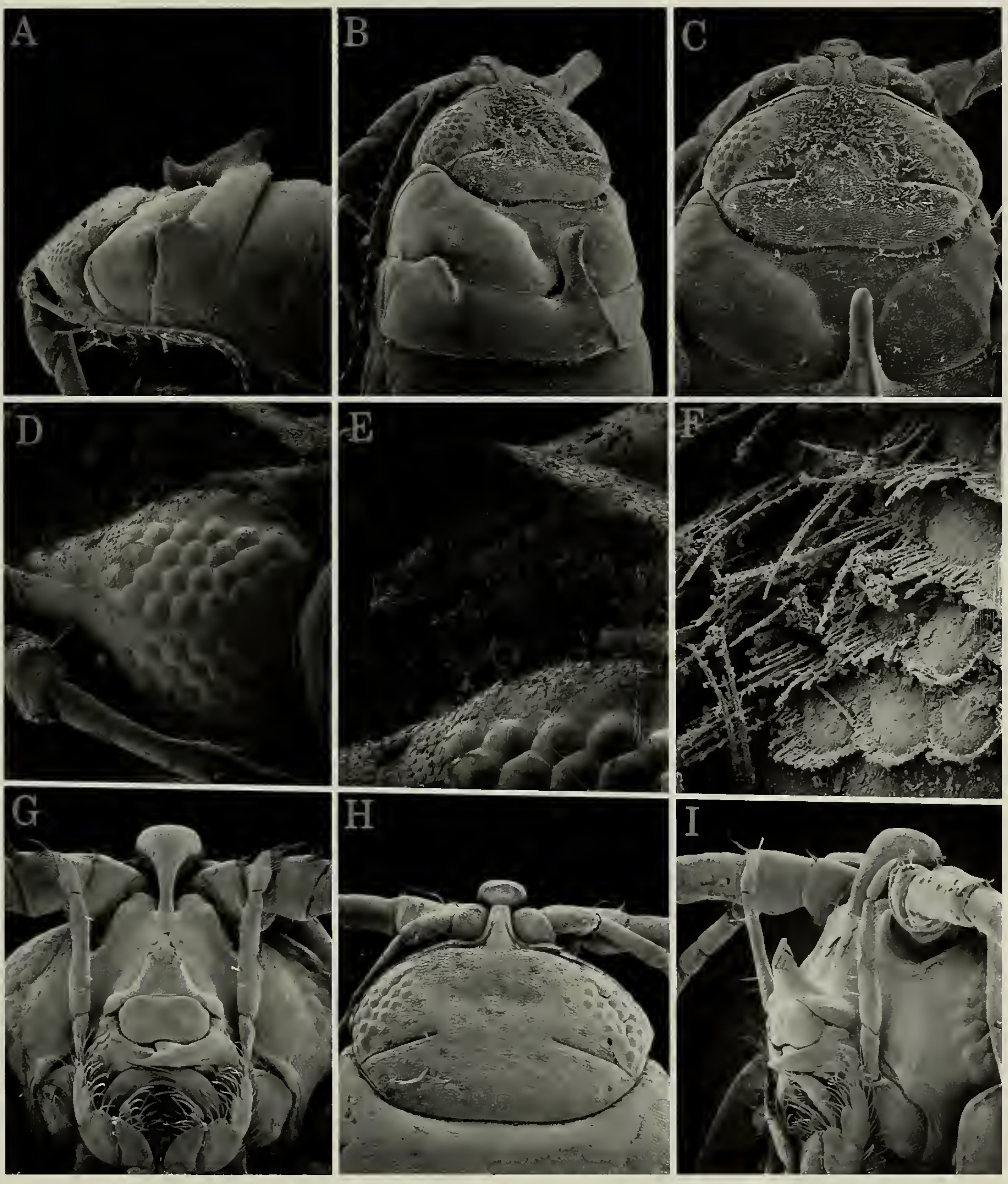

Fig. 3. *Annina mannai,* new species. A, lateral view of anterior, ♂. B, cephalon and pereonites 1, 2 of ♂. C, cephalon and pereonites 1, 2 of ♂. D, eye. E, interocular area of cephalon, closeup. F, detail of setae on scales of cephalon. G, cephalon, ventral view. H, cephalon, dorsal view, ♀. I, ventrolateral view of cephalon.

pleonites and anterior part of telson; pigment absent from medial area of pleon, forming inverted triangular shape.

Antenna 1 reaching pereonite 4; flagellum with 15–16 articles. Antenna 2 flagellum with 9 articles in female, unknown in male; peduncle more robust and longer in male. Mandible tricuspidate; spine row composed of 9 spines, several fine setae also present. Maxilla 1, exopod with 1 seta and 12 spines

Fig. 4. Distribution of known *Annina* species. ● Type localities. ■ Additional record for *A. fustis*. ⊛ Additional records for *A. lacustris*.

(most with accessory spinules) as figured; endopod typical of genus. Maxilla 2 bearing 8 setae on both palp and exopod; endopod with about 11 setae, simple and plumose. Maxilliped typical of genus.

Pereopods ambulatory. Posterior margin of pereopod 1 with dentate, cleft spines. Pereopods 2 and 7 with many spines and setae, as figured.

Pleopod 1 with 4 coupling hooks and 3 plumose setae. Pleopod 2 with 3 coupling hooks and 4 plumose setae, appendix masculina not reaching apex of endopod. Pleopod 3 and 4 each with 3 coupling hooks and 3 setae; pleopod 5 without hooks or setae. Exopods and endopods of pleopods 1–2 with plumose marginal setae, endopods of pleopods 3–5 lacking setae. Rami of all pleopods undivided. Penes short, apically rounded.

Etymology.—The species is named for its collector, Dr. A. K. Manna, Professor of Zoology at Sripat Singh College, West Bengal, India.

Remarks.—Dr. Manna (pers. comm.) reported that the species, present year-round, is abundant in its Ganges River habitat during the rainy season and was found to be feeding on dead shrimp (*Caridina* sp., Family Atyidae), suggesting that it is a scavenger. An isopod, *Tachaea* sp., was also found in association with these shrimp.

Annina mannai is the only known member of the genus with a single, salient middorsal process on pereonite 2 in the male. In all others the processes are paired and sublaterally placed. Below is presented a key to the five species of *Annina*, modified from that of Jones (1983) and based on characters of the adult male.

Key to *Annina* species

1. Posterior margin of telson truncate ....*A. lacustris* Budde-Lund
– Posterior margin of telson not truncate 2
2. Male with 1 large middorsal projection of pereonite 2 .. *A. mannai* n. sp.
– Male with 2 dorsolateral projections or horns on pereonite 2 3
3. Projections club-shaped in lateral view, longer than half-length of pereonite 1 .... *A. fustis* Bowman & Iliffe
– Projections short (less than one-half length of pereonite 1), either blunt or acute 4
4. Paired and pointed horns on cephalon and pereonites 1 and 2 ....*A. kumari* (Bowman)
– Paired horns, short and blunt, on pereonite 2 only ....*A. mesopotamica* (Ahmed)

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REDESCRIPTION OF *IAIS ELONGATA* SIVERTSEN & HOLTHUIS, 1980, FROM THE SOUTH ATLANTIC OCEAN (CRUSTACEA: ISOPODA: ASELLOTA)

Brian Kensley

Abstract.—*Iais elongata* is redescribed from a freshwater stream on Inaccessible Island, Tristan da Cunha archipelago. The presence of several males, each in amplexus with a stage 1 manca, demonstrates that precopula or mate guarding, which also provides some measure of offspring protection in a swift-flowing stream, occurs in this species.

About 130 specimens of a tiny asellote isopod were collected from a freshwater stream on Inaccessible Island (37°02′S, 12°12′W) in the Tristan da Cunha archipelago of the South Atlantic, by Mrs. Helen James of the Albany Museum, Grahamstown, South Africa. The collection was made in the course of a survey of the invertebrate fauna of the island, and submitted to the Smithsonian Institution for identification. The bulk of the collection is housed in the Albany Museum; a representative sample has been deposited in the National Museum of Natural History, Smithsonian Institution.

Although the isopods were determined to be a recently described species, it was decided to provide a fuller redescription with illustrations, especially as some interesting details of the biology were revealed.

Family Janiridae

Iais elongata Sivertsen & Holthuis, 1980

Figs. 1–5

Iais elongata Sivertsen & Holthuis, 1980: 104, Fig. 34. [Described from 2 ♂ and 1 ♀].

Material examined.—Trondheim University Museum, Holotype, ♂ TL 1.2 mm, paratypes 1 ♂, 1 ♀, (3 slide preparations), sta 136, pool of brackish water in cave 2 m above beach, North Point, Inaccessible Island.—Stream flowing to Blenden Hall beach, Inaccessible Island, 37°02′S, 12°12′W: Sample TDC 2A, 2 ovig. ♀, 21 ♀, 16 ♂ (6 ♂ with manca), 13 Oct 1989.—Sample TDC 11I, 4 ovig. ♀, 20 ♀, 10 ♂ (1 ♂ with manca), 23 Oct 1989.—Sample TDC 1I, 5 ovig. ♀, 26 ♀, 30 ♂ (3 with manca), 23/24 Oct 1989 (3 ovig. ♀, 10 ♀, 10 ♂ in NMNH collection).

Description.—Body (Fig. 1A) about 3.5–3.8 times as long as wide. Integument bearing short scattered setae, some stouter than others. Cephalon about one-third wider than midlength, slightly narrower than pereonite 1; anterior margin with broadly rounded rostrum reaching to about midlength of first antennular article. Eyes well pigmented, of 2 ommatidia each. Coxae visible in dorsal view on all pereonites. Pereonite 1 slightly shorter than pereonite 2; pereonites 2–4 subequal in length and width, each with setose anterolateral rounded lobe; pereonite 5 shortest and narrowest; pereonites 6 and 7 with setose posterolateral tergal lobes. Pleon consisting of single short anterior segment plus pleotelson; latter subequal in length to pereonites 6 and 7, lateral margins weakly convex with about 15 short setae, posterior margin weakly convex between uropodal insertions.

Antennule (Fig. 1C) of 6 articles, almost

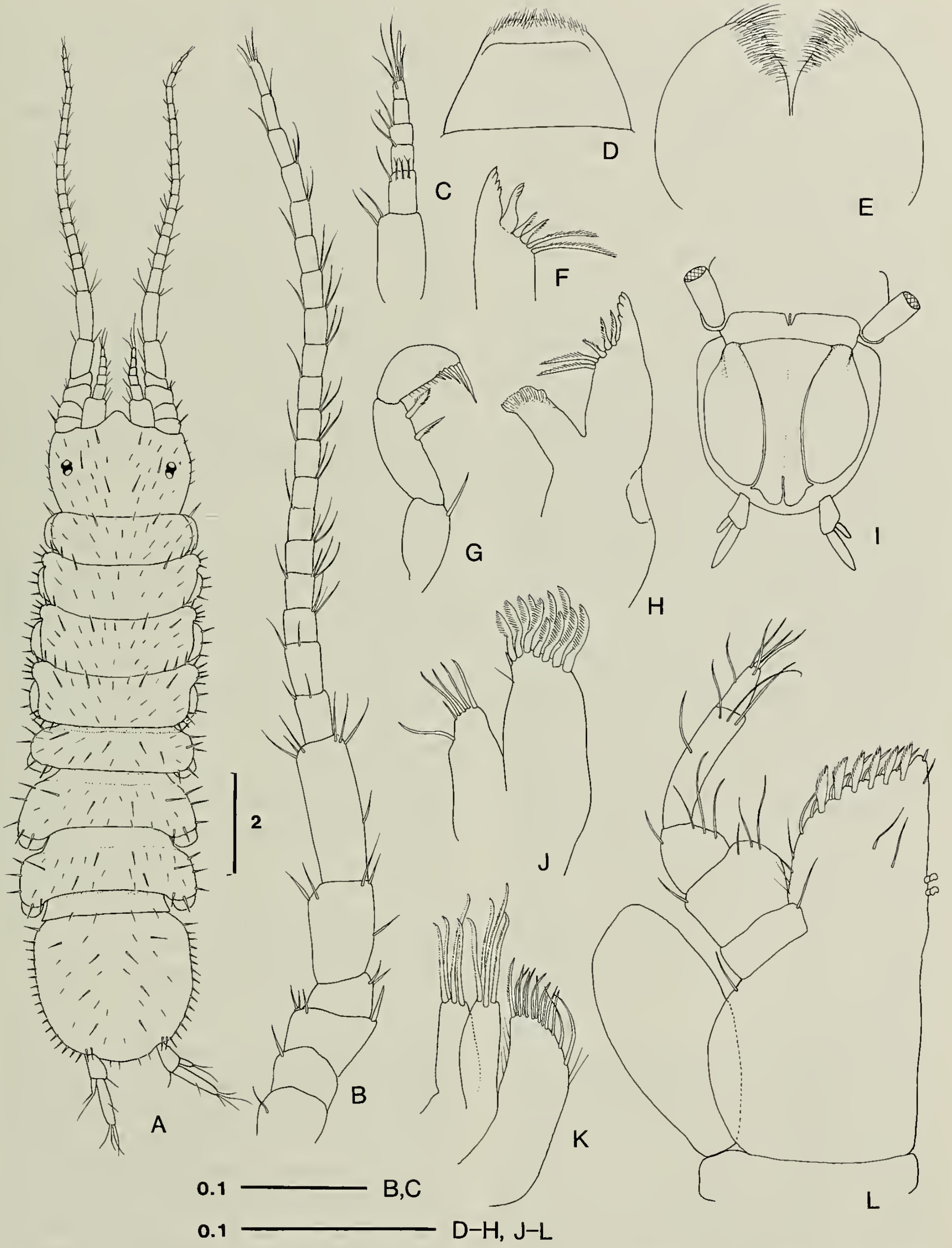

Fig. 1. *Iais elongata*: A, Adult in dorsal view, scale = 0.2 mm; B, Antenna; C, Antennule; D, Upper lip; E, Lower lip; F, Distal part of left mandible; G, Mandibular palp; H, Right mandible; I, Ventral view of last pereonite and pleon of male; J, maxilla 1; K, Maxilla 2; L, Maxilliped.

reaching distal margin of antennal article 5, article 1 widest and longest, twice length of article 2; terminal article bearing single aesthetasc. Antenna (Fig. 1B) equal in length to cephalon plus pereonites 1–5 and half of pereonite 6; peduncle articles 1–4 shorter than wide; article 3 with minute distolateral scale bearing 2 short setae; articles 5 and 6 longer than wide, article 5 about three-fourths length of article 6; flagellum of about 19 setose articles in male, 16 in female. Upper lip (Fig. 1D) about 1.8 times broader basally than midlength, distally broadly rounded, setose. Mandibular palp (Fig. 1G) of 3 articles, article 1 about two-thirds length of article 2, with single strong distolateral seta; article 2 bearing 2 strong bilaterally pectinate setae laterally in distal half; article 3 with mesial margin convex, lateral margin straight with 5 spines increasing in length distally; mandibular molar cylindrical, grinding surface sclerotized, truncate; incisor of 4 sclerotized cusps; spine row of 3 short and 2 elongate spines (left, Fig. 1F), 4-toothed lacinia mobilis, 2 short and 2 elongate spines (right, Fig. 1H). Lower lip (Fig. 1E) deeply cleft, lobes laterally broadly convex, mesiodistally strongly setose. Maxilla 1 (Fig. 1J) with mesial lobe bearing 1 distomesial and 6 distal simple setae; lateral lobe bearing 11 stout toothed spines distally. Maxilla 2 (Fig. 1K), mesial lobe bearing about 13 mostly simple setae mesiodistally; 2 lateral lobes each with 4 elongate unilaterally pectinate setae.

Maxillipedal palp (Fig. 1L) of 5 articles, article 1 broader than long, article 2 twice length and slightly wider than article 1, article 3 three-fourths length and two-thirds width of article 2, articles 4 and 5 slender, article 4 2.7 times length of article 5; endite reaching to midlength of palp article 4, with 2 coupling hooks on mesial margin, distal margin with submarginal row of 6 stout pectinate spines, marginal row of 7 slender setae; epipod ovate, distally broadly rounded, reaching palp article 3. Pereopods (Figs. 2, 3) all ambulatory, pereopod 1 only slightly shorter than pereopod 2, with biunguiculate dactylus; pereopods 2–3 and 5–7 in male and pereopods 2–7 in female essentially similar, becoming more elongate posteriorly, with basis moderately broad, bearing strong seta on anteroproximal margin, ischium with 2 or 3 setae on anterior margin, merus with group of 3 anterodistal setae, carpus subequal in length to merus and ischium together, with short posterodistal spine, propodus about half width and subequal length of carpus, with short posterodistal spine, dactylus with 3 hooked claws. Pereopod 4 in male about two-thirds length of pereopod 3 or 5, propodus with stout posterodistal spine, dactylus bearing terminal hooked claw, and reflexed subterminal claw.

Female pleopod 2 forming broad operculum (Fig. 4A), midlength subequal to greatest width, distally broadly rounded with 2 submesial setae. Male with short conical penes (Fig. 4B) on posterior sternal margin of pereonite 7, just reaching base of pleopod 1. Male pleopods 1 and 2 together forming operculum; pleopod 1 elongate (Fig. 4B), rami with fused portion 3.5 times longer than free, distal rami rounded and bearing about 7 simple setae, distolateral projection short, narrowly rounded. Pleopod 2 (Fig. 4C) peduncle roughly triangular, lateral margin convex; exopod with 2 articles subequal, article 2 distally rounded; endopod with article 1 about half length of article 2, latter slender, curved, tapering to narrow apex reaching distal end of peduncle, with narrow open furrow. Pleopod 3 (Fig. 4D) with exopod of 2 articles subequal in length, article 1 wider than 2, lateral margin convex, setose; article 2 tapering distally lateral and mesial margins setose, with single simple setae apically, endopod roughly ovate, with irregular margin, reaching distal half of exopod article 2. Pleopod 4 (Fig. 4E) exopod of single slender article bearing single elongate distal seta; endopod broad, roughly ovate, with irregular margin. Pleopod 5 (Fig. 4F) of single irregular roughly ovate ramus.

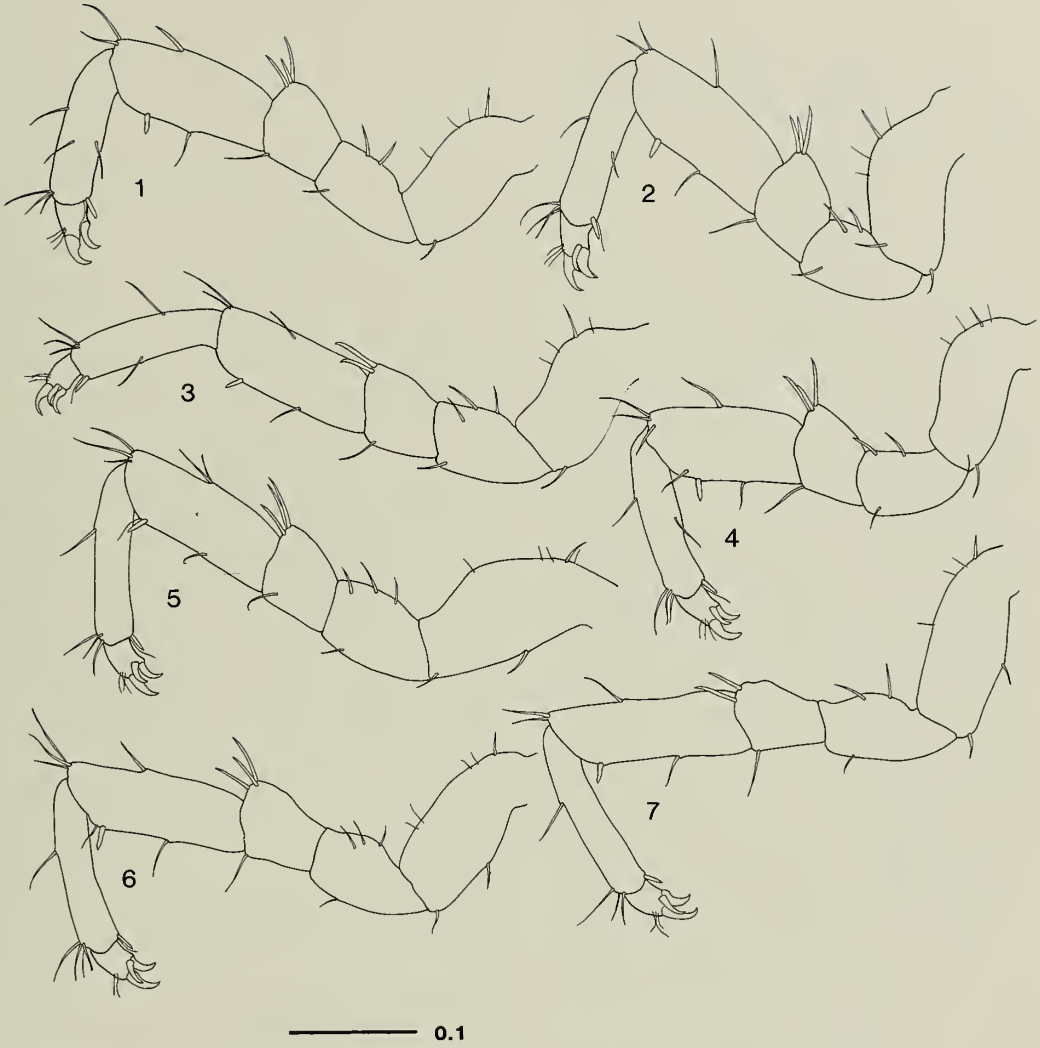

Fig. 2. *Iais elongata,* female, pereopods 1–7.

Uropod (Fig. 4G) about half length of pleotelson, peduncle with single strong distomesial seta; endopod 2.8 times length of exopod, with several terminal simple setae; exopod with 3 terminal setae.

Habitat.—The specimens were collected from a narrow, fairly swiftly flowing stream (about 60 cm wide, 50 cm deep), arising from a spring and running less than one kilometer before dropping to a boulder beach. The stream water was clear, pH neutral; the grass *Spartina arundinacea* was growing closely along the banks. The specimens were found under stones in the stream, usually several animals per stone.

Gut contents.—Determined from 2 cleared specimens: several kinds of diatoms, spore-like structures, and fine filamentous algal-like structures in addition to unidentifiable fragments. The female paratype, cleared and mounted on a microscope slide, has the entire gut packed with diatoms.

Size.—Males total length (tl) 1.08–1.30 mm, possibly in 2 size-groups; males with

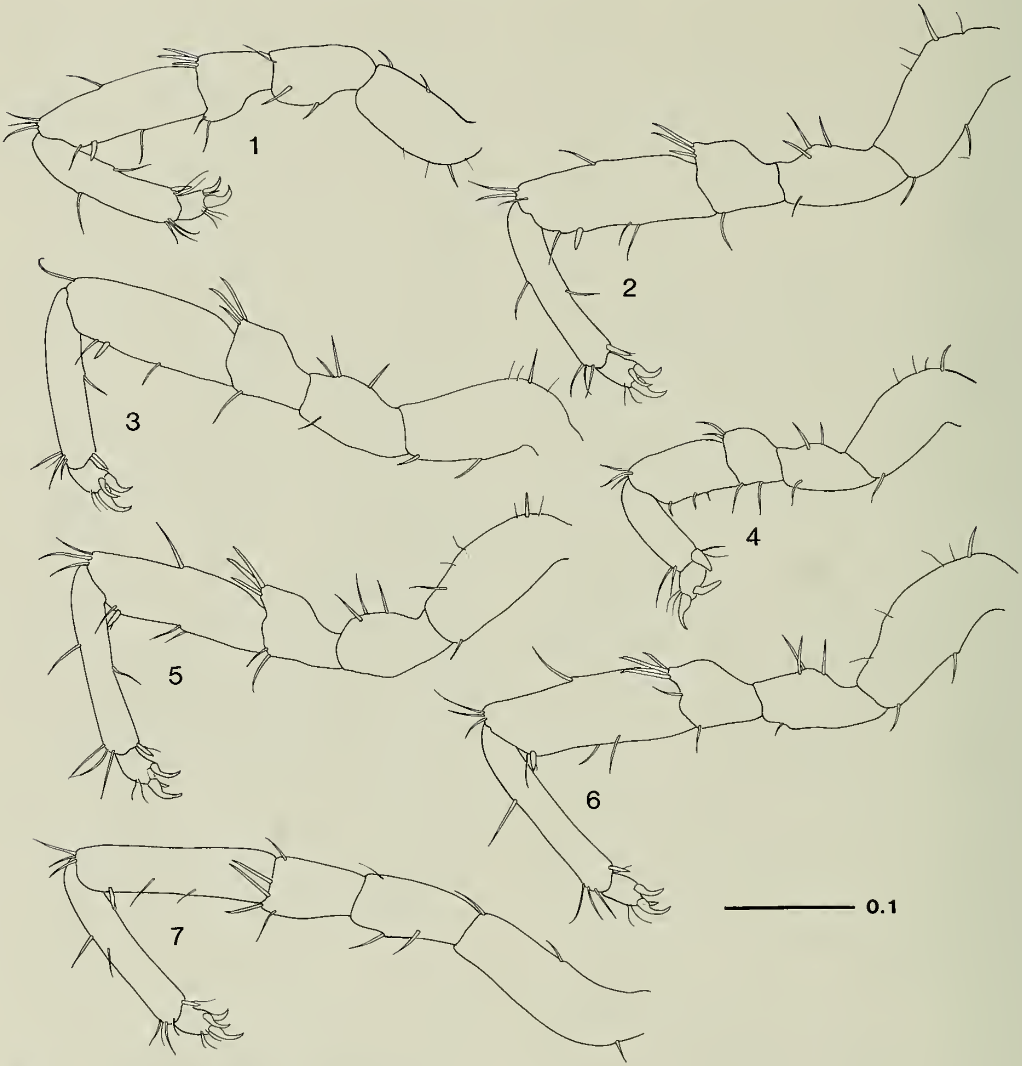

Fig. 3. *Iais elongata,* male pereopods 1–7.

manca tl 1.13–1.30 mm, manca tl 0.43 mm; females tl 0.75–1.45 mm, possibly in 2 size-groups; ovigerous females tl 1.20–1.48 mm.

Ovigerous females (average for 11 specimens tl 1.32 mm) somewhat larger than mature males (average for 9 specimens tl 1.22 mm).

Brood size.—Contents of brood pouch in ovigerous females: 1 egg—1, 2 eggs—2, 3 eggs—2, 2 manca—4, 3 manca—1.

Mate guarding.—Ten of the 56 males collected were each found to be carrying a single large manca, tucked between the pereopod bases (Fig. 5). All the mancas (manca I stage, 0.43 mm total length) were female; all were oriented in the same way, i.e., dorsum of manca pressed to ventrum of male, head directed posteriorly with respect to the male. This is clearly a case of mate guarding, with the juvenile partner held in precopula. The fourth pereopods of the male, which hold the manca in position, are two-thirds

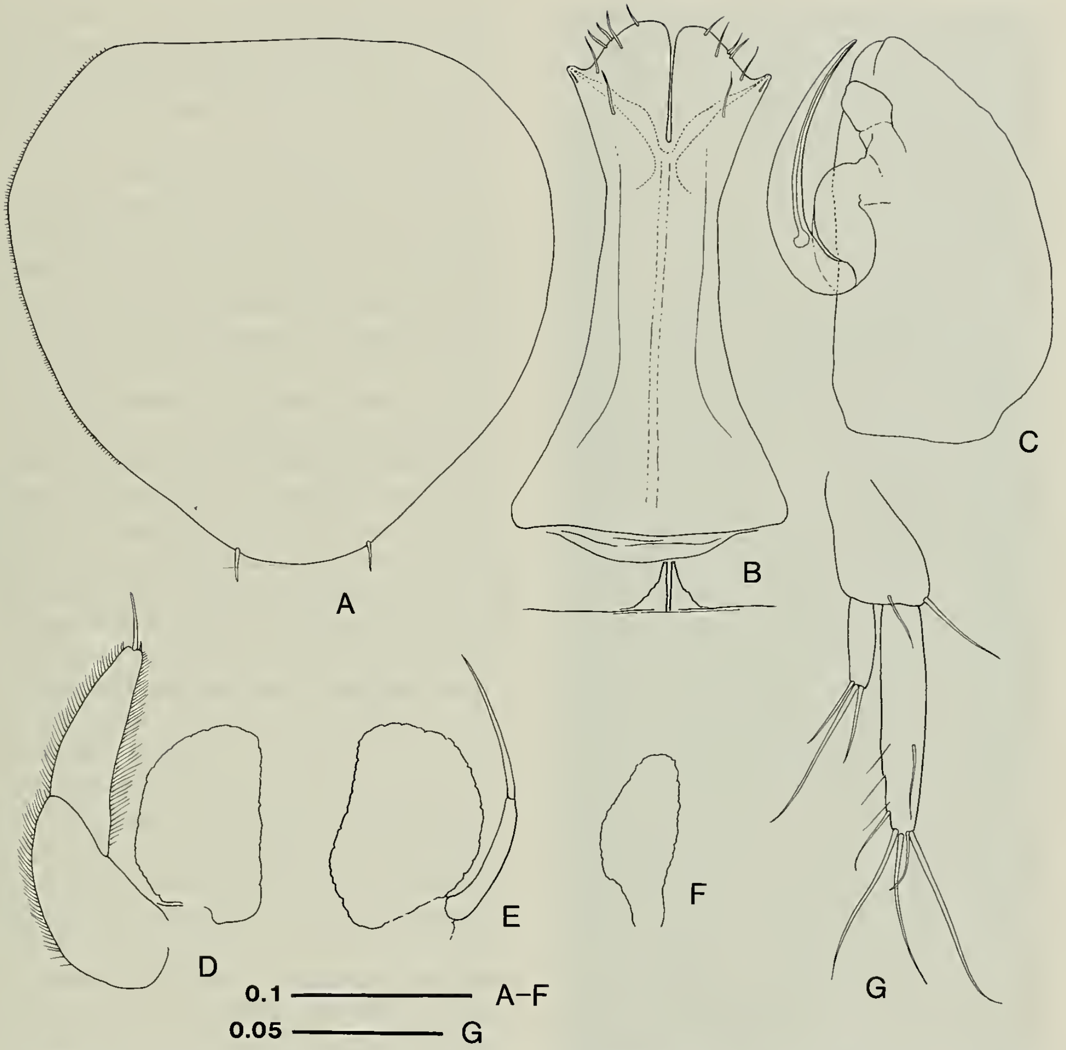

Fig. 4. *Iais elongata*: A, Female pleopod 2 operculum; B, Male pleopod 1 and penes; C, Male pleopod 2; D, Pleopod 3; E, Pleopod 4; F, Pleopod 5; G, Uropod.

the length of the third or fifth pereopods, and have one of the dactylar claws reflexed.

This precopulatory mate guarding strategy (see Dunham & Hurshman 1991, Franke 1993) has been observed in a number of crustaceans (Ridley 1983) including isopods. Precopula ensures that the male is present when a female is receptive during the brief biphasic molt, either by being passively attached to the female, or by actively carrying her around.

Copulation in isopods takes place during the biphasic molt to the adult brooding phase. The posterior half molts first, followed by insemination, then the anterior half molts, along with deployment of oostegites. Eggs are released into the broodpouch once molting is complete (Veuille 1978). Most isopods have internal insemination (Ridley 1983). Several asellote genera have been noted to resort to mate guarding; species of *Jaera* and *Munna* carry

Fig. 5. *Iais elongata,* composite SEM photograph of adult male holding female manca.

around potential mates (Veuille 1980, Hessler & Strömberg 1989, Franke 1993). As in the present species, in *Jaera* the fourth pereopod of the male is shortened and bears specialized spines for clasping the female during precopulation and copulation (Veuille 1980). The same leg is used in amplexus in the primitive asellotes *Caecidotea* (Lewis & Bowman 1981) and *Asellus* (Gruner 1965).

At a maximum total length of 1.48 mm, this species is within meiofaunal size-range. Many meiofaunal organisms exhibit regressive evolution of body size (Swedmark 1964) accompanied by reduction in number of eggs and offspring per brood. In this case, four eggs was the maximum number observed within a brood-pouch while two manca per brood pouch was the commonest number ($n = 4$) of manca observed. Given this very low number of offspring per brood, continued care of offspring after release from the brood-pouch would greatly improve the survival rate, especially given the habitat of a fairly swiftly flowing stream. This post-marsupial care is afforded by the male's use of precopulatory mate guarding of the female manca. The male is already adapted for amplexus, and this adaptation becomes a form of offspring care. This double use of an adaptation is more parsimonious than if the female, which lacks any clasping modifications, were to provide some form of post-marsupial care. The use of the fourth pereopod of the male for hanging onto the female is probably a primitive character within the Asellota, being found in the asellids, while the loss of one of the three dactylar ungui, and the flexing of one of the remaining ungui along with marked shortening of the leg seen in the janirids, represent a more advanced state than that seen in the asellids.

Remarks.—The genus *Iais* Bovallius, 1886, at present contains five species (see Nierstrasz 1941:53; Menzies & Barnard 1951:138; Coineau 1977:436). Menzies & Barnard, 1951, expressed the opinion that true species of *Iais* are always found in association with sphaeromatid isopods, and that the free-living species may well belong to a different genus. There are at least three records of free-living *Iais*: *I. pubescens* of Barnard, 1965 from Gough Island, *I. aquilei*

Coineau, 1977 from St. Helena Island, and *I. elongata* Sivertsen & Holthuis, 1980 from Inaccessible Island in the Tristan archipelago. All three of these South Atlantic island records are from freshwater habitats at varying (but never great) distances from the sea. Possibly we are dealing with a complex of island species of a genus other than *Iais.* Material from Tristan da Cunha, taken from the fully marine sphaeromatid *Isocladus tristanensis* and identified as *I. pubescens* by Barnard (South African Museum, A2286, A2452) appears to be closely similar to *I. pubescens,* widespread through the southern ocean. Examination of commensal material from Auckland, New Zealand, taken from *Exosphaeroma gigas,* from southern Peru taken from *Sphaeroma peruvianum,* along with the abovementioned Tristan material reveals considerable variation in body and appendage proportions, suggesting a complex of species rather than a single circumpolar species, masquerading under the name *I. pubescens.*

Iais elongata is very similar to *I. aquilei* from St. Helena Island, even in the total length of adult males and females. Coineau's thorough description and figures (1977), however, do reveal some subtle differences: the basal article of the antennule is relatively broader in *I. aquilei*; the third article of the mandibular palp has 3 distal spines (5 in *I. elongata*); the maxillipedal endite has 8 distal broad spines (6 in *I. elongata*); maxillipedal palp article 4 is relatively longer in *I. elongata*; there are fewer distal setae on pleopod 1 ♂ in *I. elongata*; the endopod of pleopod 3 is relatively smaller compared with the exopod in *I. elongata*; the exopod of pleopod 4 and especially the single distal seta are relatively larger compared with the endopod in *I. elongata*; the uropodal exopod is relatively more elongate compared to the endopod in *I. aquilei.*

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I am grateful to Mrs. Helen James of the Albany Museum, Grahamstown, South Africa, for making the material of *I. elongata* available for study. The expedition to Inaccessible Island that yielded this material was organized by the Percy Fitzpatrick Institute for African Ornithology at the University of Cape Town. I thank Mrs. Michelle van der Merwe of the South African Museum, Cape Town, and Dr. Tor Stromgren of the Trondheim University Museum, Norway, for the loan of comparative material. Dr. George Wilson of the Australian Museum generously shared his thoughts on asellote evolution, in correspondence over this paper.

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A NEW GENUS AND SPECIES OF CIROLANID ISOPOD FROM THE WESTERN INDIAN OCEAN (CRUSTACEA: PERACARIDA)

Brian Kensley and Marilyn Schotte

Abstract.—*Seychellana expansa* new genus, new species, is diagnosed and described from shallow water off the Seychelles Islands, western Indian Ocean. The genus is characterized by the possession of a slender, blade-like frontal lamina, a somewhat reduced pereopod 7, a strongly bipartite epimeron on pleonite 2, a broadly expanded epimeron on pleonite 3, and a ventrally inserted uropod.

Records of the cirolanid isopod fauna of the western Indian Ocean are scattered through a number of publications (see Bruce & Jones 1978, Bruce & Javed 1987, Javed & Yasmeen 1990); the steady stream of new taxa being described, though, would indicate that many new forms await discovery. To date, the majority of records are from coastal intertidal and very shallow waters. Very little is known of the peracaridan fauna of the tropical oceanic islands of the Indian Ocean, as is demonstrated by the present record of a new genus from what is relatively shallow water in the Seychelles, an area that has received less attention than some.

The material was collected in the course of an environmental survey carried out for the government of the Republic of Seychelles, and was submitted to the Smithsonian Institution for identification.

Suborder Flabellifera
Family Cirolanidae
Seychellana, new genus

Diagnosis.—Cephalon lacking rostrum. Frontal lamina slender, blade-like, posteriorly well separated from flattened, non-projecting clypeus. Mandibular molar not reduced; incisor broad. Maxillipedal endite having 2 coupling hooks. Pereopods 1–3 with merus anterodistally somewhat produced. Pereopods 4–7 ambulatory, articles not markedly flattened, bases lacking natatory setae. Pereopod 7 noticeably shorter and more slender than pereopod 6. Epimeron of pleonite 2 bipartite, consisting of strong acute dorsal and ventral parts. Epimeron of pleonite 3 enormously enlarged, overlapping pleonites 4 and 5 laterally. Pleonite 5 with free lateral margin overlapped by epimeron 3. Endopods of pleopods 3 and 4 with marginal setae, of pleopod 5 lacking setae; all exopods with marginal setae. Uropod inserted ventrally; peduncle produced along mesial margin of endopod; latter fairly slender, lateral margin excavate.

Type species.—By present designation, *Seychellana expansa*, new species.

Discussion.—The present material essentially resembles a species of *Eurydice*, overlain with a number of specializations. The similarities with *Eurydice* can be seen in the structure of the frontal lamina, clypeus, antennule, pleon, and in the ventral insertion of the uropods. The specializations include the reduced pereopod 7 (one-third shorter and less robust than pereopod 6); the lack of a complete transverse suture on any of the pleopodal rami; the strongly bipartite epimeron of pleonite 2 embracing that of pleonite 3; the enormously enlarged epimeron of pleonite 3 which completely overlaps those of pleonites 4 and 5. While some of these features appear individually in some other cirolanid genera, e.g., the slender frontal lamina of *Pseudolana, Eurydice,* and *Natatolana,* the plate-like epimera of pleonites 2 and 3 in *Booralana,* the strongly expanded epimeron of pleonite 3 as in *Aatolana schioedtei* (Miers 1884) (see Bruce 1986, fig. 135c; 1993:5, 9), none of the presently recognized genera exhibit all of these specializations, along with a considerably reduced pereopod 7 (compared to pereopod 6), and ventrally inserted uropods.

Etymology.—The generic name is a combination of Seychelles, the type locality, and 'lana', the suffix frequently used in cirolanid taxonomy.

Seychellana expansa, new species

Figs. 1–4

Material.—Holotype, USNM 252889, ♂ tl 6.6 mm, Paratypes, USNM 252890, ♂ tl 6.3 mm, ♀ tl 4.2 mm, sta C2R1, 6/1/92; ♂ tl 6.0 mm, SEM whole mount, sta C2R2; ♂ tl 6.4 mm, sta C2R3, 6/1/92 (dissected); 4°41'N, 55°33'E, 30 m, Van Veen grab on sandy bottom, off Anse aux Pins, Mahé, Seychelles, coll. J. Elliott, S. Elliott, & P. Harper, 1 Jun 1992.

Description.—Male: Body length about 3 times greatest width at pereonite 3. Red-brown chromatophores scattered over most of dorsum of cephalon, pereonites and pleonites, pleotelson dorsally almost unpigmented. Cephalon with anterior margin mesially broadly rounded but lacking distinct rostrum; bases of antennules separating cephalon from frontal lamina; latter anteriorly rounded in ventral view, posteriorly elongate, narrowed, well separated from broadly rounded clypeus. Eyes large, well pigmented. Coxal plates of pereonites 2 and 3 posteriorly truncate, of pereonites 4–6 becoming larger and slightly produced, of pereonite 7 posteriorly acute, much smaller than and almost hidden by coxa of pereonite 6. Posterior margins of pereonites and pleonites finely denticulate. Pleonites 1–5 free; pleonite 1 short, with very short free epimeron; pleonites 2–4 subequal in length, epimeron of pleonite 2 bipartite, with strong acute dorsal and ventral portions embracing enlarged epimeron of pleonite 3; latter broadly ovate, reaching posteriorly beyond pleonites to protopod of uropod, completely covering short epimera of pleonites 4 and 5; pleonite 5 longer than 4, with posterior margin mesially convex. Pleotelson as long as wide, strongly arched, with finely crenulate posterior margin broadly rounded, bearing 12 short plumose setae; lateral and posterior margins directed ventrally.

Antennular peduncle with articles 2 and 3 each bearing 2 spines on inner (ventral) surface; flagellum consisting of 9 articles, row of 3 or 4 aesthetascs on articles 2–7, penultimate article with single aesthetasc. Antennal peduncle articles 1 and 2 short, articles 3–5 increasing in length distally, article 4 with 2 stout distal spines, article 5 with 5 distal spines; flagellum of 21 articles, reaching posteriorly to level of pereonite 5. Mandibular incisor of 3 cusps on each side, mesial cusp somewhat elongate and acute, 2 lateral cusps rounded; 7 or 8 spines in spine row; molar having row of 20 spines on upper surface; palp of 3 articles, article 1 subequal in length to article 3; article 2 2.5 times length of article 1, bearing 10 setae on distal half of lateral margin; article 3 bearing 13 fringed spines increasing in length distally. Maxilla 1, endopod having 3 stout mesiodistal circumplumose setae; exopod having 8 distal entire, comb, and denticulate setae. Maxilla 2, palp bearing 2 distal elongate setae; exopod with 7 mesiodistal setae; endopod broadly rounded, with several simple and circumplumose setae on mesial margin. Maxillipedal endite reaching base of article 2 of palp, bearing 4 sparsely plumose setae distally, 2 coupling hooks on mesial margin of both left and right appendage; palp articles 2–5 bearing setae on mesial and lateral margins.

Pereopod 1, merus somewhat anterodistally produced, bearing strong terminal

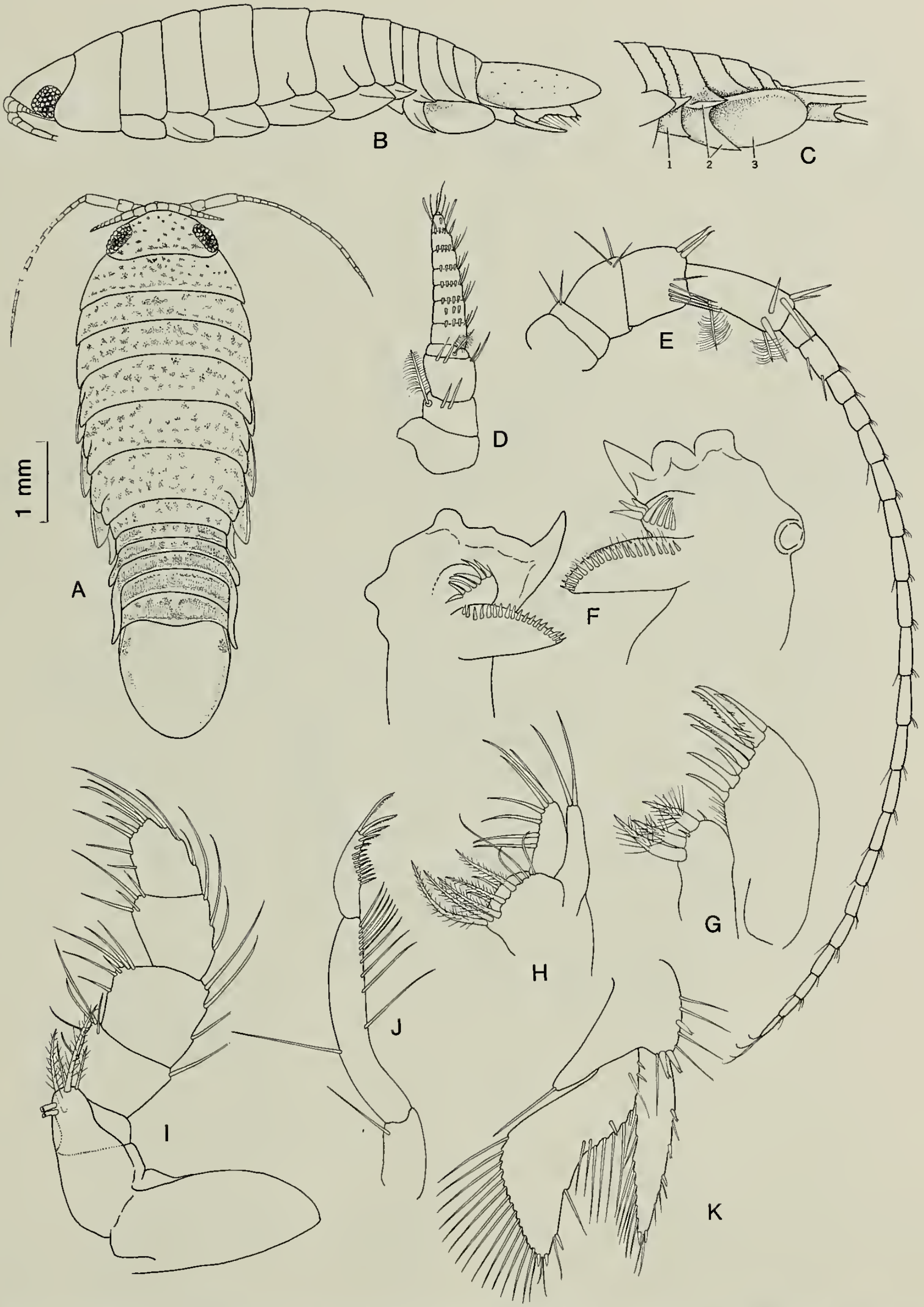

Fig. 1. *Seychellana expansa.* A, Holotype in dorsal view, scale = 1 mm; B, Holotype in lateral view; C, Lateral pleon enlarged, with epimera 1, 2, and 3 indicated. D, Antennule; E, Antenna; F, Left and right mandibles; G, Maxilla 1; H, Maxilla 2; I, Maxilliped; J, Mandibular palp; K, Uropod.

Fig. 2. *Seychellana expansa.* Pereopods 1–7.

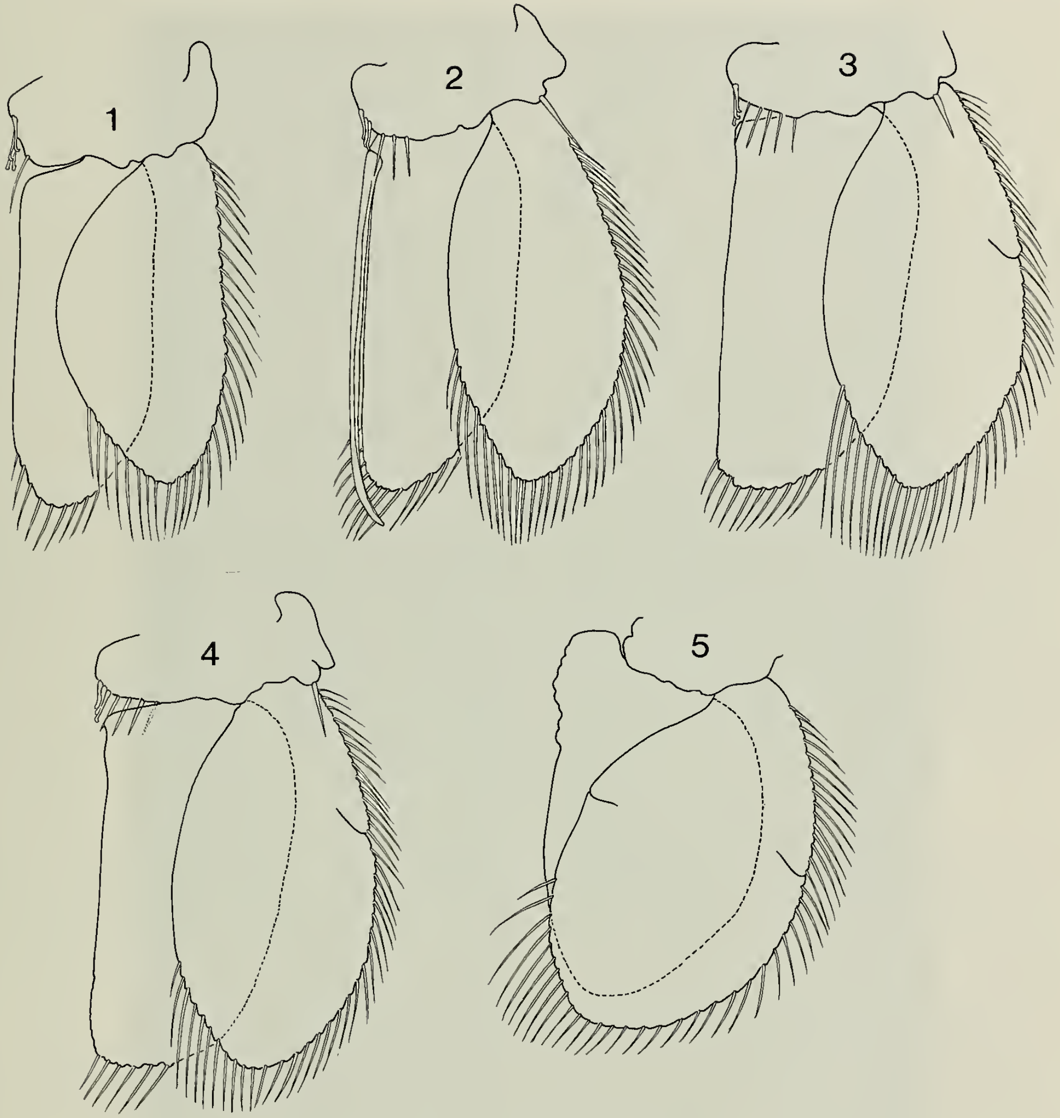

Fig. 3. *Seychellana expansa.* Pleopods 1–5.

spine, posterior margin having single elongate and several short spines; carpus short, triangular, lacking free anterior margin; propodus with 5 short spines on posterior margin; dactylar unguis lacking accessory spine. Pereopod 2, basis with 2 elongate setae on anterior margin; ischium with single strong anteromesial and posteromesial spine; merus with short anteromesial lobe bearing several spines; carpus having free anterior and posterior margin, with 2 short posterodistal spines; propodus with 2 posterodistal spines. Pereopod 3, basis with row of palmate setae on anterior margin; ischium with few small spines at posterodistal angle, single strong spine at anterodistal angle; merus with several strong anterodistal spines, posterior margin sinuous, bearing

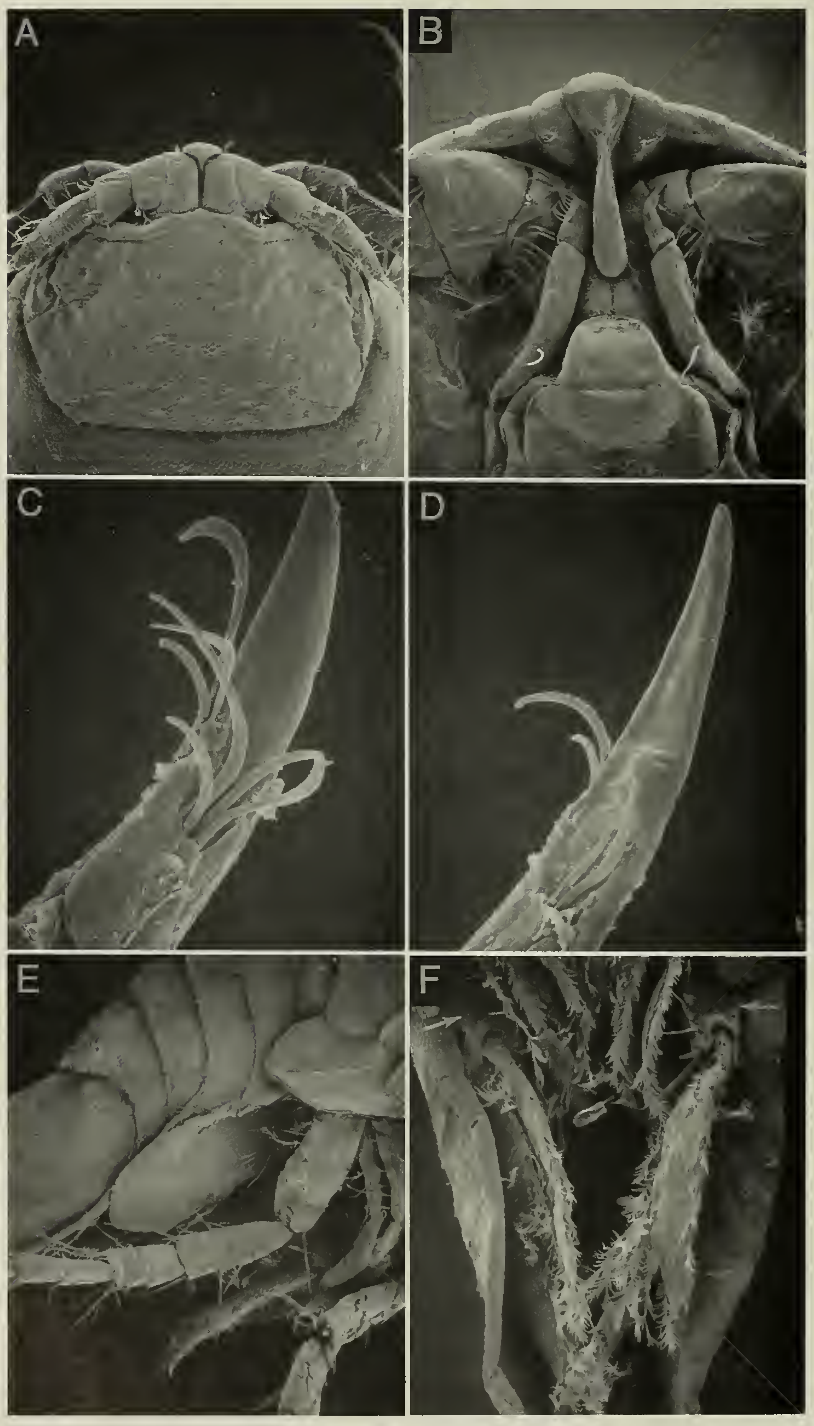

Fig. 4. *Seychellana expansa.* A, Cephalon, antennular bases, and apex of frontal lamina in dorsal view; B, Anterior cephalon in ventral view; C, Dactylar unguis of pereopod 1; D, Dactylar unguis of pereopod 5; E, Pleon in lateral view; F, Pleon in ventral view, showing ventral insertion of uropods (protopods indicated by arrows).

about 7 short and long spines; carpus, propodus, and dactylus as in pereopod 2. Pereopod 4, basis with row of elongate setae on lateral surface; ischium with anterodistal clump of spines, clump of spines at midlength and at posterodistal angle of posterior margin; merus and carpus each with anterodistal and posterodistal clump of spines; propodus slender, elongate, with single spine at about midlength of posterior margin, 2 small posterodistal spines. Pereopods 5 and 6 similar, basis with double row of setae; ischium with 3 clumps of spines on posterior margin, clump of anterodistal spines; merus and carpus with clump of spines at midlength of posterior margin, plus anterodistal and posterodistal clump; propodus with clump of spines at midlength of posterior margin, 2 small posterodistal spines. Pereopod 7 about one-third shorter and less robust than pereopods 5 and 6, basis with double row of setae; ischium with slender spines and setae on anterior and posterior margins; merus with clumps of slender spines at midlength of posterior margin, anterodistal and posterodistal angles; carpus with numerous slender distal spines; propodus with single spine at midlength of posterior margin, 2 spines at posterodistal and anterodistal angles. Penes on sternite 7 well separated low rounded structures.

Pleopod 1, protopod with 4 retinaculae; endopod slightly longer and narrower than exopod, with few distal plumose marginal setae; exopod ovate, with distal third of mesial margin and all of lateral margin bearing plumose setae. Pleopod 2, protopod with 3 retinaculae; copulatory stylet articulating at base of endopod, slender, distally curved and barely surpassing apex of rami; ovate exopod with plumose marginal setae on distal third of mesial margin and all of lateral margin. Pleopods 3 and 4 similar, protopod with 3 retinaculae; endopod with mesial margin straight, few plumose marginal setae distally; exopod ovate, with plumose marginal setae on distal third of mesial margin and all of lateral margin, latter having incomplete suture forming small notch at about midlength. Pleopod 5, protopod lacking retinaculae; endopod ovate, having rounded proximomesial lobe; exopod ovate, bearing plumose marginal setae on distal third of mesial margin and all of lateral margin, with incomplete suture forming small notch just short of midlength of both mesial and lateral margins. Uropodal protopod inserted ventrally and completely hidden by pleotelson in dorsal view, produced distomesially for about one-third length of endopod; latter with lateral margin excavate, ramus appearing flexed, with numerous setae on distomesial margin, few spines and setae on lateral margin; exopod slender, lanceolate, with 4 short spines and few setae along lateral margin, several setae along mesial margin, apex having 2 short spines.

Etymology.—The specific epithet, from the Latin *expansus,* expanded or spread out, refers to the expanded character of the epimeron of pleonite 3.

Acknowledgments

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A NEW SPECIES OF *PALAEMONETES* (CRUSTACEA: DECAPODA: PALAEMONIDAE) FROM NORTHEASTERN MEXICO

Ned E. Strenth

Abstract.—*Palaemonetes hobbsi* is described from the headwaters of the Río Mante near Ciudad Mante in the state of Tamaulipas, México. While this new species is similar to *Palaemonetes mexicanus* Strenth from the nearby state of San Luis Potosí, it differs with respect to rostral dentition, first maxilliped morphology, and spination of the appendix masculina. It also exhibits a disjunct nonoverlapping range. Standard starch gel electrophoretic comparisons also confirm that this new taxon exhibits biochemical differences that are distinct from *P. mexicanus.*

Resúmen.—Se describe una nueva especie de *Palaemonetes* de agua dulce de México. Esta especie de camarón ocurre en las aguas de cabecera del Río Mante y Río Frío cerca de Ciudad Mante en el estado de Tamaulipas. Es similar a *Palaemonetes mexicanus* Strenth conocida del estado de San Luis Potosí. Se distingue esta especie nueva de la especie *P. mexicanus* por las diferencias en la dentición del rostro, en la morfología del primer maxilípedo, en la disposición de las espinas del appendix masculina, y el análisis de bioquímica.

Following a review (Strenth 1976) of the North American species of freshwater *Palaemonetes* Heller, continued field work in northeastern Mexico revealed the presence of several populations of shrimp from two large springs near Ciudad Mante in the state of Tamaulipas. It was apparent from collections made during 1980 and 1983 that these populations differed morphologically only slightly from specimens of *P. mexicanus* Strenth from San Luis Potosí. Field work was continued in Mexico during the middle and late 1980's to establish the range of *P. mexicanus* as well as the Ciudad Mante populations. It was during this time that Hobbs & Hobbs (1989) reported the presence of these shrimp as a range extension of *P. mexicanus.* Subsequent field work now appears to support the conclusion that these populations are in fact quite distinct and separate in their distribution from that of *P. mexicanus.*

This undescribed taxon is restricted to the springfed headwaters of the Río Mante and Río Frío. More importantly, this aquatic decapod inhabits the headwaters of a separate and independent drainage system from that of *Palaemonetes kadiakensis* Rathbun or *P. mexicanus* which are also known from northern Mexico (Strenth 1976). The Río Mante and Río Frío flow into the Río Guayalejo which is a part of the Río Tamesí system. *Palaemonetes kadiakensis* is not known to occur south of the Río Bravo del Norte (Río Grande) drainage system and the distribution of *P. mexicanus* is restricted to the headwaters of a small stream which flows into the Río Tampaón which is a part of the Río Pánuco drainage system to the south in the states of San Luis Potosí and Veracruz. Extensive downstream collections from the type locality of *P. mexicanus* have failed to produce specimens from either the Río Tamuin or the Río Pánuco.

Similar downstream collections from the Río Mante and Río Frío conducted in the Río Guayalejo and Río Tamesí have likewise failed to yield specimens of freshwater *Palaemonetes.*

Recent laboratory analyses confirm that the Río Mante population exhibits biochemical differences that are distinct from *P. mexicanus.* It is now evident that this population represents a currently undescribed taxon. This conclusion is based upon morphological differences, restricted distribution, and the absence of overlapping ranges of this form with any other currently known species of *Palaemonetes.*

Materials and Methods

Specimens selected for biochemical analysis were immediately frozen in liquid nitrogen in the field and returned to the laboratory. Abdominal tissue samples of 20 specimens collected from the headwaters of the Río Mante were biochemically compared with similar tissue samples of 20 specimens of *P. mexicanus* from the type-locality west of Ciudad Valles in San Luis Potosí. These samples were subjected to electrophoretic analysis using standard horizontal starch gel techniques (Selander et al. 1971, Murphy et al. 1990). Four of 11 isozyme systems examined were observed to exhibit significant variation between the two populations. Specimens which were preserved in alcohol upon collection are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM) and the Instituto de Biología de la Universidad Nacional Autónoma de México, Mexico City (EM).

Palaemonetes hobbsi, new species

Fig. 1

Palaemonetes mexicanus Strenth, 1976.—Hobbs & Hobbs, 1989:222.

Type material.—Nacimiento del Río Mante, 8 km southwest of Ciudad Mante, Tamaulipas, México, 20 May 1980, coll. N. E. Strenth. Male holotype, USNM 264749; one male, one gravid female, paratypes, USNM 264748; one male, one gravid female, paratypes, EM 11972.

Description.—Rostrum (Fig. 1a) high; upturned at end; extending to near anterior margin of scaphocerite; dorsal margin with 5 to 6 teeth, one of which is placed behind the orbit; ventral margin with 2 teeth. Antennal spine sharp, distinct; overreaching anterior margin of carapace. Branchiostegal spine sharp and distinct; situated on anterior margin of carapace just below branchiostegal groove.

Abdomen normal; pleura of third somite rounded; pleurae of fourth and fifth somites angular; sixth somite 1.5 times as long as fifth. Telson (Fig. 1b) equal in length to sixth somite; anterior pair of dorsal spines located ⅓ of telson length from posterior margin; posterior pair on or near posterior margin. Posterior margin of telson with sharp median point flanked by 2 pair of spines and 1 pair of plumose setae; lateral pair of spines short, failing to reach median point of telson; mesial pair of spines elongate extending 3 to 4 times length of lateral spines.

Eyes (Fig. 1a) well developed; cornea globular and well pigmented. Stylocerite (Fig. 1e) sharp and extending ⅓ length of basal segment of antennular peduncle; anterolateral spine sharp, extending to anterior margin of segment; lateral antennular flagellum with rami fused for 13 to 22 articles; free portion of shorter ramus consisting of 3 to 7 articles. Scaphocerite (Fig. 1d) almost 3 times as long as wide, lateral margin slightly concave, blade extending well past lateral tooth.

Mouthparts (Figs. 1f–k) typical for the genus. First maxilliped (Fig. 1i) with endopod; epipod nonbifurcate. First pereopod (Fig. 1l) extending to distal margin of third segment of antennular peduncle; dactyl and propodus without teeth, bearing numerous setae distally; carpus twice as long as chela, 1.2 times as long as merus. Second pereopod

(Fig. 1m) extending to anterior margin of scaphocerite; dactyl and propodus without teeth, bearing few setae distally; carpus 1.4 times as long as chela; merus and chela equal in length. Third pereopod (Fig. 1n) extending to base of third segment of antennular peduncle; propodus 1.8 times as long as carpus; merus 1.9 times as long as carpus. Fourth pereopod extending to anterior margin of second segment of antennular peduncle; fifth pereopod extending to near anterior margin of scaphocerite.

Appendix masculina (Fig. 1c) of male with 4 apical spines which extend to distal margin of endopod; appendix interna ½ length of appendix masculina. Eggs of gravid females 1.2–1.5 mm in length. Lateral ramus of uropod with or without movable spine between fixed distolateral tooth and margin of blade.

Size.—Males with carapace lengths to 6 mm (including rostrum, to 11 mm); females, to 7 mm (including rostrum, to 12 mm).

Variation.—The movable exopod spine on the lateral ramus of the uropod is quite variable; both movable spines may be present, both may be absent, or only a left or right one may be present. No specimens were observed to exhibit a subapical tooth on the ventral margin of the rostrum.

Color.—Living specimens are transparent. The eggs of gravid females are dark green in coloration.

Range.—This species is currently known only from the headwaters of the Río Mante and Río Frío near Ciudad Mante in the state of Tamaulipas, México.

Etymology.—This species is named in honor of Dr. Horton H. Hobbs, Jr. of the Smithsonian Institution in Washington D.C., and Dr. Horton H. Hobbs III of Wittenberg University, Springfield, Ohio.

Remarks.—*Palaemonetes hobbsi* shares characteristics with *P. mexicanus* as well as with *Palaemonetes texanus* Strenth from the southwestern United States. All three species are similar in the variation of movable exopod spination of the uropods. *Palaemonetes hobbsi* is similar to *P. mexicanus* with respect to the number of fused articles of the lateral antennular flagellum. *Palaemonetes hobbsi* ranges from 13–22 fused articles while *P. mexicanus* ranges from 14–24. *Palaemonetes texanus* differs somewhat in exhibiting 19–29 fused articles. *Palaemonetes hobbsi* is similar to *P. texanus* in that both species exhibit angular pleurae of the fourth and fifth somites. The first maxilliped of *P. hobbsi* is similar to *P. texanus* in exhibiting an endopod; this same structure is also similar to *P. mexicanus* in possessing a non-bifurcated epipod. This intermediacy of characters is possibly related to the fact that the distribution of *P. hobbsi* lies between the distributions of both *P. mexicanus* and *P. texanus.* All three species appear to be closely related.

Palaemonetes hobbsi differs, however, from both *P. mexicanus* and *P. texanus* with respect to rostral dentition and spination of the appendices masculinae. *Palaemonetes hobbsi* exhibits only five or six dorsal rostral teeth while *P. mexicanus* exhibits six or seven and *P. texanus* ranges from five to eight. *Palaemonetes hobbsi* exhibits four apical setae on the appendix masculina while *P. mexicanus* and *P. texanus* exhibit five and six apical spines respectively. In addition, there is virtually no significant difference in the size of adult male and female specimens of *P. hobbsi.* Female specimens exhibit carapace lengths that are less than 10% longer than male specimens. Female specimens of both *P. mexicanus* and *P. texanus* are considerably larger and exhibit carapace lengths that are 28 to 45% longer than their male counterparts.

In addition to the above anatomical differences, preliminary electrophoretic analyses of both *P. mexicanus* and *P. hobbsi* reveal differences in the isozyme production of malate dehydrogenase 1, malate dehydrogenase 2, phosphoglucomutase and a-glycerophosphate dehydrogenase. These differences are considered significant in light

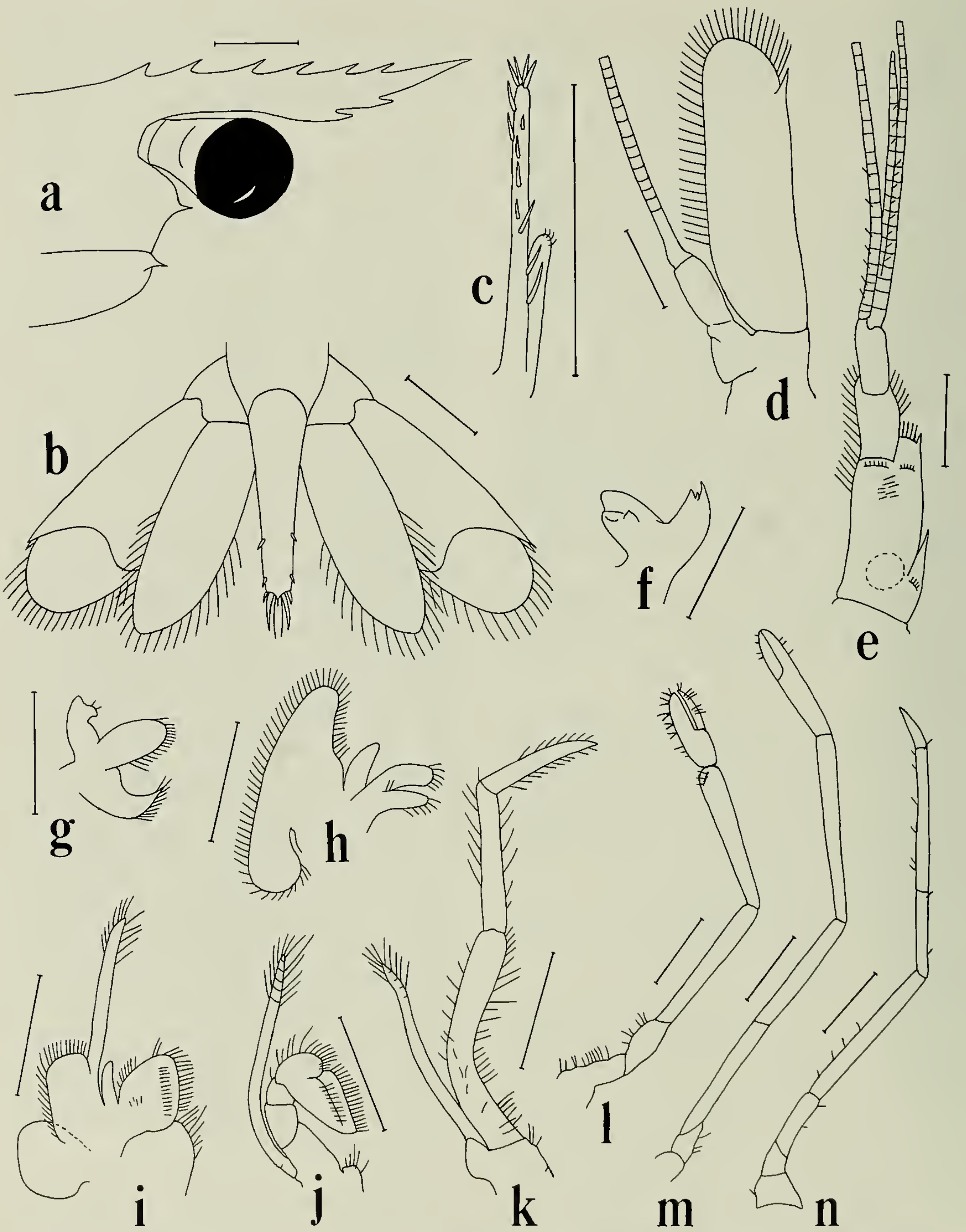

Fig. 1. *Palaemonetes hobbsi*, new species, holotype, male: a, anterior region; b, telson and uropods; c, appendix masculina; d, first antenna; e, second antenna; f, mandible; g, first maxilla; h, second maxilla; i, first maxilliped; j, second maxilliped; k, third maxilliped; l, first pereopod; m, second pereopod; n, third pereopod. (Scales = 1.0 mm).

of the fact that palaemonids are known to exhibit low levels of allozyme variation (Boulton & Knott 1984). While the exact nature of the above biochemical variation is under current investigation, it is interpreted here only as additional supportive evidence of the premise that *P. hobbsi* represents a taxon which is morphologically distinct and geographically separate from *P. mexicanus.*

Acknowledgments

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A REVISION OF THE TYPE MATERIAL OF SOME SPECIES OF *HYPOLOBOCERA* AND *PTYCHOPHALLUS* (CRUSTACEA: DECAPODA: PSEUDOTHELPHUSIDAE) IN THE NATIONAL MUSEUM OF NATURAL HISTORY, WASHINGTON, D.C., WITH DESCRIPTIONS OF A NEW SPECIES AND A NEW SUBSPECIES

Gilberto Rodríguez

Abstract.—The descriptions of a number of species of freshwater crabs from Panama and Colombia held in the USNM are revised. These are *Hypolobocera andagoensis* (Pretzmann 1965), *H. beieri* Pretzmann, 1968, *H. canaensis* Pretzmann, 1968, *H. martelathami* (Pretzmann 1965), and *H. smalleyi* Pretzmann, 1968, and three species of *Ptychophallus* from Panama, *P. cocleensis* Pretzmann, 1965, *P. goldmanni* Pretzmann, 1965, and *P. lavallensis* Pretzmann, 1978. The present work provides illustrations of the first gonopods of the above species and corrects several inaccuracies in their descriptions and those of *H. chocoensis* Rodríguez, 1980, and *P. colombianus* (Rathbun 1893). The collections included a new species, *Ptychophallus micracanthus,* and a new subspecies, *Hypolobocera bouvieri rotundilobata,* which also are described.

Due to the scarcity of reliable taxonomic characters in the carapace and appendages of the Pseudothelphusidae, the systematics of this family of neotropical freshwater crabs is based almost exclusively on the morphology of the male first gonopods. For this reason, the taxonomic status of species described without an adequate illustration of these appendages is uncertain (Rodríguez 1982). This is the case with three lots of crabs obtained by E. A. Goldman near the Panama Canal in 1912, and by Marte Latham in Colombia in 1957 and 1962, from which Pretzmann (1965, 1968) described five new species of *Hypolobocera.* Unfortunately illustrations of the first gonopods were not included with the original descriptions, and a latter work (Pretzmann 1972) provided only photographs in which morphological details are not discernible. Descriptions of the first gonopods were not included for the species of *Ptychophallus* from Panama obtained by several collectors, and described by Pretzmann in 1965, 1978, and 1980. The present work provides illustrations of the gonopods of the holotypes and other materials of these species in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and corrects several inaccuracies in the descriptions of these taxa.

A new species of *Ptychophallus* and a new subspecies of *Hypolobocera bouvieri* were discovered among the materials in these collections. Abbreviations used are cb. for carapace breadth, and cl. for carapace length.

Pseudothelphusidae Ortmann, 1893

Genus *Hypolobocera* Ortmann, 1897

Hypolobocera andagoensis (Pretzmann, 1965)
Fig. 1A–C

Strengeria (Strengeria) andagoensis Pretzmann, 1965:6.

Hypolobocera (Hypolobocera) andagoen-

sis.—Pretzmann, 1971:17; 1972:51, figs. 170–172.

Hypolobocera andagoensis.—Rodríguez, 1982:67, figs. 21c, e.—von Prahl, 1988: 183.

Material.—Colombia: Andagoya, Chocó, May 1957, leg. Marte Latham, No. 996, 1 male holotype, cl. 19.2 mm, cb. 31.6 mm (USNM 106405).—Colombia: no data, leg. Marte Latham, 1957, 15 males, largest cl. 21.3 mm, cb. 35.8 mm, smallest cl. 11.9 mm, cb. 18.2 mm, 2 females, cl. 17.6 and 21.0 mm, cb. 29.0 and 35.0 mm (USNM 106407).—Colombia: no data, leg. Marte Latham, 23 males, 28 females (USNM 106409).

Diagnosis.—First gonopod with caudal ridge long, straight; lateral lobe prominent, square, faintly crenulated; apex small, rounded, strangled. Endognath of first maxilliped strongly reduced, approximately 0.25 length of ischium of endognath.

Remarks.—In his original description Pretzmann (1965) designated the male (cb. = 31.6 mm) specimen in lot USNM 106405 as holotype, but later (Pretzmann 1972) stated the number of the holotype to be USNM 106407. In the same work 14 males and two females in lot "106405" (presumably 106407) were designated as paratypes and that author incorrectly stated that the two lots were from the same locality.

Pretzmann (1972) illustrated the whole animal (figs. 170, 171; the negatives were inverted so that the animal appears left handed), and a first gonopod which had been removed from the animal (figs. 311, 312). This appendage, however, does not belong to the holotype (USNM 106405) since this specimen still had the first gonopods attached until the present author removed them. The first gonopod of the original holotype of *H. andagoensis* (USNM 106405) is illustrated in figs. 1A–C.

Hypolobocera beieri Pretzmann, 1968
Fig. 2D

Hypolobocera (*Hypolobocera*) *bouvieri beieri* Pretzmann, 1968:9; 1971:17; 1972:46, figs. 176–181, 308, 309.

Hypolobocera beieri.—Rodríguez, 1982:46, figs. 19a, i, 20b, g, 24 a–d.—von Prahl, 1988:172, fig 2.

Hypolobocera (*Hypolobocera*) *monticola steindachneri.*—Pretzmann, 1972:46 (part).

Material.—Colombia: Bitaco, Valle del Cauca, Andes Occidentales, May 1957, leg. Marte Latham, 1 male holotype, cl. 22.8 mm, cb. 40.6 mm (USNM 106410).—Same, 2 male paratypes, cl. 18.9 and 17.0 mm, cb. 33.5 and 27.2 mm (USNM 128123 ex 106410).—Mountainous area of upper San Juan River, Chocó jungle, Department of Chocó, nearest village Playa de Oro, 28 Mar 1962, leg. Marte Latham, 3 males, cl. 46.2, 32.2 and 31.5 mm, cb. 68.4, 49.9 and 46.9 mm (USNM 240101).

Diagnosis.—First gonopod with caudal ridge straight, well defined; lateral lobe small, rounded, placed relatively far from apex, with conspicuous depression below; apex small, rounded, moderately strangled, with two rounded and flat papillae on distal surface. Endognath of first maxilliped strongly reduced, approximately 0.3 length of ischium of endognath.

Remarks.—Pretzmann (1972) reassigned the paratypes of this species to *Hypolobocera monticola steindachneri,* but characters of the gonopods and carapace clearly place these paratypes in *H. beieri.*

Hypolobocera bouvieri rotundilobata, new subspecies
Fig. 2A–C

Material.—Colombia: Mountains of upper San Juan River, Chocó jungle, Department of Chocó, nearest village Playa de Oro, 28 Mar 1962, leg. Marte Latham, 1 male holotype, cl. 46.2 mm, cb. 68.4 mm (USNM 240103).—Same data, 5 male paratypes, largest cl. 32.2 and 31.5 mm, cb. 49.9 and 46.9 mm (USNM 240104).

Fig. 1. A–C, *Hypolobocera andagoensis* (Pretzmann), holotype, USNM 106405, left gonopod; D–F, *Hypolobocera martelathami* (Pretzmann), holotype, USNM 106408, right gonopod; G–I, *Hypolobocera smalleyi* Pretzmann, holotype, USNM 54042, left gonopod; J–N, *Hypolobocera canaensis* Pretzmann, holotype, USNM 54039, left gonopod. A, D, G, J, caudal view; B, E, H, K, lateral view; C, F, I, L, apex, distal view.

Diagnosis.—Caudal ridge of first gonopod strong, with transverse wrinkles; lateral lobe small, semicircular, covered by minute pores and scattered short setae, without crenulations over distal margin; apex funnel-form, subtriangular in distal view. Endognath of first maxilliped reduced, approximately 0.4 length of ischium of endognath. Fixed finger of chelipeds without conspicuous tubercle at its base. Upper margin of front advanced, angled, marked by conspicuous row of coalescent papillae.

Description (based on holotype and 5 male paratypes).—Carapace relatively narrow (cb/cl = 1.48–1.55). Cervical grooves sinuous, deep, narrow, attaining margins of carapace. Postfrontal lobes small, rounded, well marked; median grooves not deeply impressed between lobes, but making deep incision on upper margin of front; this margin advanced, marked by conspicuous row of coalescent papillae and strongly bilobed in dorsal view; lower orbital margin strongly bent upward in holotype (probably a malformation). Exognath of third maxilliped 0.38–0.40 length of ischium of endognath. Cheliped without a large tubercle over base of fixed finger, but with scattered papillae over palm and merus, particularly on inner surface; fingers tinged reddish brown. First gonopod slender, with small semicircular lateral lobe, covered by minute pores and scattered short setae; strong caudal rib with transverse wrinkles; apex funnel-form, subtriangular in distal view.

Remarks.—*Hypolobocera bouvieri* is widely distributed over the Cordilleras of northern South America, with four subspecies: *H. bouvieri angulata* in the Sierra of Santa Marta, Sierra of Perijá and the Venezuelan Andes; *H. bouvieri bouvieri* and *H. bouvieri stenolobata* in the Eastern Cordillera of Colombia; and *H. bouvieri monticola* on the slopes of the Western Cordillera which descend to the Cauca valley. *H. bouvieri rotundilobata* is the only subspecies so far recorded from the Pacific slopes of the Andes. The type locality, close to the town of Playa del Oro (5°20′N, 76°23′W), is near the headwaters of the San Juan River, where the areas of distribution of *H. andagoensis, H. chocoensis* and *H. malaguena* von Prahl, 1988 overlap. Although the San Juan River runs parallel, and next to, the Cauca River, where *H. bouvieri monticola* occurs, these two river basins are separated by the water divide of the Western Cordillera of Colombia.

Hypolobocera bouvieri rotundilobata can be clearly distinguished from the other subspecies by the semicircular lateral lobe of its first gonopod. In addition, the new subspecies differs from *H. b. bouvieri* and *H. b. monticola* in the absence of a large tubercle at the base of the fixed fingers of chelipeds; and from *H. b. bouvieri, H. b. angulata,* and *H. b. stenolobata* in the absence of crenulations over the distal margin of the lateral lobe. The tuberculation of the upper border of the front in the new subspecies somewhat resembles that of *H. b. angulata* and *H. b. stenolobata,* but it is clearly different from that of *H. b. bouvieri* and *H. b. monticola.*

Etymology.—The subspecific name is from the Latin "rotundus," rounded, and "lobatus," lobed, a reference to the shape of the lateral lobe of gonopod.

Hypolobocera canaensis Pretzmann, 1968

Fig. 1J–L

Hypolobocera (*Hypolobocera*) *canaensis* Pretzmann, 1968:3; 1971:17; 1972:47, figs. 211–213, 313–315.

Material.—Panama: Cana, altitude 850 m, 24 May 1912, leg. E. A. Goldman (U.S. Biological Survey donation), 1 male holotype, cl. 32.6 mm, cb. 51.2 mm (USNM 54039).—Cana, altitude 760 m, 21 May 1912, leg. E. A. Goldman (U.S. Biological Survey donation), 1 immature female paratype (fragmented) (USNM 54036).—Cana, Setiganti River, altitude 610 m, 24 Mar 1912, leg. E. A. Goldman (U.S. Biological Survey donation), 1 immature female paratype, cl. 45.7 mm, cb. 72.8 mm (USNM 54037).—Cana, altitude 760 m, 1 Jun 1912, leg. E. A. Goldman (U.S. Biological Survey donation), 1 male with broken carapace, cl. 34.2 mm, cb. 53.8 mm (USNM 54038).

Diagnosis.—First gonopod slender, slightly arched; caudal ridge straight, long, narrow; lateral lobe long, narrow, more expanded distally; apex funnel-form, elliptic in distal view, with 1 flat rounded papilla on distal surface. Endognath of first maxilliped strongly reduced, approximately 0.3 length of ischium of endognath.

Remarks.—It is doubtful whether the two paratype specimens listed by Pretzmann (1972) belong in this species since both are immature females collected at lower altitudes on different days. There are only fragments of the carapace and some pereopods of one of them (USNM 54036). For details of the type locality Cana see below under *Ptychophallus goldmanni.*

Hypolobocera chocoensis Rodríguez, 1980

Hypolobocera (*Hypolobocera*) *dubia.*—Pretzmann, 1972:48, figs. 224–226, 230–232, 236, 237 (not *Pseudothelphusa dubia* Colosi, 1920).

Hypolobocera chocoensis Rodríguez, 1980: 891; 1982:59, figs. 19f, q, 21b, d, 31 a–d.

Material.—Colombia: Mountains of upper San Juan River, Chocó jungle, Department of Chocó, nearest village Playa de Oro, 28 Mar 1962, leg. Marte Latham, 10 males, the largest cl. 22.8 mm, cb. 36.7 mm, 26 females, the largest cl. 23.8 mm, cb. 39.7 mm (USNM 240102).

Diagnosis.—First gonopod strongly constricted below lateral lobe, with caudal ridge long, irregular; lateral lobe wide proximally, narrow distally; apex funnel shaped, expanded, rounded in distal view, with two flat, wide papillae on distal surface and small subtriangular spine on mesial side. Endognath of first maxilliped strongly reduced, approximately 0.2 length of ischium of endognath.

Remarks.—The following characters should be added to the description of the species: The regions of the carapace (Rodríguez 1982) are strongly marked; the postfrontal area is excavated. The front is well defined by a tuberculated ridge; the surface of the front is conspicuously excavated. The postorbital notch is very deep; the anterolateral border is not continuous with the margin of this notch, but runs dorsally to it, forming a rounded lobe. The anterior portion of the carapace is covered by rough papillae, barely visible to the naked eye. The male chelipeds are strongly unequal; when fully developed the fingers of the largest chela are strongly gapping, the dactylus is recurved; the distal half of the dactylus, the tip of the fixed finger and the teeth of both fingers are brown black.

Hypolobocera chocoensis closely resembles *Hypolobocera malaguena* von Prahl, 1988. The lateral lobe of the first gonopod of *H. malaguena* is smaller and almost rounded; the apex in lateral view is not strangled or funnel-shaped like in *H. chocoensis.* In distal view the apex is clearly triangular, not rounded, and possesses a well developed transverse mesial lobe. Other features which separate *H. malaguena* from *H. chocoensis,* include the smooth carapace with weakly marked regions and unexcavated frontal and postorbital regions, the upper border of the front which is weak toward the sides, and the anterolateral margin of the carapace which is continuous with the margin of the postorbital notch.

Hypolobocera martelathami
(Pretzmann, 1965)
Fig. 1D–F

Strengeria (*Strengeria*) *martelathani* (sic) Pretzmann, 1965:6.

Hypolobocera (*Hypolobocera*) *martelathami* 1971:17; 1972:50, figs. 159–161, 242–244.

Hypolobocera martelathami.—Rodríguez, 1982:52.—Campos & Rodríguez, 1984: 538, figs. 4c, f.

Hypolobocera (*Hypolobocera*) *plana orientalis* Pretzmann, 1968:2; 1971:17; 1972: 60, figs. 162–164, 214–221.

Hypolobocera orientalis.—Rodríguez, 1982: 52, figs. 19d, 20c, h; 26a–c.

Material.—Colombia: No other data, 1957, leg. Marte Latham, 1 male holotype,

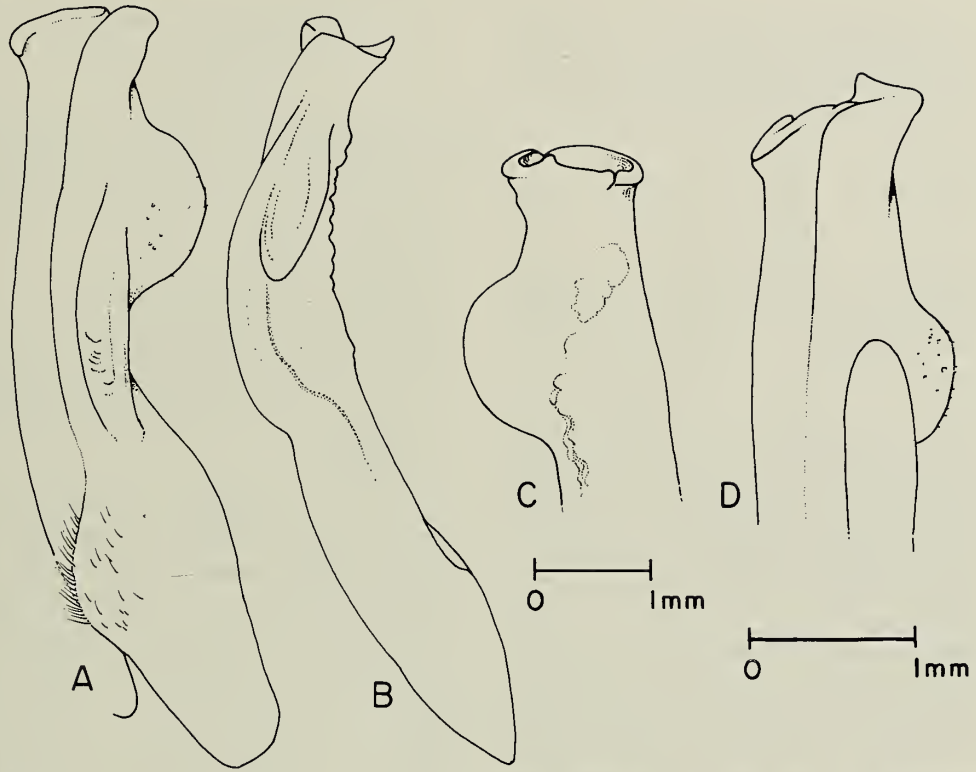

Fig. 2. A–C, *Hypolobocera bouvieri rotundilobata,* new subspecies, holotype, USNM 240103: A, left gonopod caudal view; B, same lateral view; C, same caudal view; D, *Hypolobocera beieri* Pretzmann, holotype, USNM 106410, caudal view.

cl. 16.0, cb. 25.7 mm (USNM 106408).—Colombia: No other data, 1957, leg. Marte Latham, 1 male paratype, cl. 13.0 mm, cb. 20.0 mm, 7 males, cl. 12.7, 12.7, 12.1, 12.0, 10.6, 10.2, 9.8 mm, cb. 19.8, 19.8, 18.7, 15.6, 15.6, 15.2, 14.0 mm, 2 females, cl. 16.7, 15.2 mm, cb. 26.8, 23.8 mm, 1 imm. female, cl. 12.0 mm, cb. 18.4 mm, 5 juveniles (USNM 122602).

Diagnosis.—First gonopod with distal half wide in caudal and mesial views, caudal ridge straight; lateral lobe large, reaching middle of first gonopod, narrow proximally, wide distally, covered with minute wrinkles, pores and scattered short setae; apex not funnel-shaped or conspicuously expanded, oblong or rectangular in distal view, 2 flat rudimentary papillae on distal surface. Endognath of first maxilliped moderately reduced, approximately 0.55 length of ischium of endognath.

Remarks.—The first gonopod of *H. martelathami* is identical to that of *Hypolobocera orientalis* Pretzmann, 1968. According to Pretzmann (1968) this last species has a broader carapace, and the exognath of third maxilliped is longer, and does not possess an exorbital tooth. Actually the mean cb/cl ratio is 1.54 in both *H. martelathami* (n = 12) and *H. orientalis* (n = 10, Rodríguez 1982); the mean ratio of the exognath to ischium of the endognath is 0.65 in *H. orientalis* (Rodríguez 1982) and 0.55 (n = 9; spread 0.46–0.66) in *H. martelathami* (USNM 106408, USNM 122606); the postorbital area is similar in both species. Consequently, *Hypolobocera orientalis* should be considered as a junior synonym of *Hy-*

polobocera martelathami, as has already been suggested by Rodríguez (1982). *Hypolobocera plana* (Smith 1870) is an incertae sedis species (Rodríguez 1982).

Hypolobocera smalleyi Pretzmann, 1968
Fig. 1G–I

Hypolobocera (*Hypolobocera*) *smalleyi* Pretzmann, 1968:4; 1972:50, figs. 233–235, 238, 239.
Hypolobocera smalleyi.—Rodríguez, 1982: 60.

Material.—Panama: Cana, Canal Zone, altitude 760 m, 1912, leg. E. A. Goldman (U.S. Biological Survey don.), 1 male holotype, carapace broken, cl. 39.5 mm, cb. 24.7 mm (USNM 54042).

Diagnosis.—First gonopod with caudal ridge long, straight; lateral lobe prominent, rounded, more expanded distally, with conspicuous coalescent papillae on cephalic side; apex funnel shaped, expanded, subtriangular in distal view, with 1 acute papilla on distal surface. Endognath of first maxilliped strongly reduced, approximately 0.3 length of ischium of endognath.

Genus *Ptychophallus* Smalley, 1964
Ptychophallus cocleensis Pretzmann, 1965
Fig. 3D, E

Ptychophallus (*Ptychophallus*) *montanus cocleensis* Pretzmann, 1965:5.
Ptychophallus (*Ptychophallus*) *cocleensis.*—Pretzmann, 1971:21; 1972:88, figs. 505–507, 534, 535.

Diagnosis.—First gonopod with lateral projection divided in 2 lobes by deep median notch, distal lobe small, rounded close to apex, proximal lobe finger-like, directed distally; distal caudal ridge short; 2 mesial apical processes large, triangular.

Material.—Panama: Rio Coclé del Norte, 1951, leg. M. W. Stirling, 1 male holotype (USNM 119869).—Barro Colorado Island, Wheeler trail, 9 Jul 1969, leg. R. Foster, 1 male (USNM 230097).

Ptychophallus colombianus (Rathbun, 1893)
Fig. 3A–C

Pseudothelphusa colombiana Rathbun, 1893:653, pl. 74, fig. 10, pl. 75, fig. 1; 1898:533.—Young, 1900:219.—Rathbun, 1905:302.—Coifmann, 1939:107.—Smalley, 1964:10.
Ptychophallus (*Semiptychophallus*) *columbianus* (sic).—Pretzmann, 1965:5.
Ptychophallus (*Semiptychophallus*) *columbianus* (sic) *columbianus* (sic).—Pretzmann, 1971:21; 1972:88, figs. 514, 515, 525, 526.

Material.—Panama: Chiriquí, David River, about lat. 8°28′N, long. 82°24′W, elevation 1220 m above sea level, very rapid stream, descending from Mount Chiriquí, Jul 1883, leg. J. A. McNeil, 2 female types (USNM 5512).—Volcán, Rio Chiriquí Viejo, 1 Mar 1924, leg. Foster, 1 male (soft shell) cl. 14.8 mm, cb. 26.8 mm (USNM 58182).—Chiriquí, Hato del Volcán, Pacific drainage, c. 3000 m altitude, 18 Jun 1960, leg. Robinson et al., 5 specimens (USNM 230098).

Diagnosis.—First gonopod with lateral projection narrow, with slight depression at middle; distal caudal ridge short, narrow; mesial apical process small, triangular.

Remarks.—Rathbun (1893) based her description on two female syntypes. Pretzmann (1972) assigned to this species the male specimen from Volcán, Panama, mentioned above (that he stated to be a female, USNM 58182), and two specimens (male and female) from Chiriquí, Panama, in the Zoologisches Museum, Berlin. Examination of the USNM material revealed that the illustration of the carapace in Pretzmann's (1972, figs. 514, 515) corresponds to one of the female paratypes (USNM 5512), and that the first gonopod illustrated in figs. 525 and 526 was taken from the specimen from Volcán (USNM 58182). Morphological details of the first gonopods are not clearly discernible from these figures and has been redrawn in the present work.

Fig. 3. A–C, *Ptychophallus colombianus* (Rathbun), USNM 58182: A, left gonopod, caudal view; B, same, meso-caudal view; C, same, apex, distal view; D, E, *Ptychophallus cocleensis* Pretzmann, holotype, USNM 119869: D, left gonopod, caudal view; E, same, apex, cephalic view; F–H, *Ptychophallus goldmanni* Pretzmann, holotype, USNM 54044: F, left gonopod, caudal view; G, same, cephalic view; H, same, apex, distal view; I, J, *Ptychophallus lavallensis* Pretzmann, USNM 240100: I, left gonopod, caudal view; J, same, apex, cephalic view.

Ptychophallus goldmanni Pretzmann, 1965
Fig. 3F–H

Ptychophallus (*Microptychophallus*) *goldmanni* Pretzmann, 1965:5; 1971:21; 1972:90, figs. 527–529, 544–546.
Ptychophallus goldmanni. —Rodríguez, 1982:86.

Material.—Panama: Cana, 850 m, 24 May 1912, leg. E. A. Goldman, U.S. Biological Survey, 1 male holotype (USNM 54044).

Diagnosis.—First gonopod with lateral projection almost absent, except for small lobe located distally; caudal ridge forming distally large triangular process which extends slightly beyond apex; strong longitudinal ridge on cephalic surface ending distally in flat round lobe; mesial apical process rounded.

Remarks.—The name "Cana" refers to Mount Cana, altitude 1615 m, 7°48'N, 77°32'W, in Darien Province, Panama. The locality is situated in the northern outskirts of the Serranía del Baudo. The area is drained by the Balsas River which empties into a southern extension of the Gulf of San Miguel. In this mountain, E. A. Goldman also collected *Hypolobocera canaensis* and *H. smalleyi* (see above) at altitudes between 610 and 850 m.

Ptychophallus lavallensis Pretzmann, 1978
Fig. 3I–J

Ptychophallus (*Ptychophallus*) *exillipes lavallensis* Pretzmann, 1978:1; 1980:651–666.

Material.—Panama: Coclé, headwaters of Rio Indio, N of La Mision, above El Valle, where 3 springs begin stream, c. 700 m altitude, 14 Sep 1962, leg. Loftein and Kosan, 3 males, cl. 21.7, 13.7 and 12.3 mm, cb. 37.0, 21.9 and 19.2 mm (USNM 240100).—El Aguacate, 22 Feb 1973, leg. A. Smalley, 1 male, cl. 23.4 mm, cb. 39.8 mm (USNM 184338).—Same data, 1 male, cl. 23.5, cb. 29.9 mm (USNM 184339).

Diagnosis.—First gonopod with lateral projection very wide, simple, its proximal margin transverse and slightly concave, its distal margin convex, both with minute setae; distal caudal ridge short, weak; apex strongly bent toward cephalic side, making contact with cephalic surface, field of spines directed laterally.

Description.—Cervical grooves recurved backward, narrow and shallow; do not reach margins of carapace; anterolateral margins with shallow postfrontal notch, rest of border entire. Postfrontal lobes wide, delimited anteriorly by transverse depression; median groove narrow, deep, making deep incision on upper margin of front. Surface of carapace between postfrontal lobes and front flat, horizontal, only slightly inclined downward. Upper margin of front slightly convex in dorsal view, thin, well marked, with few small tubercles; lower margin thin, moderately sinuous; front between upper and lower margin high, vertical.

Exognath of third maxilliped 0.68 length of ischium of endognath. Palm of largest cheliped moderately swollen, lower and upper margins convex; fingers with rows of black points on external surfaces. Lateral lobe of first gonopod very wide, simple; proximal margin transverse and slightly concave, distal margin convex; apex strongly bent toward cephalic side, with field of spines directed laterally; distal caudal ridge short, weak; margin of lateral lobe only have minute setae.

Remarks.—This species was only briefly diagnosed by Pretzmann (1978, 1980) and no illustration of the first gonopod was published. The description given above, which supplement Pretzmann's short description, is based on the specimens from Rio Indio and El Aguacate, Panama, recorded above. The Rio Indio runs parallel to, and approximately 30 km from, the valley of Rio Coclé, where the type locality of the species is found.

The first gonopod of *P. lavallensis* has a wide undivided lobe, like *P. exillipes* (Rath-

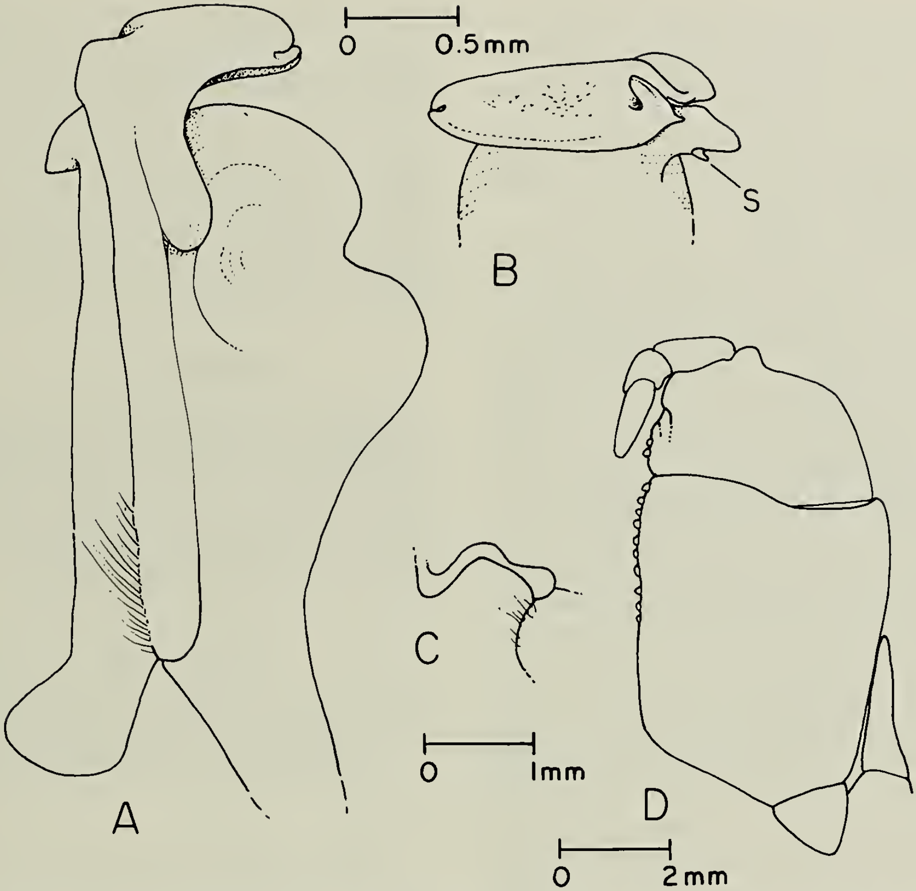

Fig. 4. *Ptychophallus micracanthus,* new species, holotype, USNM 240106: A, left gonopod, caudal view; B, same, apex, cephalic view; C, opening of left efferent channel; D, third maxilliped; s, cephalic spine.

bun 1898), but it has a different shape and lacks the long setae; the apex is relatively smaller, more strongly bent toward the cephalic side, making contact with the cephalic surface of the appendage; the distal caudal ridge is weaker, and relatively smaller.

Ptychophallus micracanthus, new species
Fig. 4A–D

Material.—Panama: Pacific drainage, 1971, leg. L. G. Abele, 1 male holotype, cl. 24.6 mm, cb. 42.4 mm (USNM 240106).—Same data, 1 female paratype, 36 juveniles (USNM 240107).—Same data, 4 males, 2 females, 22 juveniles (USNM 240108).—San Blas, tributary to Rio Carti Grande at trail NW from Nuragandi, 5 Mar 1985, leg. R. W. Bouchard, 9 juveniles (USNM 240105).—San Blas, Quebrada Pingandi at Llando-Carti road, 4 Mar 1985, leg. R. W. Bouchard, 3 males (USNM 240110).—San Blas, Nuragandi off Llando-Carti road, 1 Mar 1985, leg. R. W. Bouchard, 1 juvenile male (USNM 240111).—Tributary to Pacora River, creek by road about 8 miles N of Cerro Azul, 27 Aug 1962, leg. Loftein and Kosan, 3 males, 1 female, 3 juveniles (USNM 240109).

Diagnosis.—First gonopod with large lateral projection divided in 2 subequal rounded lobes by median notch, margins with minute setae; distal caudal ridge short, strong; mesial apical process small, triangular, with conspicuous spine on cephalic surface; apex strongly bent toward cephalic side, with field of spines directed toward latero-cephalic side.

Description of holotype.—Cervical grooves recurved backward, narrow and shallow, not reaching margins of carapace; anterolateral margins with shallow postorbital notch, rest of borders entire. Postfrontal lobes wide, delimited anteriorly by transverse depression; median groove narrow, deep, making incision on upper margin of front. Surface of carapace between postfrontal lobes and front flat, horizontal, only slightly inclined downward. Upper margin of front slightly convex in dorsal view, thin, well marked, with few small tubercles; lower margin thin, moderately sinuous; front between upper and lower margin high, vertical.

Exognath of third maxilliped 0.54 length of ischium of endognath. Palm of largest cheliped moderately swollen, with lower and upper margins convex; fingers slightly gaping, with rows of small black-brown points on external surface. First gonopod with large lateral projection divided in 2 subequal rounded lobes by median notch, margins with minute setae; distal caudal ridge short, strong; mesial apical process small, triangular, with conspicuous spine on cephalic surface; apex strongly bent toward cephalic side, with field of spines directed toward latero-cephalic side.

Remarks.—The first gonopod of *P. micracanthus* resembles that of *P. tumimanus* (Rathbun, 1898) in the shape of the lateral lobe, but in *P. micracanthus* it is less expanded laterally and the middle notch is deeper. This species differs from all others in the genus by the presence of a small but clearly visible spine on the mesial projection of the first gonopod.

The species is well represented in the collections of the National Museum of Natural History, but the only fully mature male is the holotype specimen (USNM 240106). However, immature crabs are easily identifiable by means of the spine located on the mesial apical process of the gonopod which is present even in specimens with a carapace length of 10.8 and 12.5 mm.

Etymology.—The specific name is from the Greek "mikros," small, and "acanthus," spine, in reference to the spine on the mesial process of the gonopod.

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PARAPINNIXA CUBANA, A NEW PEA CRAB FROM CUBA (CRUSTACEA: BRACHYURA: PINNOTHERIDAE)

Ernesto Campos

Abstract.—One male specimen of *Parapinnixa cubana*, new species, was collected on Diego Pérez Reef, Cuba. *Parapinnixa cubana* most closely resembles *P. magdalenensis* Werding & Müller, 1990, and can be distinguished from this and all other species of the genus by the shape and proportions of the carapace and chela.

Resúmen.—Un especímen macho de *Parapinnixa cubana*, nueva especie, fue colectado en el Arrecife Diego Pérez, Cuba. *Parapinnixa cubana* se asemeja mayormente a *P. magdalenensis* Werding & Müller, 1990, y se puede distinguir de ésta y todas las otras especies del género por la forma y proporciones del caparazón y la quela.

During the study of the marine crustacean fauna of Cuba by J. C. Martínez-Iglesias and colleagues, Instituto de Oceanología, Academia de Ciencias de Cuba (ACC), one male pinnotherid specimen was collected on Diego Peréz Reef. The specimen was sent to me for study and proved to be a new species of *Parapinnixa*. The holotype of the new species has been deposited in the Crustacean Collection, ACC. Abbreviations used in this paper include: third maxilliped as MXP3, carapace length as CL, carapace width as CW, and pereopods as P1 (the cheliped) to P5. Measurements are in millimeters.

Parapinnixa cubana, new species
Figs. 1, 2

Material.—Diego Pérez Reef, Golfo de Batabano, Cuba, 20 m depth, Jul 1991, male holotype (CW = 3.0, CL = 1.8), coll. J. C. Martínez-Iglesias, ACC 1880.

Description of holotype.—Carapace elliptical, width 1.6 times length, dorsally and laterally with short setae (Fig. 1A); front deflexed, triangular, with shallow medial groove, covered with minute setae; posterior margin almost straight. Eyes large, filling orbits, extending far beyond anterior margin of carapace; orbital hiatus occupied by basal antennal article (Fig. 1B). Antennulae plicate in wide fossettes, fronto-orbital distance subequal to carapace length. Buccal area triangular, epistome linear. MXP3 (Fig. 2A–B) with merus widely triangular, outer and distal margin almost straight, outer margin with plumose setae; carpus rounded, with long setae, and longer than combined length of elongated propodus and minute, inconspicuous dactylus; dactylus distally with 2 long tufts of setae (Fig. 2C); exopod ovate, without flagellum (Fig. 2D).

P1 stout (Fig. 1C–D), as long as P2, merus dorsally subtriangular, with setae (Fig. 1C), lateroexternal surface trapezoidal and flattened (Fig. 1D); carpus rounded, setae shorter than those on merus. Chelae symmetrical, tomentose; length of palm subequal to height, longer than fingers. External surface of palm somewhat convex proximally, slightly concave distally, with fingers ornamented with several teeth; internal surface slightly swollen and with tuft of setae at summit, dorsally convex with tubercles, ventral margin somewhat sinuous. Fingers

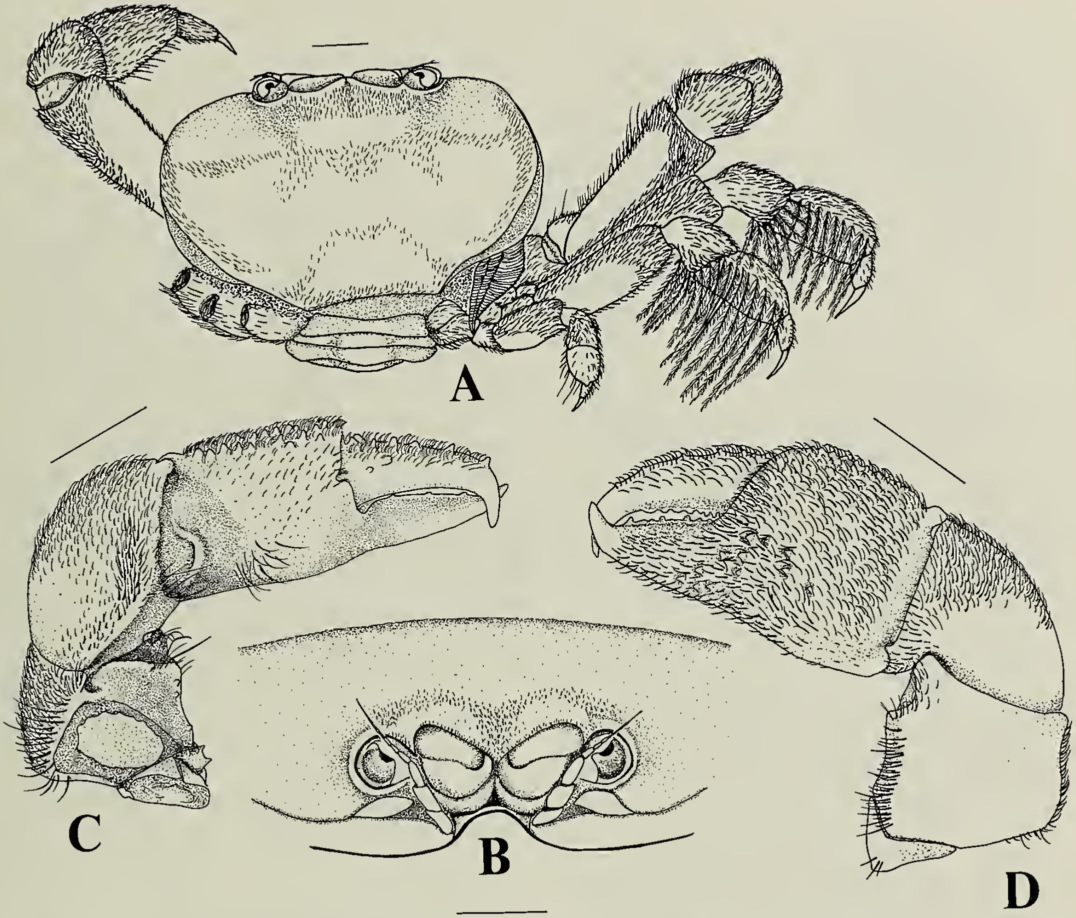

Fig. 1. *Parapinnixa cubana,* new species, male holotype, A, Dorsal view; B, frontal view; C and D, left cheliped, inner and outer view respectively. Scales equal 0.5 mm. Plumose setae omitted on dactylus and ventral margin of carpus and propodus of P3 and P4; subacute teeth not visible on inner surface of dactylus in C.

triangular, curving at tip where they cross; cutting surface of both fingers with row of subacute teeth. Dorsal surface of dactylus with crest of 7 subacute and acute teeth.

Walking legs (Fig. 1A) decreasing in length and width from P2 to P5, meri flattened, dorsally and ventrally pubescent, P5 much the shortest. Carpi dorsally subelliptical and convex, laterally subtriangular, with short setae. Propodi tapering distally. Fringe of extremely long plumose setae on outer surface of carpus, propodus and dactylus of P3 and P4, others placed on ventral margin of carpus and propodus of same legs. Dactyli triangular, naked at long corneus tip, those of P2 to P4 somewhat falcate, that of P5 straighter.

Abdomen (Fig. 2E) with 7 free somites, third widest and with convex lateral margins, fourth through seventh gradually tapering, seventh longest, subtriangular, its length/width ratio 1.66.

Gonopods (Fig. 2F) almost straight toward proximal third, folding mesially and tapering distally, ending in pore of spermatic channel.

Comparison with other species of Parapinnixa.—Parapinnixa cubana mainly differs from its congeners as follows: *P. nitida* (Lockington 1876), *P. glasselli* Garth, 1939,

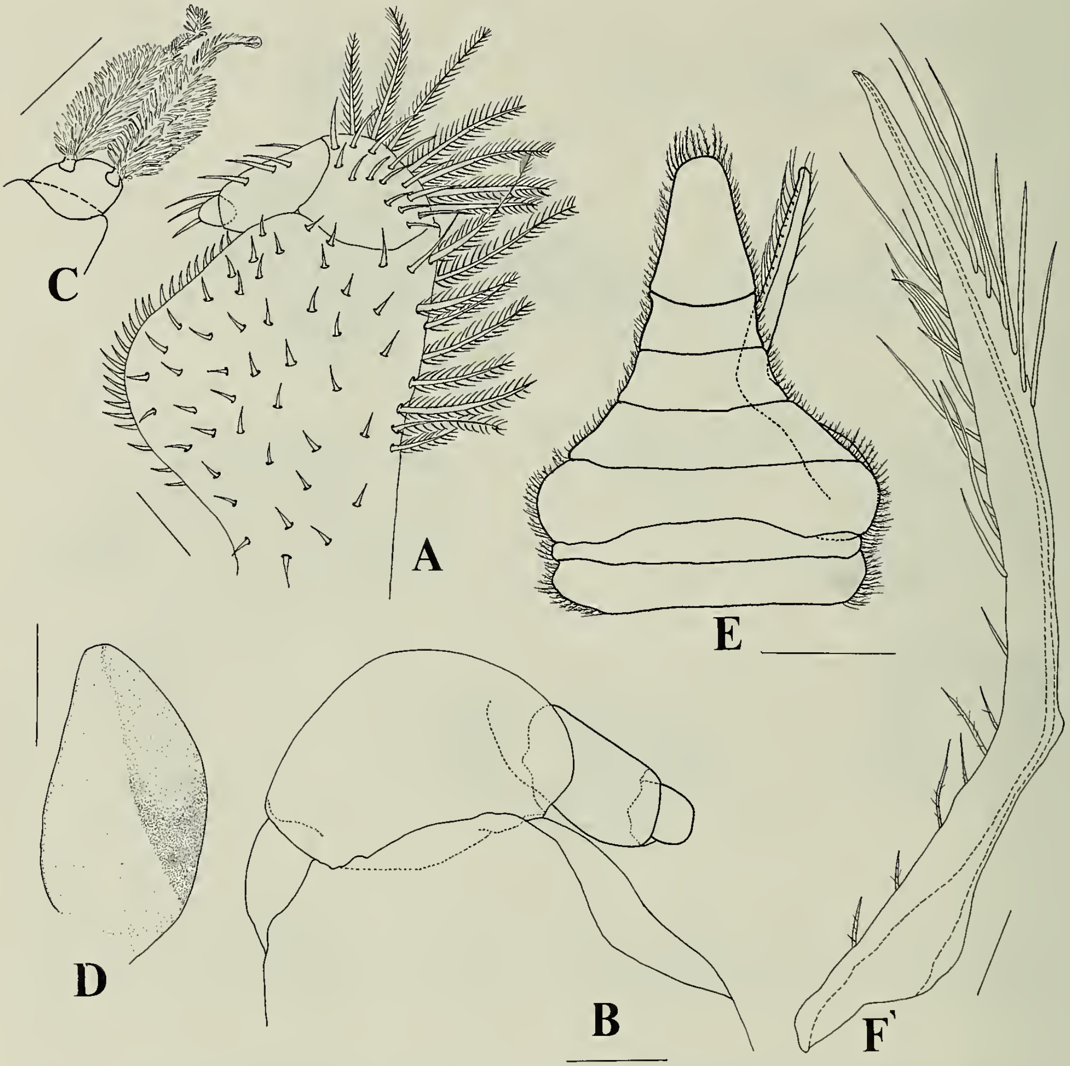

Fig. 2. *Parapinnixa cubana,* new species, male holotype. A–D, third maxilliped; A, outer view; B, palp, inner view; C, dactylus; D, exopod; E, abdomen; F, gonopod. Scales equal 0.125 mm (A–B, D, F), 0.05 mm (C), 0.5 mm (E).

and *P. hendersoni* Rathbun, 1918 have a CW which is more than twice the CL, instead of 1.6 as in *P. cubana.* In addition, the three former species have two rows of hairs on the outer surface of the smooth palm, which contrast with the absence of such hairs and the presence of sub-acute and acute tubercles on the surface of the palm in *P. cubana* (see Garth 1939: plate 9, fig. 4; Williams 1984: fig. 358). *Parapinnixa affinis* Holmes, 1900 has the dactylus of the chela hooked and a row of hairs on the surface of the palm which are lacking in *P. cubana* (see Glassell 1933: fig. 1–2). *Parapinnixa bouvieri* Rathbun, 1918, and similarly *P. affinis,* have small eyes (see Williams 1984: fig. 357) and the fronto-orbital width about one third the CW, whereas *P. cubana* has large eyes and the fronto-orbital width larger than one third the CW. In addition P3 and P4 are smaller in *P. bouvieri* than in *P. cubana. Parapinnixa beaufortensis* Rathbun, 1918 has a tuft of hair on either side of the dorsal surface of the carapace near the lateral margin, which are absent in *P. cubana.* A male specimen identified with hesitation as *P. beaufortensis* by Werding & Müller (1990: fig. 1a and 1e) has, in addition to the tufts noted above, a less elongated abdomen and more robust gonopod than does *P. cubana.*

Parapinnixa cubana most closely resembles *P. magdalenensis* Werding & Müller (1990). The two species are easily distinguished by the articles of the palp on MXP, and the pattern of setation on the carapace, chelipeds and walking legs. Furthermore the antero-lateral margin of the carapace is crenulate in *P. magdalenensis* but not in *P. cubana*; the merus of the cheliped is more elongated and possesses tubercles in *P. magdalenensis* than in *P. cubana.* Finally, the posterior margin of the caparace is wider than the fronto-orbital margin, and the gonopod is more robust in *P. magdalenensis* (see Werding and Müller 1990: fig. 2a–e) than in *P. cubana.*

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I am indebted to Juan Carlos Martínez-Iglesias for allowing me to study and describe *Parapinnixa cubana.* I gratefully acknowledge the help of my wife Alma Rosa who illustrated and prepared the figures for publication. My deep gratitude is due to Raymond B. Manning and Rafael Lemaitre (National Museum of Natural History, Smithsonian Institution), and Deborah Zmarzly (Marine Biology Laboratory, San Diego) for reviewing my manuscript with great care. This work has been supported by project "Crustáceos simbiontes de Baja California" of the Facultad de Ciencias, Universidad Autónoma de Baja California, and the 1989 Scientific Collaboration Agreement between México (Consejo Nacional de Ciencia y Tecnología) and Cuba (ACC).

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PETROLISTHES EXTREMUS, A NEW PORCELAIN CRAB (DECAPODA: ANOMURA: PORCELLANIDAE) FROM THE INDO-WEST PACIFIC

Roy K. Kropp and Janet Haig

Abstract.—*Petrolisthes extremus,* new species, is described from several locations in the Indo-west Pacific. The new species is most similar to *P. coccineus* and *P. carinipes,* with which it shares a transversely rugose carapace, sinuously triangular front, and one epibranchial spine. *Petrolisthes extremus* is distinguished from the *P. coccineus* by having the lateral margins of the carapace not converging strongly between its widest point and the epibranchial spines and by having the carpus of the cheliped relatively shorter and wider. *Petrolisthes extremus* is distinguished from *P. carinipes* by having a narrower front of the carapace that has sharply oblique lateral lobes. The new species is known from Cocos Keeling, the Kermadec Islands, Lord Howe Island, Easter Island, the Mariana Islands, and Taiwan.

Among several collections of porcellanid crabs from the Indo-west Pacific were specimens belonging to an undescribed species of *Petrolisthes.* Study of the material revealed that several previous literature records also could be referred to the new species.

The material used in this study is located in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), the Natural History Museum of Los Angeles County (the collections formerly were associated with the Allan Hancock Foundation), Los Angeles, California [LACM (AHF)], the Bernice P. Bishop Museum, Honolulu, Hawaii (BPBM), the Australian Museum, Sydney, Australia (AM), the National Museum of New Zealand, Wellington, New Zealand (NMNZ), and the Institute of Zoology, Academia Sinica, Taipei, Taiwan (IZAS).

Abbreviations used are: cl, carapace length; cw, carapace width; coll., collector; ft, feet; m, meters; mm, millimeters; and ovig., ovigerous.

Petrolisthes extremus, new species
Fig. 1

Petrolisthes, sp.—Whitelegge, 1889:36 [list, Lord Howe Island].

Petrolisthes lamarcki.—Gillett & McNeill, 1959:158, pl. 152, figure at bottom of page [Lord Howe Island]. [Not *Petrolisthes lamarckii* (Leach, 1820)].

Petrolisthes coccineus.—Gillett & McNeill, 1962:158, pl. 152, figure at bottom of page; Gillett and McNeill, 1967:158, pl. 152, figure at bottom of page [Lord Howe Island]. [Not *Petrolisthes coccineus* (Owen, 1839)].

Petrolisthes n. sp. 2 [Haig, ms].—Kropp et al., 1981:39 [Guam]; Kropp & Eldredge, 1982:125 [Cabras Island, Guam].

Type material.—Holotype: Mariana Islands: Guam; Asan Point; shore at low tide; 13 Jun 1980; coll. R. K. Kropp; 1 ♂ LACM 80-151.1 (AHF 8014). Paratypes: Cocos Keeling Island: West Island (ocean side); cove on N end (12°8′22″S, 96°49′0″E); dead coral; <1 m; 22 Feb 1974; coll. Smith-

Vaniz et al., 1 ♀ (ovig.) USNM 190765. Kermadec Islands: Sunday Island; 1909–1910; coll. R. S. Bell & W. R. B. Oliver; 9 ♂, 7 ♀ (3 ovig.) NMNZ. Taiwan: Hsan Tiao Chiao; 10 May 1969; coll. Ting; 1 ♂ IZAS. Yeh Liu Pi; poison station; 2 m; 28 Jun 1978; coll. L. G. Eldredge; 2 ♂, 1 ♀ (ovig.) LACM 78-237.1 (AHF); Kuei-An; 47 km S of Hualien; subtidal under rock; 2 Jul 1978; coll. L. G. Eldredge; 1 ♀ (ovig.) USNM 210587. Mariana Islands: Guam; Asan Point; shore at low tide; 13 Jun 1980; coll. R. K. Kropp; 1 ♀ (ovig.) LACM 80-151.2 (AHF); Piti Bay; outer reef flat W of Camel Rock; down 1–2 m in consolidated rubble; 11 Jun 1986; coll. B. D. Smith & H. Conley; 2 ♀ (ovig.) BPBM. Easter Island: from starfish stomach; Jan 1965; coll. I. Efford & J. Mathias; 1 ♂ LACM 65-325.2 (AHF 654); Anakena; 20–25 ft [7–8 m]; 15 Jan 1965; coll. I. Efford & J. Mathias; 1 ♂ (damaged) LACM 65-325.1 (AHF); Motu Iti; rock; 8 Aug 1972; coll. H. I. Moyano; 1 ♀ LACM 72-358.1 (AHF).

Other material examined.—Taiwan: Kuei-An; 47 km S of Hualien; on *Pocillopora danae* Verrill and *Stylophora pistillata* (Esper); 1–3 m; 23 Jul 1979; coll. R. K. Kropp; 3 ♀, 2 ♂ USNM 210585, 210586; San Hsien Tai; on *Pocillopora danae;* 3 m; 25 Jul 1979; coll. R. K. Kropp; specimen parasitized by rhizocephalan, USNM 210584. Mariana Islands: Anatahan; "Observation Spot"; intertidal under rocks; 19 Jul 1981; coll. L. G. Eldredge; 3 ♀ USNM 210588; subtidal under rock; 5–7 m; 19 Jul 1981; 1 ♀ USNM. Pagan; Katsu; subtidal under rock; 2 m; 7 Mar 1981; 2 ♀ USNM; "Palapala Bay"; under rock; 1 m; 15 Jul 1981; 1 ♀ USNM. Guam; Piti Bay; outer reef flat; intertidal; 13, 15 Jun 1980; 3 Jun 1981; 3 ♂, 2 ♀ (1 ovig.) USNM; outer reef flat; down 1–2 m in consolidated coral rubble; 18 May, 11 Jun 1986; coll. B. D. Smith & H. Conley; 2 ♂, 2 ♀ (ovig.) USNM; Luminao; reef front under rock; 6 m; 8 Sep 1980; coll. V. Tyndzik; 1 ♂ USNM. Pago Bay; outer reef flat; intertidal; 3 May 1980; 1 juv.; reef front under rock; 2–3 m; 24, 31 May 1986; 1 ♂, 1 ♀ (ovig.) USNM. Lord Howe Island: collected before 1900; 1 ♀ AM G.2420, 2 ♂, 2 ♀ AM G.2512; collected before 1909; coll. A. R. McCulloch; 2 ♀ AM P.1131; 1921; coll. A. R. McCulloch; 2 ♂ AM P.5248, 1 ♂, 5 ♀ AM P. 5429; collected before 1924; coll. G. P. Whitely; 4 ♂ AM P.6883; Ned's Beach; Jul 1959; coll. E. Pope; 1 ♀ AM P.15168; Ned's Beach; from coral; Oct 1962; coll. J. Booth; 1 ♂ AM P.15169; 6 Mar 1963; coll. J. Booth; 1 ♂, 2 ♀ AM P.15170.

Measurements.—Holotype: cl, 6.6 mm, cw, 6.5 mm. Paratypes: largest male: cl, 11.3 mm, cw, 10.5 mm; largest female: cl. 9.8 mm, cw, 9.7 mm; smallest ovigerous female: cl, 5.0 mm, cw, 4.6 mm.

Diagnosis.—Carapace with distinct transverse rugae each with anterior row of setae, 1 epibranchial spine present; front sinuously triangular, margin serrated, supraocular spine present. Chelipeds slightly unequal in size; carpus with squamate median longitudinal ridge, anterior margin with 3–4 spine-tipped teeth, posterior margin with 3 spines; dorsal surface of manus divided by longitudinal squamous ridge, outer portion with granules, outer margin serrated and with 6 or more spines on proximal half; inner edges of fingers serrated, gape with very short setae, projecting only slightly above surfaces of fingers. Merus of walking legs with transverse striations, anterior margin with 3–8 spines and fringed with plumose setae, posterodistal spines 2, 2, 0; carpus of first walking leg with or without anterodistal spine.

Description.—Carapace slightly longer than broad, broadest at posterior branchial region, lateral margins strongly converging anteriorly, cristate. Front sinuously triangular, lateral lobe oblique, less produced than median lobe; margin crenulate; protogastric lobes fringed anteriorly with plumose setae, divided by median groove. Supraocular lobe well-developed, spine usually present, occasionally obsolescent. Orbits shallow, very oblique; outer orbital angle not produced, or produced into very small tooth. Epibranchial spine well-developed. Gastric region with strong transverse striae, sometimes interrupted at midline; hepatic, anterior branchial, outer margin of posterior branchial with shorter striae; frontal region crossed with fine transverse lines; cardiac, posterior branchials except near margins finely punctate, appearing smooth. Striae of carapace lined anteriorly with very fine, short setae, extending less than half way between crests of adjacent striae.

Basal segments of antennules with several irregularly-spaced denticles of varying size on anterior margin. First movable segment of antennae with strong, spinnule-tipped lobe on anterior margin; second rugose or strongly granulate along anterior margin, tubercle sometimes developed anteroproximally; third smooth.

Dorsal extension of ocular peduncle onto cornea triangular, lined with simple setae, single larger seta distally (often missing in preserved specimens); cornea round in lateral view.

Merus of chelipeds transversely rugose on dorsal and ventral surfaces; inner margin with strong rugose tooth or lobe, its edges crenulate; distal margin with one or two spines, lined distally with plumose setae; median or subproximal spine usually present on outer portion of dorsal surface. Carpus (excluding inner marginal teeth) about twice as long as wide; inner margin with 3–4 strong teeth, these serrate or crenulate along edges, often with smaller denticles between them; series of 5–6 spines along distal half of outer margin, including 1 at outer distal angle; dorsal surface with median longitudinal row of broad, flat squamae, inner portion (including marginal teeth) covered with smaller flattened granules; ventral surface with transverse rugae. Palm with outer margin thin, strongly curved, serrated and proximally spinulate in smaller specimens, crenulate or with blunt teeth in larger ones; dorsal surface with strong longitudinal crest extending from base of dactyl nearly to articulation with carpus; surface inside this crest with oblique rugae or flattened squamae; surface to outside covered with flattened or somewhat upstanding granules; ventral surface obliquely rugose. Dactyl with longitudinal row of prominent, flattened squamae; surface of fixed finger slightly concave, usually granulate; cutting edges meeting for entire length; in some individuals of both sexes, fingers of 1 cheliped gaping and cutting edge of dactyl with strong conical tooth proximally; ventral surfaces of fingers with flattened granules, inner side with short, sparse pubescence or none. All segments of cheliped with very short, fine setae arising from distal side of granules and rugae, but these scarcely visible except at margins; in smaller specimens a fringe along outer margin of chela; in larger adults this fringe absent or confined to proximal portion of margin; usually fringe of plumose setae along distal side of each inner carpal tooth.

Walking legs rugose dorsally; dorsal surface of all segments with simple setae of varying length; merus with thick fringe of plumose setae along anterior margin. Leg 1: merus with 6–9 spines on anterior margin, 2 well-developed posterodistal spines (the smaller, more anterior spine occasionally obsolescent); carpus with anterodistal spine; propodus with 2–3 movable spinules along midline of posterior margin. Leg 2: merus with 4–8 spines on anterior margin, 2 well-developed posterodistal spines (the smaller, more anterior spine occasionally obsolescent); carpus without anterodistal spine; propodus with 2–3 movable spinules along midline of posterior margin. Leg 3: merus with 3–5 spines on anterior margin, posterodistal margin unarmed; carpus without anterodistal spine; propodus with 2 movable spinules along midline of posterior margin. Dactyls of all legs with 3 movable spinules on posterior margin.

Coloration.—Overall color of carapace, chelipeds, and walking legs mottled light green, blue, and bright white with scattered

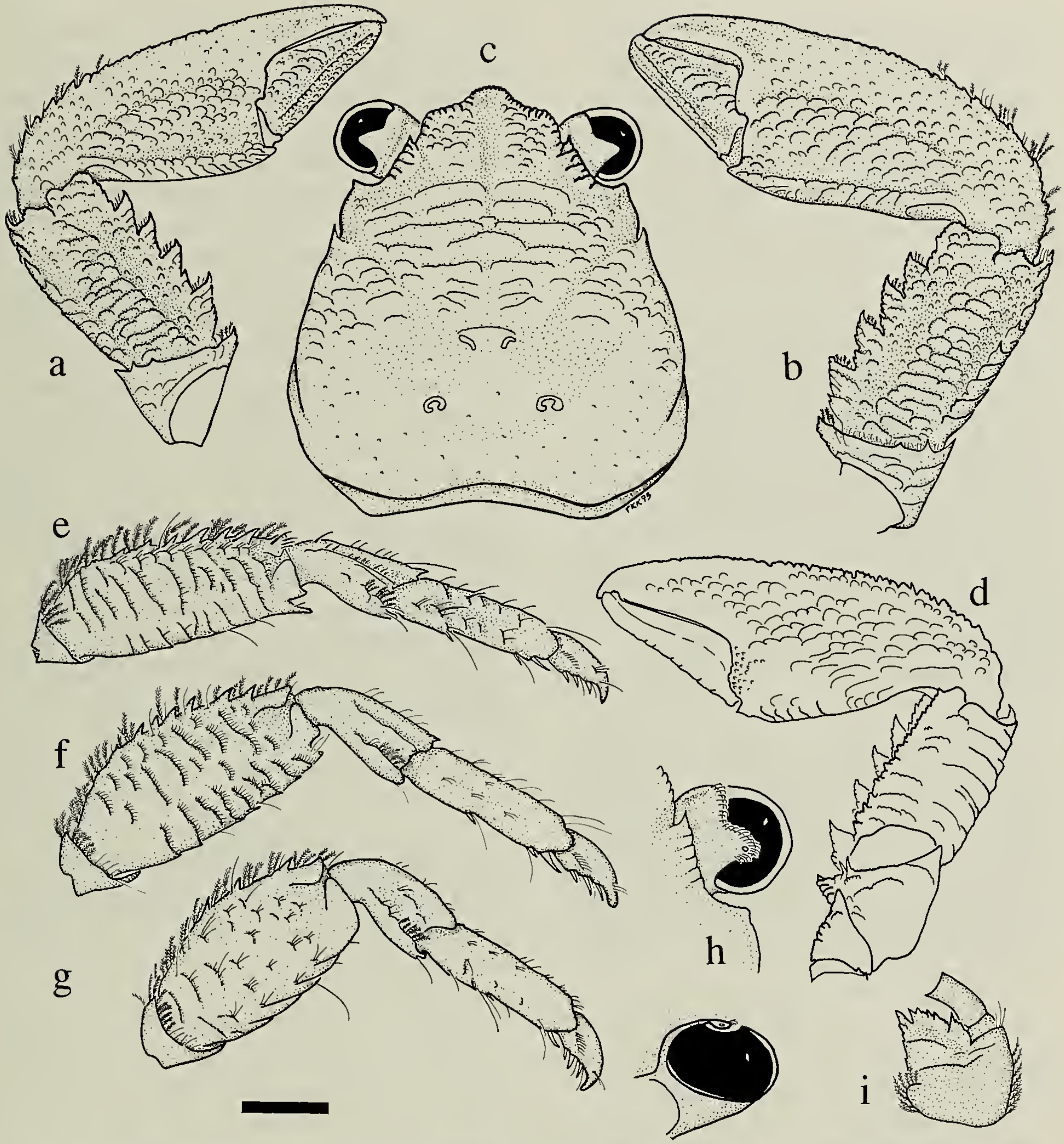

Fig. 1. *Petrolisthes extremus,* new species, paratype ♂ (Kermadec, NMNZ): a, b, chelipeds (dorsal view); c, carapace; d, left cheliped (ventral view); e–g, right walking legs 1, 2, 3; h, right eye (dorsal, lateral views); i, basal segment of right antennule. Scale: 2.2 mm (a, b, d); 1.5 mm (c, e–g); 1 mm (h–i).

burgundy spots; red setae line rugae of carapace. Propodus and dactylus of walking legs with transverse burgundy and white bands.

Remarks.—In the Indo-west Pacific, *P. extremus* is most similar to *P. coccineus* (Owen) and *P. carinipes* (Heller), with which it shares a transversely rugose carapace, sinuously triangular frontal region, a supraocular spine, and a single epibranchial spine. The ranges of the three species overlap in the western Pacific. *Petrolisthes extremus* ranges from Taiwan and the Mariana Islands south to Lord Howe Island and east to Easter Island. *Petrolisthes carinipes* occurs from the Red Sea and western Indian

Ocean to the Ryukyu, Ogasawara, Mariana, and Chesterfield Islands in the western Pacific (Haig 1983, 1987). *Petrolisthes coccineus* ranges throughout the Indian Ocean, the western Pacific from Indonesia to Japan, and extends eastward from the Ogasawara and Mariana Islands to the Hawaiian Islands and the Tuamotu Archipelago (Haig 1983).

The coloration of the three species differs sharply. In contrast to the mottled light green, blue, and bright white with scattered burgundy spots marking the carapace and chelipeds of *P. extremus,* those of *P. carinipes* are dark red-brown, appearing black to the unaided eye (RKK, personal observation of material from Guam). The carapace of *P. carinipes* also is marked with white spots at the tip of the rostrum, at the supraocular spines, and along the lateral and medial regions. White spots also occur on the chelipeds of *P. carinipes.* In *P. coccineus,* the carapace is pale blue-green with the gastric region marked with pale yellow-orange and a dark yellow-orange gastric ridge (RKK, personal observation of material from Guam). The manus of *P. coccineus* is blue-green and marked with a distinctive orange longitudinal crest and yellow-orange along the outer margin.

Petrolisthes carinipes and *P. extremus* are very similar in the striation pattern of the carapace and in the form and armature of the chelipeds and walking legs. However, in *P. carinipes* the lateral carapace margins are evenly convex between the epibranchial and posterolateral angles, the lateral lobes of the front are nearly transverse, and the orbits are regularly concave between the supraocular spine and the outer orbital angle. In *P. extremus* the carapace is strongly divergent posteriorly, the lateral lobes of the front are sharply oblique, and the orbits oblique between the supraocular spine and the outer orbital angle.

Petrolisthes extremus may be most easily distinguished from *P. coccineus* by the relative proportions of the carpus of the cheliped and the spination on the posterior margin of the merus of the third walking leg. The carpus of the cheliped is about twice as long as wide in *P. extremus,* but much more than twice as long as wide in *P. coccineus.* The posterodistal margin of the third walking leg is unarmed in *P. extremus,* but armed with one or two spines in *P. coccineus.* Also, in *P. coccineus* the front is narrowly triangular with the lateral lobes even more oblique and obscure than in *P. extremus;* the strong transverse striae on the gastric region are interrupted in the midline by a short but distinct interspace; and the number of spines on the anterior margin of the merus of the walking legs averages a little higher (5 to 9, 7 to 9, and 5 to 8 on legs 1, 2, and 3, respectively).

Etymology.—From the Latin, *extremus,* meaning outermost or farthest away. When study of this taxon began by one of us (JH), the only material available had been collected from Lord Howe, Kermadec, and Easter Islands, the "outposts" of the tropical or subtropical Indo-west Pacific. Although later collections from Taiwan and the Marianas counter the idea that the species is an "outpost taxon," the initial name was retained, at least in part, to refer to the interesting distribution of the taxon in the southern hemisphere portion of its range.

Habitat.—In the Mariana Islands, found under rocks, generally subtidal to a depth of 7 m; occasionally in the intertidal zone. In Taiwan, also on base of pocilloporid corals.

Distribution.—*Petrolisthes extremus* ranges from Taiwan and the Mariana Islands in the western Pacific south to Lord Howe Island and eastward to the Kermadec Islands and Easter Island.

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A NEW FRESHWATER CRAB OF THE GENUS *GEOTHELPHUSA* (CRUSTACEA: DECAPODA: BRACHYURA: POTAMIDAE) FROM KAGOSHIMA PREFECTURE, SOUTHERN KYUSHU, JAPAN

Hiroshi Suzuki and Eiji Tsuda

Abstract.—A new freshwater crab, *Geothelphusa exigua,* is described from Kagoshima Prefecture, southern Kyushu, Japan. It is differentiated from *G. dehaani* (White 1847) and *G. candidiensis* Bott, 1967, in possessing distally narrowed eyes, presence of granules both on the lower edge of the epistome and on the groove between the subhepatic and pterygostomian regions, and laterally curved male first gonopod with a subterminal genital opening. This is the second species known from the Japanese mainland.

Among the eight species of the genus *Geothelphusa* known from Japan, *G. dehaani* (White 1847) is the only species known to occur on the Japanese mainland (north of Honshu southward to Nakano-shima of the Tokara Islands, south of Kyushu) (de Haan 1835; White 1847; Stimpson 1858; Rathbun 1898, 1904, 1905; Miyake & Chiu 1965; Miyake & Minei 1965; Bott 1967, 1970; Minei 1973, 1974b). The other seven species, *G. obtusipes* Stimpson, 1858, *G. sakamotoana* (Rathbun, 1905), *G. aramotoi* Minei, 1973, *G. tenuimana* (Miyake & Minei 1965), *G. levicervix* (Rathbun 1898), *G. candidiensis* Bott, 1970, and *G. miyazakii* (Miyake & Chiu 1965), are restricted to the Ryukyu Islands, including Amamiohshima.

During our current study of the geographical distribution of *G. dehaani* in southern Kyushu, unusual specimens of a freshwater crab of the genus *Geothelphusa* were found on the Ohsumi Peninsula of Kagoshima Prefecture. The unusual eyes and male first gonopods of these crabs indicate that they represent a new species which is herein described and illustrated.

The holotype is deposited in the National Science Museum, Tokyo (NSMT), and the paratypes are in the Marine Biological Laboratory, Faculty of Fisheries, Kagoshima University, Kagoshima (KUMB) and the Kitakyushu Museum of Natural History, Kitakyushu (KMNH). Measurements shown in parentheses under "*Material examined*" indicate the maximum carapace width in millimeters. Abbreviations used include: Cr and cr, crustacea; IvR, Invertebrate Recent.

Family Potamidae Ortmann, 1896

Genus *Geothelphusa* Stimpson, 1858

Geothelphusa exigua, new species

Figs. 1–3

Material examined.—Kimotsuki River: Futamata-gawa, 400 m alt., 11 Jul 1991; 7 ♂ (13.1–21.8), 3 ♀ (12.2–13.0), holotype, ♂ (21.0), NSMT-Cr 11314, KUMBcr 1039, KUMBcr 1041: Iwaya-gawa, 220 m alt., 25 Sep 1991; 1 ♂ (20.5), KUMBcr 1042: Nanatsudani, Kushira-gawa, 400 m alt., 11 Jul 1991; 1 ♂ (18.8), 2 ♀ (13.2, 13.4), KUMBcr 1041: Takakuma valley, Kushira-gawa, 180 m alt., 22 Oct 1991; 1 ♂ (16.8), KUMBcr 1045: Naganomaki, Aira-gawa, 180 m alt., 11 Jul 1991; 6 ♂ (13.3–22.6), 4 ♀ (15.9–24.4), KMNH-IvR 900001–900004, KUMBcr 1041. Honjo River: Sarugajo valley, 150 m alt., 22 Oct 1991; 1 ♂ (19.6), KUMBcr 1045. Ohsumi Kamino River: Hangaishi, 300 m alt., 25 Sep 1991; 1 ♂ (20.8), KUMBcr 1042.

O River: Onigauto, Fumoto-gawa, 300 m alt., 9 Aug 1989; 3 ♂ (11.2–14.8), 2 ♀ (16.2, 17.8), KUMBcr 1038, KUMBcr 1040: Uchinomaki, Shibatate-gawa, 380 m alt., 9 Aug 1989; 2 ♂ (12.6, 14.3), 4 ♀ (13.0–28.7), KUMBcr 1040: Shinden, 330 m alt., 25 Sep 1991; 1 ♂ (18.7), KUMBcr 1042: Ohfuji-gawa, 520 m alt., 9 Aug 1989; 2 ♀ (12.7, 26.7), KUMBcr 1040: Ohtakeno, Akase-gawa, 600 m alt., 9 Aug 1989; 1 young (6.9), 2 ♂ (8.7, 17.8), 3 ♀ (13.9–15.6), KUMBcr 1037, KUMBcr 1040. Hirose River: Magome, 450 m alt., 2 Oct 1991; 1 ♀ (24.7), KUMBcr 1043. Kubota River: Himekado, 160 m alt., 25 Sep 1991; 1 ♂ (20.4), KUMBcr 1042. Funama River: Gorogamoto, 380 m alt., 2 Oct 1991; 1 ♂ (9.9), 1 ♀ (19.0), KUMBcr 1043. Hitotsutani River: Uchinoura, 390 m alt., 2 Oct 1991; 1 ♂ (16.7), KUMBcr 1043. Ohura River: Uchinoura, 300 m alt., 8 Oct 1991; 1 ♂ (14.4), KUMBcr 1044. Hetsuka River: Sarutubo, 490 m alt., 8 Oct 1991; 1 ♂ (25.0), 1 ♀ (27.5), KUMBcr 1044: Doh-gabaru, 180 m alt., 8 Oct 1991; 1 ♂ (16.4), KUMBcr 1044.

All specimens were collected by H. Suzuki and E. Tsuda.

Diagnosis.—Male first gonopod saber-like, penultimate segment slightly curved laterally, ultimate segment strongly curved laterally, tapering, genital opening subterminal. Ocular peduncle swollen proximally, cornea small.

Description.—Carapace much broader than long, smooth and devoid of hair (Fig. 1a), postfrontal and postorbital regions indistinctly rugose, faint oblique striae on epibranchial and posterolateral regions, epi- and uro-gastric regions distinct, former divided into two parts by median depression, cervical groove obsolete on epibranchial region. Anterolateral margin of carapace cristate, lined with fine rounded granules, epibranchial notch rudimentary. Frontal margin 0.35 (0.33–0.40 in male, 0.31–0.38 in female) times as broad as carapace. Posterior margin of epistome divided into three parts by 2 deeper notches (Fig. 1b), granules present on lower edge of epistome, absent medially. Lower orbital margin and groove between subhepatic and pterygostomian regions lined with small rounded granules.

Eyestalk short, proximallly swollen, distally slim (Fig. 1a, b). Cornea small, slightly wider than distal portion of ocular peduncle.

Merus of third maxilliped broad, square, with deep punctum (Fig. 1c). Three-segmented palp connected on inner distal angle of merus, tip of palp not below distal margin of ischium. Exopod slender, longer than ischium, with small flagellum (Fig. 1c, d).

Chelipeds asymmetrical in males over 13.0 mm carapace width (right larger than left in 26 out of 28 males, left larger than right in remainder), symmetrical in all females and in males less than 13.0 mm; large chela 2.09 (1.82–2.27) times as long as high (Fig. 1e), palm smooth and surfaces relatively rounded, fingers with 2 longitudinal ridges on outer lateral surface (Fig. 1e, f). Carpus of large cheliped slightly smooth, with stout inner tooth below which is a low swelling (Fig. 2a). Carpus of small cheliped without any swelling below stout inner tooth.

Palp of mandible 3-segmented (Fig. 2b), distal segment uniramous and sickle-shaped, median segment longer than wide, distal half expanded, proximal segment short, stout.

Adult male first gonopod saber-like (Fig. 2c–h), penultimate segment slightly curved laterally, synovial membrane short, about 3 times as long as broad (Fig. 2c), ultimate segment strongly curved laterally (Fig. 2c, d), tapering, with genital opening subterminal in position (Fig. 2e). Tip of first gonopod papilla-like in specimen 8.7 mm carapace width (Fig. 2f), and tapered in specimens 11.2 and 14.6 mm carapace width (Fig. 2g, h). Male second gonopod slender, flat, weakly convex, with small lamella on distal one-third (Fig. 2i, j).

Sizes (carapace width).—Males, 8.7–25.0 mm; females, 12.2–28.7 mm.

Color in life.—Chocolate brown or dark brown with scattered black speckles on car-

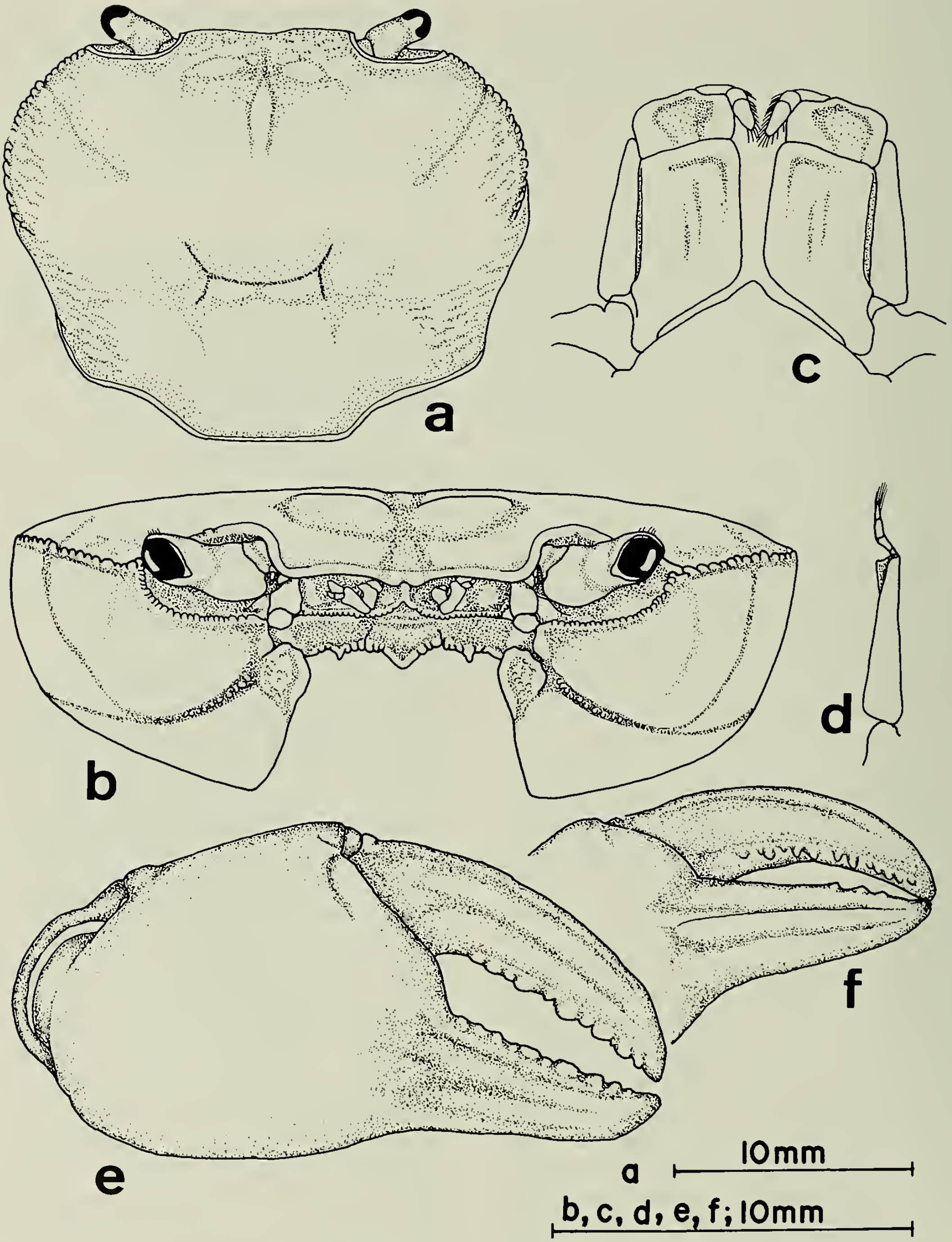

Fig. 1. *Geothelphusa exigua*, new species, male holotype (NSMT-Cr 11314): a, dorsal view; b, frontal view; c, third maxilliped, frontal view; d, exopod of third maxilliped, frontal view; e, right cheliped, lateral view; f, fingers, ventrolateral view.

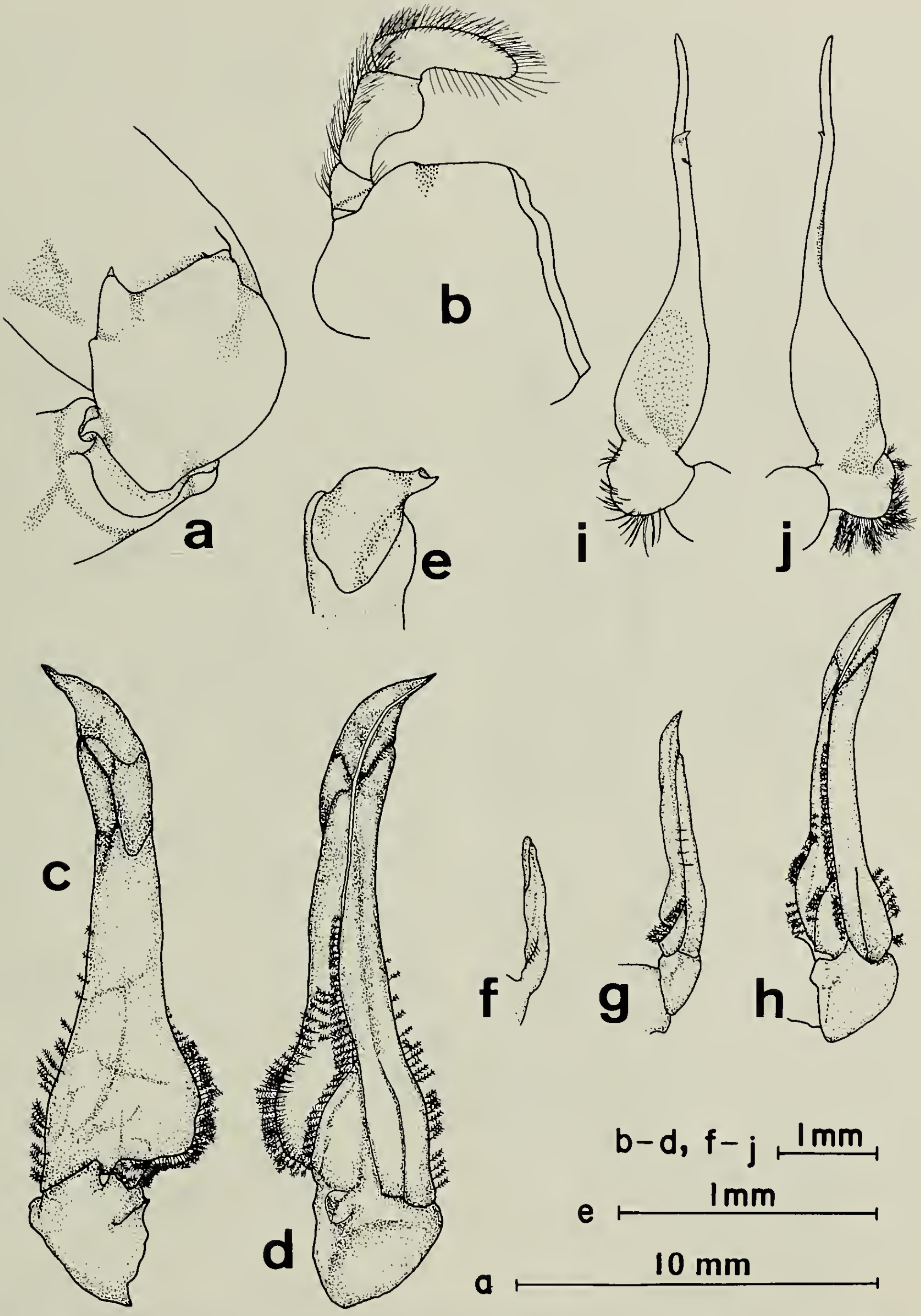

Fig. 2. *Geothelphusa exigua,* new species, male holotype (NSMT-Cr 11314): a, carpus of right cheliped, dorsal view; b, right mandibular palp, ventral view; c, left first gonopod, dorsal view; d, same, ventral view; e, distal part of same, distal view; i, left second gonopod, dorsal view; j, same, ventral view. Male paratypes (KUMBcr 1037–1039): f, left first gonopod (8.7 mm carapace width), ventral view; g, same (11.2 mm carapace width), ventral view; h, same (14.6 mm carapace width), ventral view.

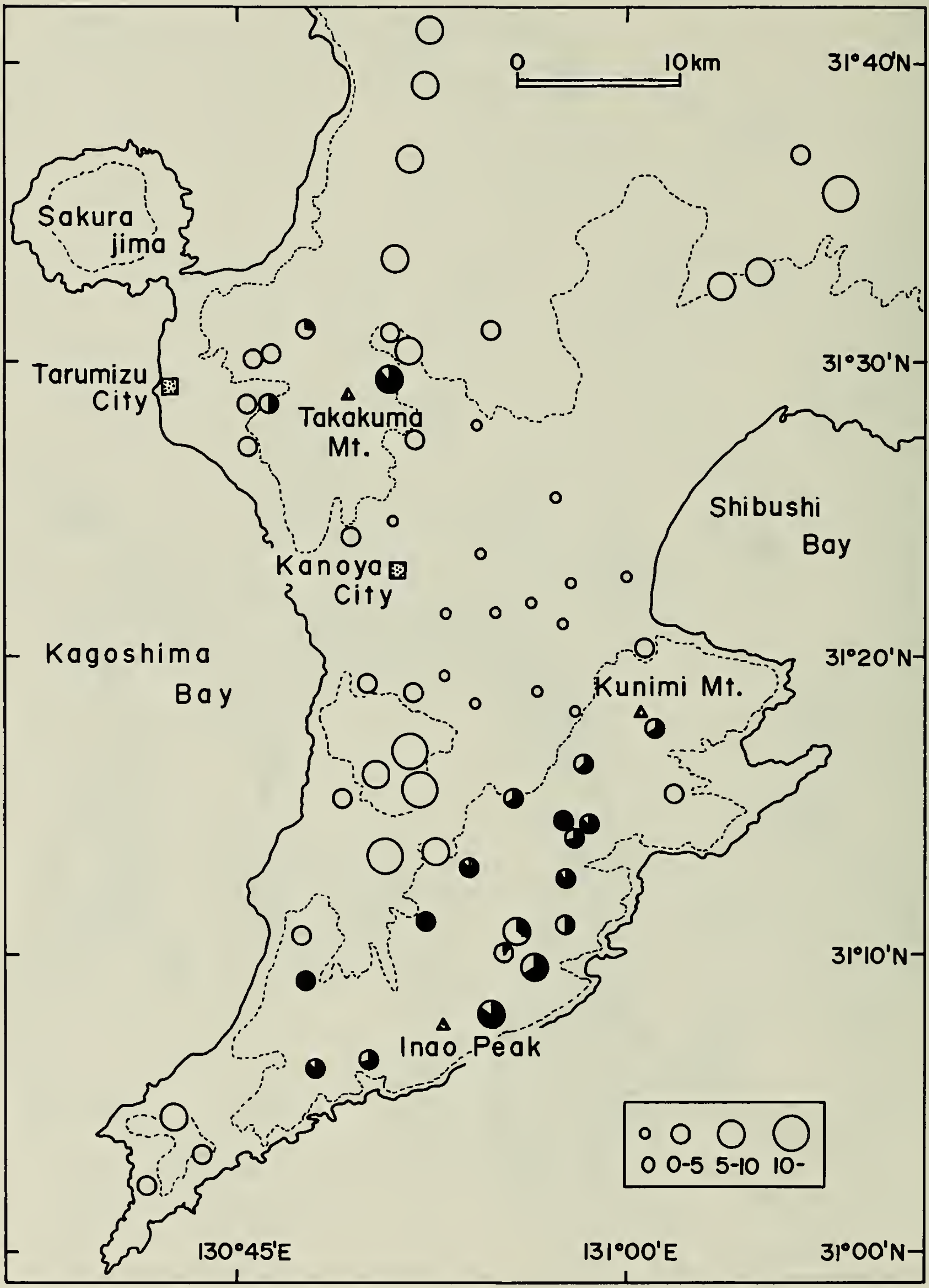

Fig. 3. Map showing the distribution and abundance of *G. exigua*, new species (black part) and *G. dehaani* (white part) in Ohsumi Peninsula, Kagoshima. Arabic numerals corresponding to size of circles in the square at bottom right indicate the numbers of crabs captured per ten minutes by one person. Broken line shows 150 m contour line.

apace and pereopods. Palm of chelae chocolate brown, fingers milk white. No color variation between sexes and sizes.

Etymology.—The specific name is derived from the Latin "exiguus" (small), alluding to the small cornea, characteristic of the new species.

Remarks.—The saber-like male first gonopod and the 3-segmented mandibular palp with an uniramous distal segment displayed by the new species are characteristics of the genus *Geothelphusa* (see Bott 1970). The medium-sized carapace, smooth palm, and broad frontal region ally the species with *G. dehaani* and *G. candidiensis,* from which it is distinguished by several features.

The most definitive differences may be seen on the male first gonopods. The ultimate segment in *G. dehaani* and *G. candidiensis* is straight or slightly curved mesially (Bott 1967, 1970; Minei 1973, 1974a), ending in a papilla-like tip with a terminal genital opening. In the new species, however, this segment is strongly curved laterally and tapering, having a subterminal genital opening. The eyestalks in both related species are constricted at the middle, and the cornea and the proximal part of the ocular peduncle are swollen. In the new species, only the proximal part of the ocular peduncle is swollen, the cornea and the distal part of the peduncle are proportionately narrower. The postorbital and epibranchial regions of the carapace bear finely crenulate striae in *G. candidiensis* (see Minei 1973), instead of faint striae as in *G. exigua.* Examination of specimens of *G. candidiensis* reported by Minei (1973), and now in the collection of the Kitakyushu Museum of Natural History, Kitakyushu (5 ♂, 4 ♀, ZLKUm 1016, Maezato, Ishigaki-jima, 28 Oct 1962, leg. S. Kudaka; 19 ♂, 18 ♀, ZLKUm 1019, Pensan-gara, Ishigaki-jima, 19 May 1963, leg. S. Kudaka), shows that there are distinct granules on the median part of the lower edge of the epistome which are barely discernible in the new species. The presence of distinct granules on the groove between the subhepatic and pterygostomian regions also differentiates *G. exigua* from *G. dehaani.* The carapace and pereopods of *G. dehaani* show color variation, for example red, orange, blue, brown, purple, or yellowish white (Chokki 1976, 1980; Suzuki & Tsuda 1991). The palm and fingers of *G. dehaani,* however, are usually yellowish white, regardless of carapace color. In *G. exigua,* the carapace and pereopods are chocolate brown or dark brown, and only the fingers are milk white. In addition, allelic substitution was observed at General protein-1 and -2, Lactate dehydrogenase, and Isocitrate dehydrogenase-2 loci between *G. exigua* and *G. dehaani* (Suzuki & Tsuda, pers. comm.).

Distribution.—The specimens of *G. exigua* examined have been obtained only in the area above 150 m altitude on Takakuma Mountain, Inao Peak, and Kunimi Mountain Ranges, in Ohsumi Peninsula, Kagoshima Prefecture (Fig. 3), where the Miocene granitic rock and quartz porphyry are exposed. *Geothelphusa exigua* and *G. dehaani* are sympatric, having been taken together at many locations.

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AEGLA PEWENCHAE, A NEW SPECIES OF CENTRAL CHILEAN FRESHWATER DECAPOD (CRUSTACEA: ANOMURA: AEGLIDAE)

Carlos G. Jara

Abstract.—The description of *Aegla pewenchae,* a new species of freshwater anomuran crab from the Rapel, Maule, Itata, Bío Bío, Imperial, and Toltén river basins is given. Its diagnostic characters are: 1) rostrum long and narrow, styliform, scarcely troughed both sides of rostral carina; 2) anterolateral angles of carapace spiniform, slightly divergent; 3) marginal scales of rostrum and hepatic lobes minute; 4) orbital spine clearly defined, with a smaller second one some distance below; 5) anterolateral angle of first hepatic lobe spiniform; 6) branchial borders smooth; 7) palmar crest wide and thin, its border deeply serrate or microdenticulate; 8) chelipeds with dorsal surface of propodus densely covered by minute lens-like scales; 9) anterolateral angle of second abdominal epimeron spiniform. *Aegla pewenchae* resembles, to a certain extent, *A. rostrata* Jara, 1977, and *A. abtao* Schmitt, 1942a.

The zone between Angostura de Paine and Chillán, in central Chile, is one of the most ancient and densely populated zones because of the fertility of its soils, mild climate and abundance of streams and rivers that provide water for agricultural irrigation. *Aegla* has seldom been registered in these fluvial bodies. However, this seems to be related more to the difficulties in identifying the specimens collected than with low collection efforts (N. Bahamonde, pers. comm.).

Bahamonde & López (1963) reported the presence of *A. laevis talcahuano* Schmitt, 1942b, from seven localities between the Zamorano River (tributary of the Cachapoal-Rapel River system) and the Ñuble River in Chillán, as well as *A. concepcionensis* Schmitt, 1942a, from the Tronco River (Colchagua Province), and *A. maulensis* Bahamonde & López, 1963, from Laguna del Maule.

This paper describes a new species of *Aegla,* which was found almost continuously between the Colchagua Province in the north and the Cautín Province in the south. The specimens were collected during an eight-year period, while sampling the Andean or upper river stretches and the Coastal or lower river stretches, on both sides of the Chilean main longitudinal highway (Carretera 5) which crosses most of the river systems along continental Chile.

Aegla pewenchae, new species
Figs. 1, 2, 3

Type material.—Holotype: Instituto de Zoología, Universidad Austral de Chile, IZUA C-338, adult male collected in the Bío-Bío River, 16 km S of Los Angeles, under bridge of Carretera 5 (37°35′45″S, 72°16′30″W), Province of Bío-Bío, VIII Región, Chile, 21 Feb 1983, by C. G. Jara.

Allotype: IZUA C-338, adult female. Paratypes: IZUA C-338, 5 adult ♂♂ (P1 to P5) and 3 adult ♀♀ (P6 to P8). Same locality and date as holotype.

Diagnosis.—Carapace longer than wide; rostrum elongate, styliform; anterolateral angles of carapace acute, slightly divergent; scales on rostral and hepatic borders very small; orbital spine well developed, dorsal to a second smaller one; anterolateral angle of first hepatic lobe spiniform; branchial borders smooth, noticeably arcuate; palmar crest laminar, expanded, its border microdenticulate to dentate; dorsum of propodus of chelae densely covered by minute lens-like scales; anterolateral angle of second abdominal epimeron sharply acute, spiniform.

Description of holotype.—Rostro-frontal end narrow, bound by slightly inflated anterolateral lobes scarcely distinct from protogastric prominences. Anterolateral lobe prolonged in conical acute spine, well separated from orbital spine, its apex reaching posterior border of cornea. Orbital spine small, slender, acute, recurved towards anterolateral angle; its length ⅓ to ¼ length of anterolateral spine. Frontal width about half precervical width. Orbits wide, comparatively shallow, their depth about half their maximum width. Extraorbital sinus well defined, wide, slightly asymmetrical. Orbital margins with four or five minute well spaced scales.

Rostrum narrow, styliform, its width at level of posterior margin of orbits ⅔ its length. Cross-section of proximal half rhombic; distal half subcircular. Apex ending in acute conical scale. Rostral margins defined only on proximal half of rostrum. Rostral carina low, narrow, reaching midpoint of rostrum flanked by shallow troughs; its proximal end marked by pair of tiny pits between protogastric lobes; its dorsum with two rows of minute scales which merge into one, distally. Carina is replaced by irregular row of well spaced scales which increase in size distally, on distal half of rostrum.

Dorsum of precervical area uniformly convex; no marginal plateau on dorsum of hepatic lobes. Epigastric prominences scarcely distinguishable, except by 1 or 2 nodules bearing 5 to 8 minute apical scales. Protogastric lobes less prominent, marked by 7 (left) and 5 (right) apical scales in arquate row. Dorsum of carapace smooth, polished, slightly punctate. Margins of carapace, between anterolateral lobe and cervical groove, almost straight. Hepatic lobes well delimited by shallow furrows; all of them with one acute apical scale. Remaining margin with irregular row of small, unequal scales.

Dorsum of postcervical carapace markedly and uniformly convex. Sutures (lineae) fine, shallow. Cardiac area and areola wide; areola slightly inflated, its dorsum leveled with gastric area. Border of branchial areas smooth, narrowly marginated and slightly recurved, with irregular row of fine acuminate scales mingled with short stiff setae.

Dorsum of abdominal tergae slightly punctate; small tufts of fine short setae protrude from punctae; tufts thicker and more numerous on flanks of epimera. Anterolateral angle of second epimeron prolonged in short, stout, conical spine, its apex overreaching adjacent branchial border. Pleural angle of third and fourth epimera sharply acute. Telson cordiform, medially articulate. Ventral surface of fourth thoracic sternum flat, slightly convex; its frontal border straight at center and slightly concave near anterolateral angles abutting in short blunt cones.

Chelipeds robust, left largest. Chelae stout, ovoidal. Left propodus markedly convex, inflated over its proximal ⅔; right subtriangular. Dorsum of propodus with oblique, blunt, low ridge between carpus-propodus and propodus-dactylus joints, and parallel to base of palmar crest. Palmar crest subrectangular, slightly excavate, its border clearly denticulate, merging anteriorly into predactylar lobe. Right crest with 7 acute denticles, left with 6, becoming progressively more recurved towards proximal end of crest; right crest ends proximally in robust denticle partially separated from preceding ones by deep, wide notch. Postcrestal sinus deep, wide. Dorsum of chelae covered by tiny, blunt, conical scales that become larger toward distal end of both propodus and dactylus where they intermingle with bundles of short stiff setae. Dactylar lobe as

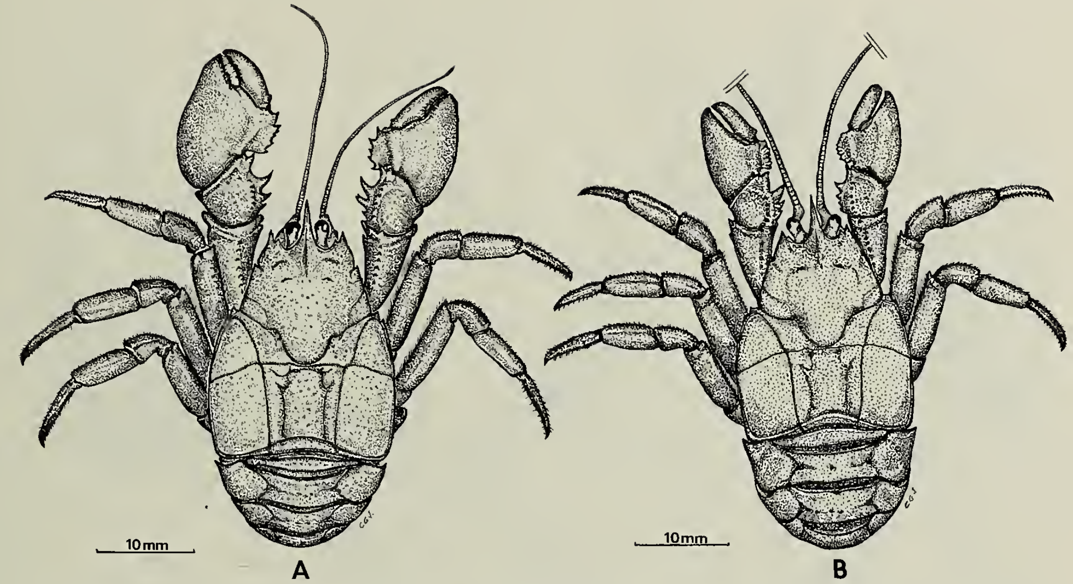

Fig. 1. *Aegla pewenchae,* new species. A, male holotype, dorsal view. B, female allotype.

low blunt tubercle with apical scale 2 or 3 times larger than those on surface of propodus. Ventral surface of chelae slightly punctate, convex, polished, without scales or setae except at propodus-dactylus joint. Dorsum of carpus globular, with field of minute conical scales over lateroexternal half. Internal border with 3 robust acute conical spines that decrease in size proximally; apex of second right spine bifid. Carpal lobe spiniform, separated from adjacent articular nodule by shallow furrow; separated from distalmost spine of carpal crest by wide sinus. Ridge along dorsum of carpus well marked, made up by 9 coalescent, little prominent, tubercles, each with 2 to 4 apical scales in oblique row. Lateroventral nodule of carpus-propodus joint with minute flattened conical scale and short setae. Ventral face of carpus gently convex, without spine. Distodorsal vertex of merus of chelipeds as spiniform tubercle crowned by 2 acute scales and some stiff short setae. Dorsal border of merus sharp, with row of spiniform cones decreasing in size proximally; distal cone twice size of subdistal; 10 (right) and 9 (left) cones; the five distalmost procumbent. Ventral borders smooth, ending in acute conical spine; inner one slightly curved; external border, next to merus-carpus articular node, with distally directed small acute cone. Ventral border of ischium slightly concave, with small tubercle crowned by conical scale and few stiff short setae at both ends. Distodorsal angle of merus of second and third pereiopods fringed by stiff short setae mingled with conical scales; 1 or 2 are central and prominent. Dorsal border of merus of second pereiopod fringed by long plumose setae; fringe absent on third pereiopod. Distal third of ventral median line of dactylus of second to fourth pereiopods with row of 3 to 7 acicular scales decreasing in size proximally.

Description of allotype.—Aside from the relatively larger abdomen and smaller chelae (secondary sexual characters), the allotype differs from the holotype in the following aspects: scales on dorsum of chelae larger, particularly over distal half of propodus and dactylus; tubercles on dorsal midline of carpus prominent, some spiniform; ventral

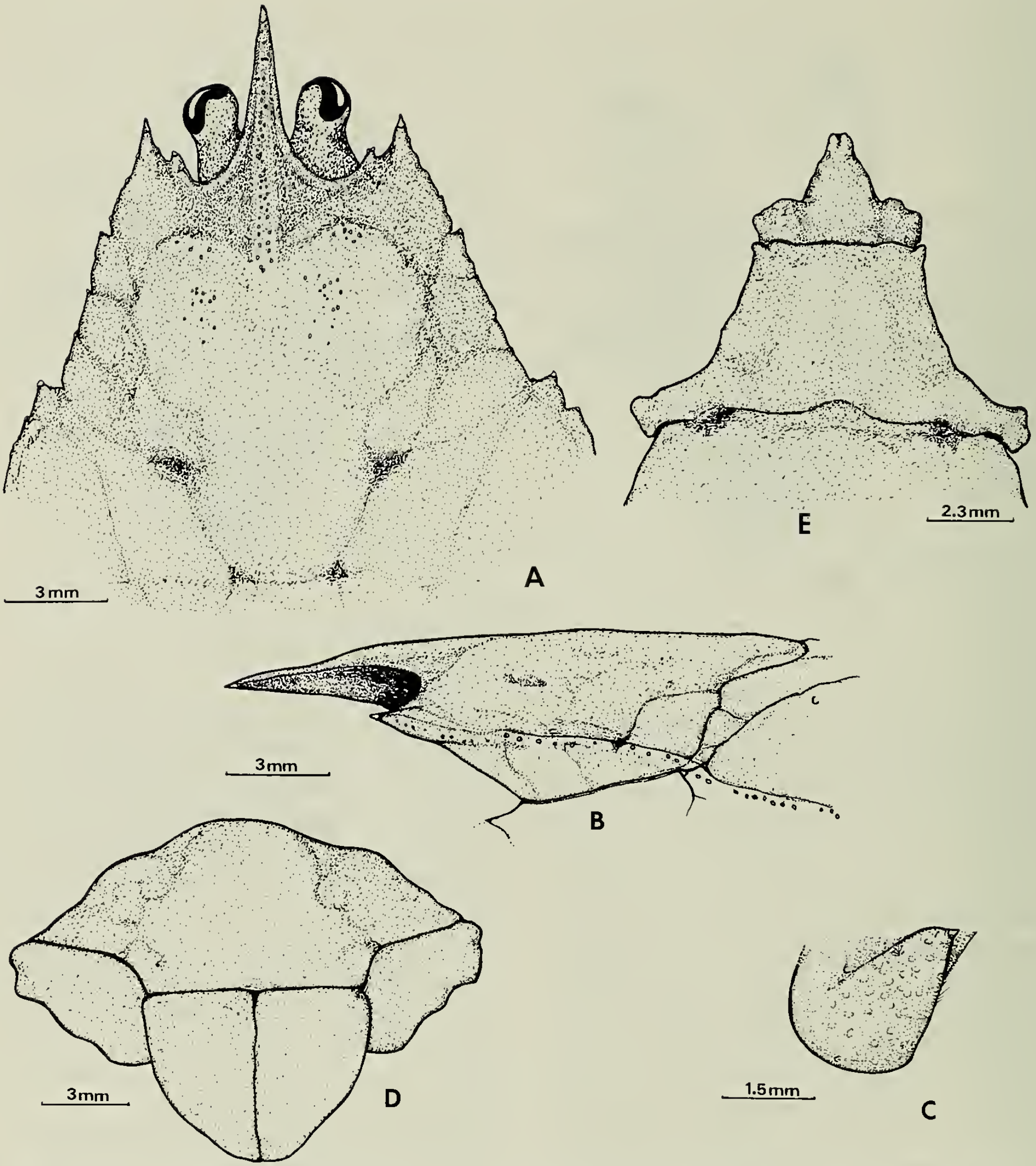

Fig. 2. *Aegla pewenchae*, new species, male holotype. A, precervical carapace in dorsal view; B, same in lateral view; C, anterolateral angle of second abdominal epimeron in lateral view; D, telson plate; E, fourth thoracic sternum.

border of merus of chelipeds with spine at limit between median and distal thirds of article; 2 similar spines at distal third of external lateroventral border of merus of right cheliped; predactylar lobe well defined, specially when seen from ventral face of chelae; midventral line of propodus of chelae with 1 (left) and 3 (right) scales forming row; anterolateral angles of fourth thoracic sternum flattened and little scalloped; external flank of carpus-propodus articular node with spiniform tubercle; punctae on dorsum of carapace coarse, deep; extraorbital sinus comparatively narrow.

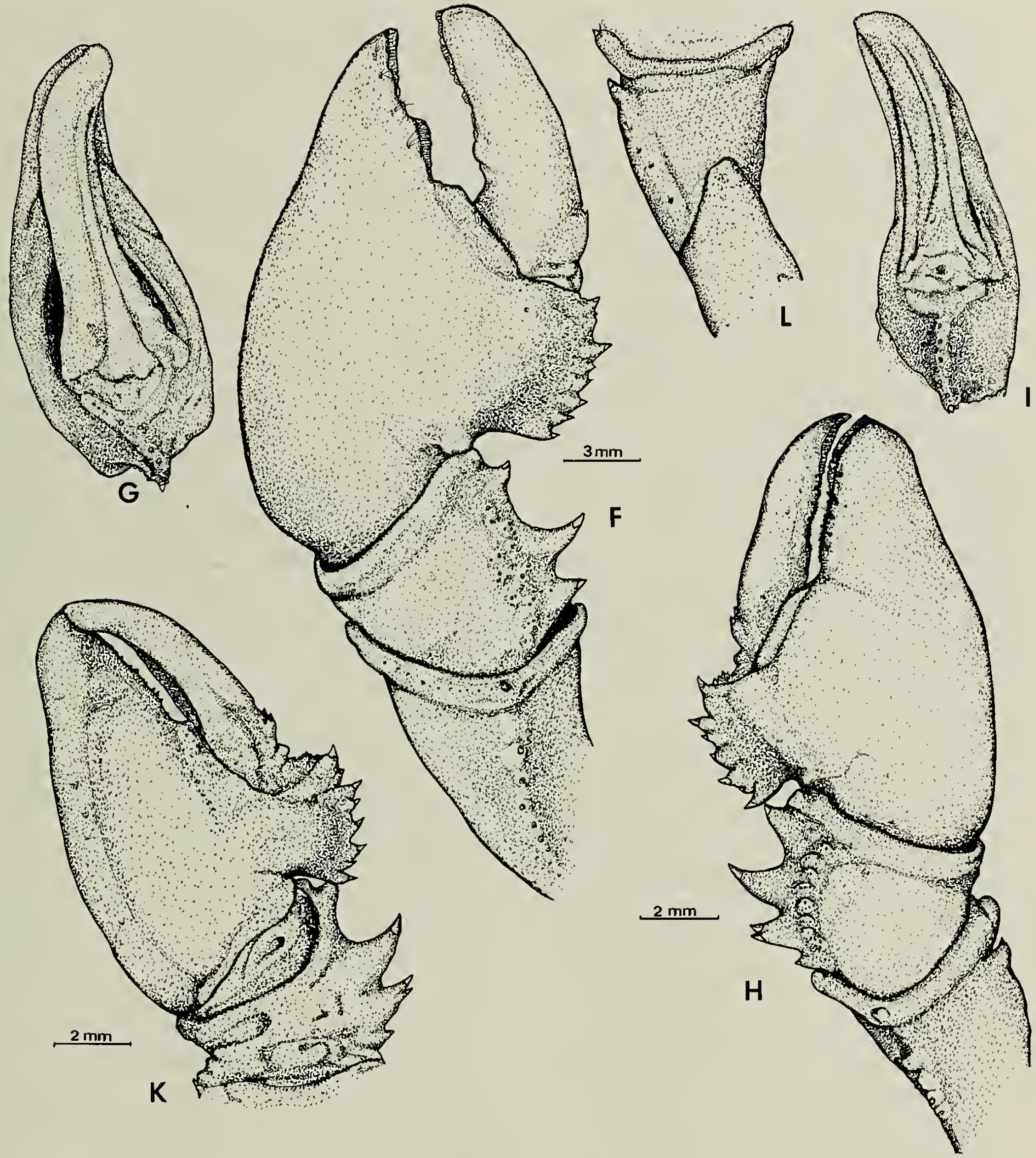

Fig. 3. *Aegla pewenchae,* new species, male holotype (continuation). F, left cheliped in dorsal view; G, left chela seen from dactylus top; H, right cheliped in dorsal view; I, right chela seen from dactylus top; K, same in ventral view; L, ischium and merus of left cheliped in ventral view.

Color.—In life, dorsum of carapace uniform in color varying among specimens from light olive green to dark green; color more intense in furrows and depressions of the carapace, over the frontorostral area and proximodorsal area of chelae. Distal zone of chelae and dactyls of pereiopods yellowish orange; intensity varying greatly among individuals. Scales amber-like, translucent, mounted on top of tubercles and spines ivory white to light yellow changing progressively to general background color of carapace toward their bases. Ventral surface white in recently molted individuals, and smokey tan in animals in pre-ecdysis.

In alcohol-preserved specimens, carapace creamy white varying from almost translucent in just molted individuals to yellowish brown with dark brown spots in individuals in pre-ecdysis. Superimposed on general background color, blueish tones mingle with other colors in varying intensity and extension. Dorsum of chelae, gastric, and cardiac areas, and dorsum of second to fourth abdominal segments of P7 and P8 light grayish blue changing to ivory white over branchial areas; center of posterobranchial areas dark rose; same hue, but more intense, stains dactylus of pereiopods of P7.

Etymology.—The name *pewenchae* is the latinized genitive feminine singular form of "pewenche," the aboriginal amerindians inhabiting the upland plateau at the origin of the Bío Bío River.

Distribution.—Table 1 contains the basic data on records of *Aegla* deemed to be conspecific with *A. pewenchae.* Noteworthy is the distribution of *A. pewenchae* which appears closely related to the Andean and pre-Andean stretches of the drainage systems of Rapel, Maule, Itata, Bío Bío, and Imperial rivers. Figure 4 shows the geographic range of *A. pewenchae.* The species is found from the Chimbarongo River, in the drainage basin of the Rapel River, to the Donguil River, tributary of the Toltén River basin. The species is distributed along 480 km of the Chilean territory. In the Bío Bío River basin *A. pewenchae* is found along most of the 380 km of mainstream, including lakes Galletué and Icalma, sources of the Bío Bío River. The absolute upper limit of the species altitude range (1150 m) is found in these lakes, while the lower limit (ca. 100 m) is found at several points along the Chilean Central Valley. In the drainage system of the Toltén River, *A. pewenchae* is only found in a small basin that drains the north-central area of the extra-Andean Valdivian territory.

Remarks.—*Aegla pewenchae* presents such a diverse combination of characters that it is difficult to advance a hypothesis about its phyletic relationships.

Aegla pewenchae resembles *A. rostrata,* from lakes in the Toltén and Valdivia river basins, in having: rostrum narrow, elongate, scarcely troughed; orbits ample; orbital spine well defined, accompanied by second one in subordinate position; palmar crest wide, lightly built, its border dentate to microdenticulate; dorsum of chelae covered by fine scales; and, dorsum of carapace dark green contrasting with marble-white ventral surface. In the Imperial River basin, both species coexist, being difficult to differentiate. *A. pewenchae* differs from *A. rostrata* in lacking denticles on the branchial border of the carapace, and in having the dorsal surface of anterior branchial area convex.

Aegla pewenchae resembles *A. abtao* Schmitt, 1942a, distributed between the Toltén River basin and the Chiloé Island, in having: comparatively short, triangular, scarcely elongate rostrum; male chelae markedly unequal in size, fingers short and robust; dorsum of carapace coarsely punctate; palmar crest thick and narrow, its border nodulate to dentate; spines on inner border of carpus and dorsal ridge of merus of chelae short, thick, and stout. *Aegla pewenchae* differs from *A. abtao* in lacking a dense row of conical scales along rostral borders and thick protuberant scales on the surface of carapace. For comparison with the holotype of *A. pewenchae,* Fig. 5 shows the frontal end and the left chela of a full grown male of *A. abtao.*

Aegla pewenchae is a phenotypically well defined species, associated with the Andean piedmont zone of several Central Chilean river systems. Towards the West its distribution extends to the Central Valley, in general coinciding with the fluvial zone where the mean current velocity allows for the deposition of gravel and sand. These gradually replace the boulders and coarse gravel that predominate in the upper part of the basins where *A. pewenchae* is commonly found.

Table 1.—Records of *A. pewenchae*, new species, in addition to the type series. All samples are deposited in the Collection of the Instituto de Zoología of the Universidad Austral de Chile (IZUA-C). R. stands for river, L. for lake, and J for juveniles (specimens in which the gonopores are not visible).

Collection number	Locality	Latitude/ longitude	Date of collection	Specimens		
				♂	♀	J
503	R. Chimbarongo	34°46'S, 71°08'W	12 Dec. 91	11	15	49
344-A	R. Claro	35°11'S, 71°24'W	14 Feb. 83	14	13	—
393-A	R. Claro	35°25'S, 71°41'W	01 Aug. 87	3	2	—
492-B	R. Lircay	35°25'S, 71°34'W	13 Dec. 91	19	21	2
347-A	R. Maule	35°28'S, 71°57'W	15 Feb. 83	23	25	24
342	R. Longaví	35°37'S, 71°46'W	17 Feb. 83	2	—	—
493-A	R. Putagán	35°46'S, 71°40'W	13 Dec. 91	15	11	32
490	R. Ancoa	35°54'S, 71°30'W	13 Dec. 91	29	22	6
395-A	R. Liguay	35°57'S, 71°41'W	10 Nov. 85	—	4	—
394-A	R. Longaví	36°00'S, 71°43'W	10 Nov. 85	2	—	—
489	R. Longaví	36°14'S, 71°30'W	13 Dec. 91	6	4	33
491-A	R. Cato	36°15'S, 71°41'W	13 Dec. 91	6	7	4
396	R. Cató	36°17'S, 71°40'W	03 Mar. 73	1	2	—
482	R. Ñuble	36°29'S, 71°45'W	07 Dec. 91	14	40	83
480	R. Bustamante	36°34'S, 71°45'W	07 Dec. 91	2	4	—
479	R. Chillán	36°41'S, 71°54'W	07 Dec. 91	8	16	6
478	R. Diguillín	36°54'S, 72°05'W	07 Dec. 91	4	9	2
477	R. Dañicalqui	37°02'S, 72°01'W	07 Dec. 91	10	12	6
481	R. Cholgüán	37°11'S, 71°59'W	06 Dec. 91	16	6	7
470	R. Huepil	37°13'S, 71°57'W	06 Dec. 91	16	14	9
336	R. Bío Bío	37°17'S, 72°43'W	19 Feb. 83	—	8	—
474	R. Laja	37°18'S, 71°58'W	06 Dec. 91	20	15	43
520-B	R. Cholguahue	37°29'S, 72°13'W	10 Oct. 92	10	16	2
472-A	R. Quilleco	37°30'S, 71°59'W	06 Dec. 91	18	22	13
425	R. Bío Bío	37°33'S, 72°35'W	26 Jun. 85	2	7	—
475	R. Duqueco	37°35'S, 72°09'W	06 Dec. 91	19	23	28
427	R. Huequecura	37°41'S, 71°46'W	09 Apr. 87	3	8	1
340	R. Mulchén	37°43'S, 72°15'W	21 Feb. 83	13	10	1
222-A	R. Malleco	37°47'S, 72°41'W	06 Jun. 81	—	4	—
335	R. Queuco	37°51'S, 71°38'W	21 Feb. 83	1	14	—
339	R. Renaico	37°51'S, 72°23'W	21 Feb. 83	3	3	—
334	R. Malleco	37°58'S, 72°26'W	22 Feb. 83	6	16	7
318	R. Traiguén	38°14'S, 72°19'W	23 Dec. 82	9	18	—
323	R. Quino	38°18'S, 72°25'W	23 Dec. 82	41	25	10
317-A	R. Colpí	38°19'S, 72°47'W	22 Dec. 82	5	4	—
324-D	R. Quillén	38°24'S, 72°47'W	22 Dec. 82	7	4	—
326-B	R. Quillén	38°25'S, 72°56'W	22 Dec. 82	3	10	7
266	R. Bío Bío	38°38'S, 71°06'W	04 Feb. 69	6	5	12
186	L. Galletué	38°40'S, 71°19'W	16 Feb. 77	6	11	—
319	R. Bío Bío	38°43'S, 71°09'W	05 Mar. 83	45	31	22
426	R. Bío Bío	38°46'S, 71°14'W	08 Apr. 87	—	16	2
187	L. Icalma	38°48'S, 71°17'W	17 Feb. 77	11	10	1
320-B	R. Quepe	38°51'S, 72°37'W	21 Dec. 82	6	3	—
327-C	R. Donguil	39°06'S, 72°41'W	21 Dec. 82	48	47	66
327-D	R. Donguil	39°06'S, 72°41'W	21 Dec. 82	63	54	46

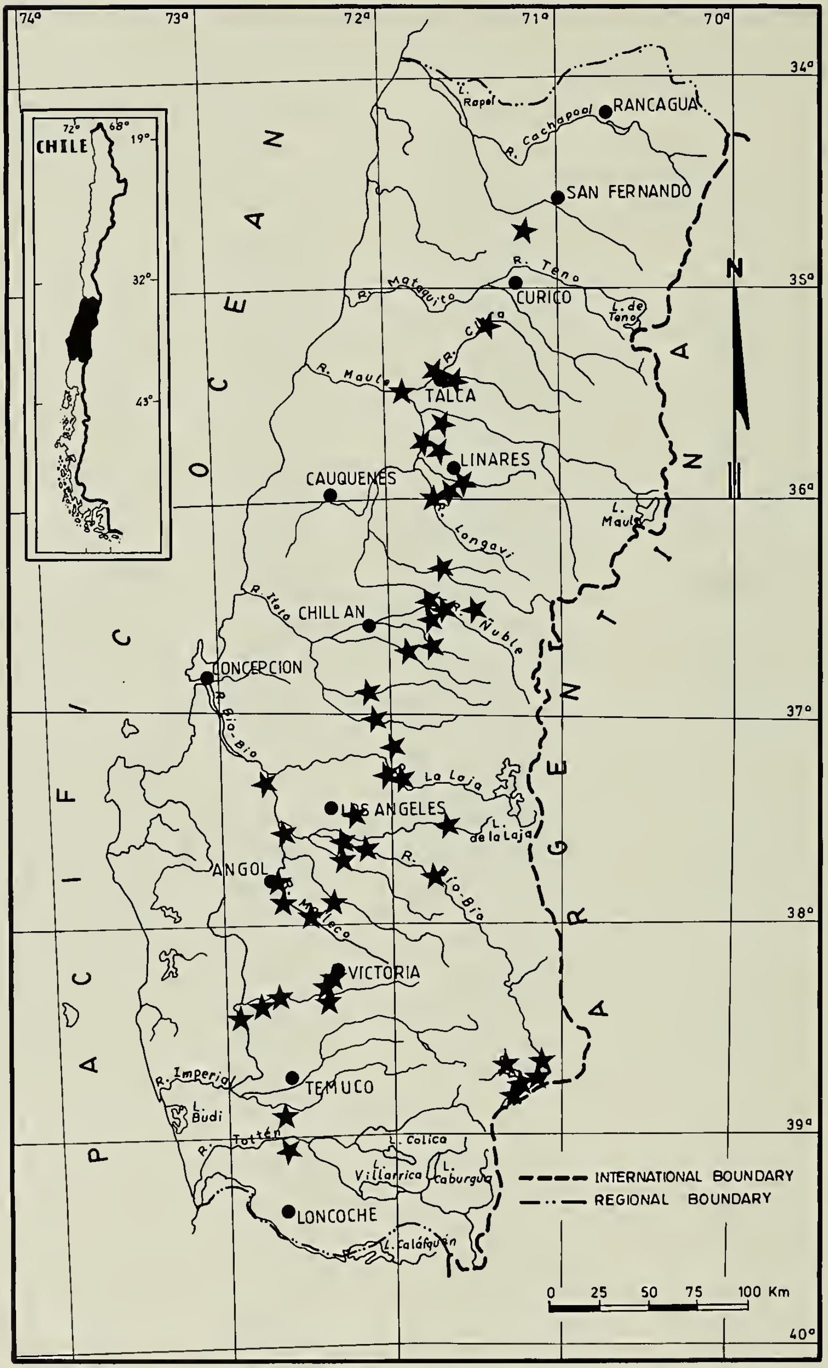

Fig. 4. Geographical range of *A. pewenchae,* new species. Stars indicate sampling localities; black dots, geographical localities.

Fig. 5. *Aegla abtao* Schmitt, adult male. A, precervical carapace, dorsal view; B, left cheliped, dorsal view.

Aegla abtao, which replaces *A. pewenchae* to the south of the Toltén River basin, also prefers this biotope (see Jara 1980:93–96; as *A. riolimayana?*). Both species share characters seemingly associated with living in moderate to fast running water environments, i.e., the smooth longer-than-wide oval carapace, the relatively short but narrow acute rostrum, and the marked heterochely of adult males. However, this morphological similarity is not necessarily indicative of common ancestry between the two, and may well be the result of convergence.

Aegla pewenchae, throughout its ample geographical range, shows a relatively wide exophenotypical variation which mostly affects the rostral and precervical morphology and the maximum size of the specimens. However, this species does not show morphological variations related to the lacustrine environment. In *A. rostrata, A. abtao* (Jara 1986a), and *A. denticulata* (Jara 1986a, 1989), the lacustrine environment does seem to induce an overspinulation or spination of the carapace edges.

The latitudinal limits of *A. pewenchae* seem to coincide, more or less, with well defined zoogeographical boundaries. In fact, its present northern limit lies at the Cachapoal-Rapel River system, just to the south of the Maipo River system where two other freshwater decapod crustacean species reach their southern limit, namely, *A. papudo* Schmitt, 1942b (unpublished data), and *Cryphiops caementarius* (Molina 1782) (Bahamonde & López 1963). A third species, the burrowing crayfish *Parastacus pugnax* (Poeppig 1835), reaches its northern limit at the Aconcagua River (Bahamonde & López 1963), just to the north of the Maipo River system. At the Toltén River basin the situation is less clearly defined. Here *A. abtao* reaches its northern limit, while *P. pugnax,* and the trichomycterid fish *Bullockia maldonadoi* (Eigenmann 1927), reach their southern limit (unpublished data).

Morphological Variations

The expression of the taxonomic characters varies among type specimens. In P1 and P5 the rostral apex overreaches corneae ca. two times their length, but in P6 and P7 it overreaches corneae by less than once their length. The orbital spine is comparatively small in the holotype and in P2, P7 and P8, its length being one fourth the length of anterolateral spine of carapace, but in P1 equaling one half the length of anterolateral spine. The first left hepatic lobe of the holotype, P1, P7, and P8 ends in one acute scale, but the right in two; the opposite occurs in P6. The curvature of branchial borders varies in relation to the relative width of carapace; it is minimum in the holotype and maximum in P1. Indentation of the palmar crest is notorious in the holotype, but insignificant in P1, P2, P3 and P5. The predactylar lobe merges completely into the palmar crest of the left chela of P1, P2 and P3, but in P5 it does in both chelae. The ventral face of carpus of chelipeds is smooth in all specimens except in P1 and P3 (left chela), and P5 (right chela), which have a spiniform tubercle. The inner ventral border of merus of chelipeds is smooth, with one distal spine in all specimens except in P1, P4, and P5, which have two, and in P8, which has three.

Table 2 contains the morphometric data of the type series. Measurements were taken with a digital caliper to the nearest 0.1 mm. The morphometric parameters here considered were defined by Jara & López (1981).

The morphological variations most commonly found among the specimens examined, additionally to the type series (Table 1), are related with the rostrum and the frontal area. Figure 6 shows the variation extremes in 29 specimens from Malleco River. A negative correlation between length and width of rostrum, and also between rostral length and frontal width appears among them. Figure 7 records the extreme variations of the rostro-frontal area in 58 specimens from River Putagán; a negative correlation seems to exist between rostrum length and the upwards inclination of its apex. Figure 5-A1 shows that the external border of the anterolateral lobes may be arquate instead of straightlined as in the type series.

Maximum size variation along the Bío Bío River basin was found to conform to a cline (Fig. 8), between Icalma Lake and Nacimiento. The most obvious environmental factors to which this phenomenon could be related are the thermic regime and the organic productivity along the river. Lake Icalma is situated at 1150 m altitude while Nacimiento is at 130 m. However, no consistent field data are available to support this hypothesis. The graph suggests that the most favorable environmental conditions for *A. pewenchae* are those found in the mesorithral facies of the river (sector B).

Natural History

Field notes characterize *A. pewenchae* as a rheophilic species, consistently associated with rithral or fast running water environments. *Aegla pewenchae* specimens were mostly found in places where water flowed over hard substrates (boulders and stone blocks) with little to no deposition of fine sediments. In the monomictic ultraoligotrophic lakes Galletué and Icalma, *A. pewenchae* was also found on boulders and hard substrate along the shoreline. In these pristine environments, the specimens typically presented clean carapaces. In contrast, when *A. pewenchae* was found in eutrophic biotopes with high fine sediment deposition rates and high benthic primary productivity, i.e., the rivers associated with intensive fruticulture, between Chimbarongo and Talca, the specimens presented dirty carapaces, covered by muddy deposits and epibionts.

The thermic conditions in which *A. pewenchae* was found also present an interesting contrast. In lakes Icalma and Galletué the thermic regime ranges between 5.5°C for Icalma Lake and 7.5°C for Galletué Lake, in winter, to 19°C and 17.5°C in summer, respectively (Parra et al. 1993). In the rivers of the fruticultural zone, water temperatures rise to approximately 25°C in summer (Jara, field notes).

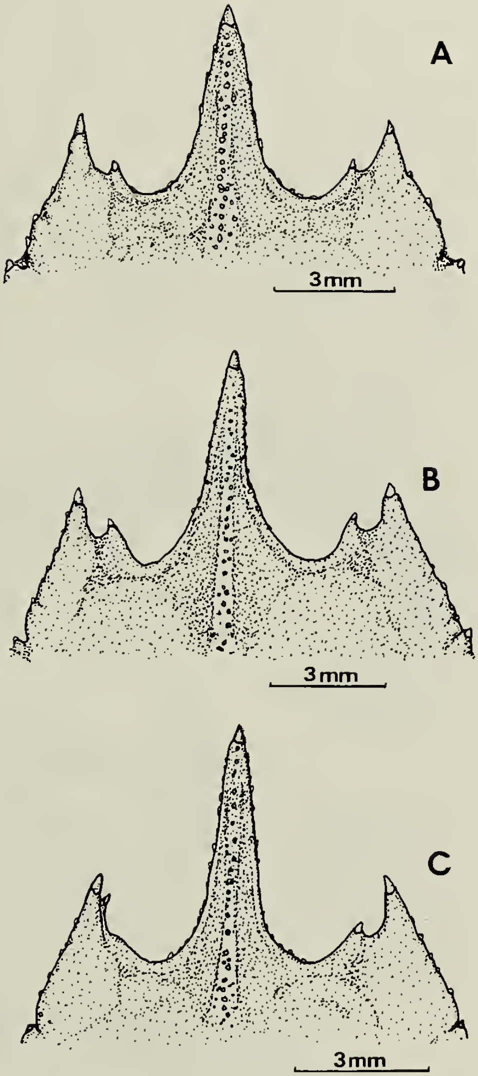

Fig. 6. Morphological variation in *A. pewenchae*, new species. Rostrum and rostral end of three males from Malleco River (IZUA C-334).

At least one instance of migratory behav-

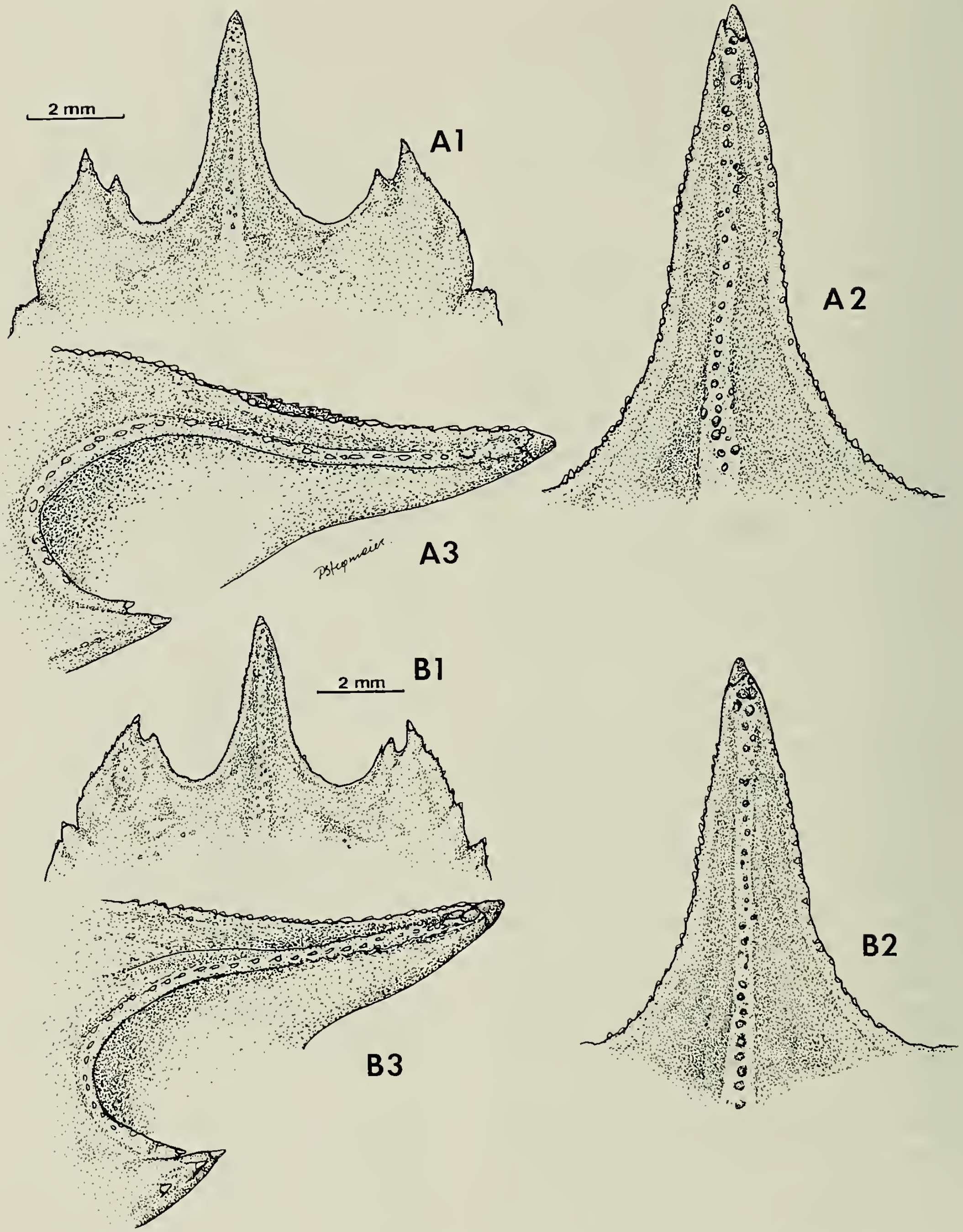

Fig. 7. Morphological variation in *A. pewenchae*, new species. Rostrum and frontal end of two extreme variant males from Putagán River (IZUA C-493). A1 & B1, rostrum and frontal end in dorsal view; A2 & B2, rostrum in dorsal view; A3 & B3, rostrum in lateral view.

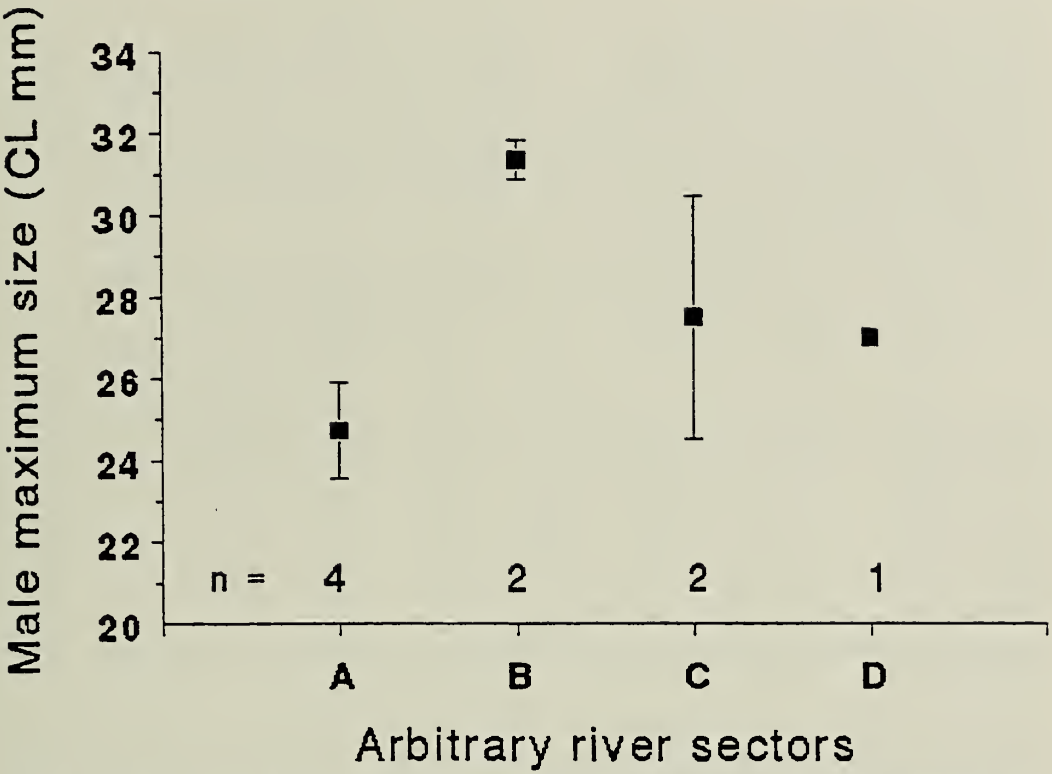

Fig. 8. Variation of male maximum size (CL, carapace length) in *A. pewenchae,* new species, along Bío Bío River mainstream. n = number of populations sampled per river sector. In each sample only the size of the largest male was recorded. Sample size ranged between 7 and 98 specimens ($\bar{X}$ = 22.5; SD = 27.2). River sectors are roughly defined as follows: A, upland river in a high mountain steppe-like environment, 0 to 20 km downstream from sources (localities: Icalma, Galletué, Marimenuco and Liucura); B, torrential river in a deep piedmont valley, 115 to 135 km from sources (localities: Queuco and Huequecura); C, lowland moderately fast running river, 185 to 210 km from sources (localities: bridge under highway #5 and Coihue); D, lowland slow running river on sandy substrate, 245 km from sources (locality: La Laja).

ior was observed for this species. On 21 February 1983, a great number of individuals, mostly adult males, were seen migrating upstream along the banks of the Queuco River (Bío Bío River basin). Animals moved at a rate of 600 to 1200 individuals per hour, 24 hours a day; the cause of this migration could not be established.

In relation to the molting period, in the Queuco River, females are known to molt in October. According to field notes, most of the individuals sampled between Los Angeles to the south and Chillán to the north during December 1991 were in advanced pre-ecdysis or in recent post-ecdysis.

No data are available about reproductive biology or trophic niche of *A. pewenchae.*

The benthic community in which *A. pewenchae* is found varies in the number of species and in the abundance of organisms from one river to another. In general, it is composed by rheophilic "clean water" species such as leptophlebiid and baetid ephemeropterans, hydropsychid, rhyacophilid, and sericostomatid trichopterans, gripopterygid and diamphipnoid plecopterans, elmid and psephenid coleopterans, and trichomycterid fishes.

Other species of *Aegla* are occasionally part of these communities. In the rivers

Table 2.—Morphometrics of *A. pewenchae*, new species, type series. All measurements in mm. M = male; F = female; Holo = holotype; Allo = allotype; P1 to P8 = paratypes. CL, carapace length, distance between rostral apex and posterior margin of cephalothorax; RL, rostral length, distance between rostral tip and a transverse line tangent to deepest point of orbits; PCL, precervical length, distance between rostral tip and midpoint of cervical groove; FW, frontal width, distance between tips of anterolateral angles of carapace; PCW, maximum precervical width, distance across third hepatic lobes; CW, maximum carapace width; LCL, left cheliped length; RCL, right cheliped length; L2PL, length of second pereiopod; L2DL, dactylar length of second left pereiopod; L4DL, dactylar length of fourth left pereiopod; TL, telson length. * = rostrum broken; e = estimated.

	Holo	Allo	P1	P2	P3	P4	P5	P6	P7	P8*
Sex	M	F	M	M	M	M	M	F	F	F
CL	25.8	23.8	29.7	26.9	26.8	26.0	25.7	23.9	23.8	24.7e
RL	5.7	4.8	6.1	4.9	5.6	6.2	4.8	4.7	4.0	4.9e
PCL	17.0	15.6	19.5	17.4	17.6	16.9	16.6	15.6	15.5	16.5e
FW	7.5	6.8	8.9	8.5	8.1	7.7	7.3	7.1	6.9	7.8
PCW	13.5	13.0	16.2	14.6	14.6	13.2	14.3	13.0	13.6	13.5
CW	19.9	18.9	24.5	21.4	21.5	19.6	20.5	19.2	19.8	20.4
LCL	35.4	27.9	43.4	40.4	38.2	32.8	36.9	27.9	28.6	29.1
RCL	32.3	27.9	40.4	37.0	35.4	30.6	35.5	27.6	27.5	28.9
L2PL	36.5	32.9	40.7	39.1	39.4	36.7	38.4	34.2	33.4	34.8
L2DL	8.4	7.5	8.8	8.7	8.9	8.0	8.4	7.4	7.6	7.8
L4DL	8.7	7.9	9.7	8.9	—	8.7	8.3	8.2	8.0	8.4
TL	5.3	5.9	5.1	5.3	5.0	4.7	4.8	5.8	5.9	5.9

Claro, Lircay, Maule, Putagán, Liguay, and Cato (Maule River system) and Cholguahue and Quilleco (Bío Bío River system) *A. pewenchae* was collected together with *A.* aff. *laevis talcahuano* Schmitt, 1942b. In rivers Malleco (Bío Bío River system) and Donguil (Toltén River system) it was collected together with *A. denticulata* Nicolet, 1849. In rivers Colpí, Quillén, and Quepe (Imperial River system) and Donguil (Toltén River system) it was collected together with *A. rostrata* Jara, 1977 (fluvial form), and in the river Cholchol (Imperial River system) it was collected with *A. spectabilis* Jara, 1986b.

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The author thanks Mr. Raúl Arriagada for his valuable collaboration during field work in December 1991, and Messrs. René Navarro and David Manriquez for their collaboration during the field work in December 1982. Thanks are extended to Miss M. C. Vásquez for the curation of IZUA's *Aegla* collection, and to P. Stegmaier for the art work. Improvement of the English version is due to Mrs. P. Araya, and two reviewers. This paper was financed by grants FONDECYT 91-0900 and DID S-91-4 of Dirección de Investigación y Desarrollo of the Universidad Austral de Chile.

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DESCRIPTION OF THE GHOST SHRIMP *EUCALLIAX MCILHENNYI,* NEW SPECIES, FROM SOUTH FLORIDA, WITH REEXAMINATION OF ITS KNOWN CONGENERS (CRUSTACEA: DECAPODA: CALLIANASSIDAE)

Darryl L. Felder and Raymond B. Manning

Abstract.—*Eucalliax mcilhennyi,* new species, is described from an intertidal sandflat bordering Fort Pierce Inlet on the Atlantic coast of Florida. The species is distinguished from known congenerics of the Eucalliinae, all of which are restricted to the western Atlantic. Detailed comparisons are made to *E. jonesi* (Heard 1989), from Bimini Harbor, Bahamas. Specimens from Florida were first thought to represent *E. jonesi* because of superificial resemblance, similarities in habitats, and proximity of collection localities. The two species differ from each other and their congenerics in a number of morphological characters, including relative development of the front and rostrum of the carapace, spination of chelipeds, shape of gonopods, and ventral plating of abdominal somites. Abbreviated larval development and limited capacity for dispersal are inferred by the large eggs found on ovigerous females of species in this genus, and may serve to maintain isolation of regional populations. This would be consistent with morphological evidence that *Eucalliax* has extensively endemized within the tropical western Atlantic, even in the absence of evidence for major historical disjunctures in appropriate habitat.

Over the last decade, we have used yabby pumps (see Hailstone & Stephenson 1961, Manning 1975) to collect extensively from intertidal substrates in the vicinity of Fort Pierce, Florida. Our efforts there have revealed a number of previously unknown infaunal decapods, some of which we have described in previous papers (Felder & Manning 1986; Manning & Felder 1989, 1992). Materials from this region have also provided a basis for systematic revisions and new distribution records, especially for members of the Callianassidae (Manning 1987, 1993; Manning & Felder 1986, 1991; Manning & Heard 1986; Manning & Lemaitre 1994).

One of our collecting sites within the southern Indian River lagoon, a small intertidal sandflat just inside Fort Pierce Inlet (see Felder & Manning 1986), has produced a particularly rich assemblage of fossorial stomatopod, thalassinid, and alpheid crustaceans. The thalassinids taken from this small area have included representatives of *Upogebia, Callichirus, Neocallichirus, Biffarius,* and a new genus (Manning & Lemaitre 1994). Our collections there have also included infrequent occurrence of two species of ghost shrimp that we assigned to a new genus, *Eucalliax* Manning & Felder, 1991. One of these species, perhaps the same as that previously reported from south Florida as "*Eucalliax quadracuta*" (Biffar 1971; specimen destroyed by fire), we have tentatively grouped with the '*Eucalliax quadracuta* complex' until such time as we can complete further comparative studies from throughout the range of that group. The other, allied to *E. jonesi* (Heard 1989) from the nearby northern Bahamas and *E. cearaensis* from Brazil (Rodrigues & Manning 1992), is herein recognized as a new species.

Material examined is listed by location followed by date, collector, number of specimens per sex and condition (imm = immature, mutl = mutilated, ov = ovigerous), and, if applicable, museum number. Size is expressed as postorbital carapace length (CL) measured in millimeters (mm), except where compared as total length under "Remarks" section. The holotype and some paratypes of *Eucalliax mcilhennyi* have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Paratypes have been deposited in the University of Southwestern Louisiana Zoological Collections, Lafayette, Louisiana (USLZ). In addition to type materials of *E. cearaensis* and *E. jonesi* available at the Smithsonian Institution, the paratype of *Eucalliax jonesi* was obtained on loan from the Gulf Coast Research Laboratory (GCRL) in Ocean Springs, Mississippi, and the types of *Eucalliax quadracuta* (Biffar, 1970) were obtained on loan from the Museum of Comparative Zoology, Harvard University, in Cambridge, Massachusetts.

Eucalliax Manning & Felder, 1991
Eucalliax mcilhennyi, new species

Figs. 1–6

Type material.—Station RBM FP-89-4, sandflat with sparse seagrass, 27°27.7′N, 80°18.7′W, south side of Fort Pierce Inlet, north side of US Highway A1A causeway between Fort Pierce and South Hutchinson Island, Indian River lagoon, St. Lucie County, Florida, 11 Aug 1989, coll. R. B. Manning, R. Brown, and W. Lee, ♂ holotype (CL 10.1 mm), USNM 267112; (same site as holotype, except where otherwise indicated) station RBM FP-85-4, voucher for color photo, 23 Jul 1985, coll. R. B. Manning and D. L. Felder, 1 ♂ (CL 9.0 mm), USLZ 3538; station RBM FP-86-1, 11 Aug 1986, coll. R. B. Manning, D. L. Felder and W. D. Lee, 1 ov ♀ (CL 10.3 mm), USNM 267113; station RBM FP-86-2, voucher for color photo, 11 Aug 1986, coll. R. B. Manning, D. L. Felder and W. D. Lee, 2 ♀ (1 ov, 1 mutl; CL 11.6 mm, 10.5 mm), USNM 267114; station RBM FP-86-3, 12 Aug 1986, coll. R. B. Manning and D. L. Felder, 1 ♀ (CL 10.9 mm), USNM 267115; station RBM FP-86-4, 12 Aug 1986, coll. R. B. Manning, D. L. Felder and W. D. Lee, 1 ♀ (CL 9.9 mm), USNM 267116; station RBM FP-86-6, 14 Aug 1986, coll. R. B. Manning, D. L. Felder and W. D. Lee, 3 ♀ (1 ov, 1 mutl; CL 11.2, 11.2, 11.0 mm), USNM 267117; no station number, 4 Jun 1993, coll. D. L. Felder, 1 ov ♀ (CL 9.7 mm), USLZ 3537; station RBM FP-88-3, hard packed sand along shore, 27°28.2′N, 80°18.2′W, south side of Coon Island, north shoreline of Fort Pierce Inlet, Indian River lagoon, St. Lucie County, Florida, "with *Pinnixa*," 21 Apr 1988, coll. R. B. Manning, W. D. Lee, M. Schotte, and C. King, 1 ♂ (CL 7.5 mm), USNM 267118.

Diagnosis.—Rostrum broad, weakly produced. Carapace dorsally lacking strong, longitudinal ridges. Antennal peduncles overreaching antennular peduncles. Chelipeds with hooked marginal spinules on ischium, lacking acute teeth or spines at distal corners of carpus. Male first pleopod originating from distinct ovoid ventral plate on abdomen, terminally bifurcate, with single, short subapical process.

Description.—Dorsally, carapace much less than (about ⅔) combined lengths of abdominal segments 1 and 2 (Fig. 1a). Frontal margin of carapace with broad, triangular rostrum; rostrum acute terminally and flanked by weakly excavate shoulders (Fig. 2a) forming anteriorly produced prominences just lateral to margins of eyestalks; rostrum extending less than ½ visible length of eyestalks in dorsal view, ventrally bearing tuft of setae, longest of which extend anteriorly between eyestalks to cornea. Carapace lacking distinct dorsal oval and cardiac

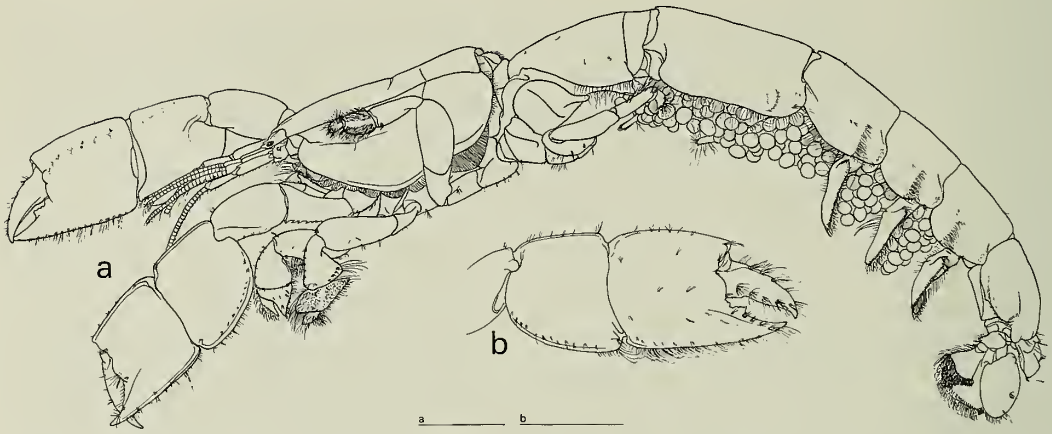

Fig. 1. *Eucalliax mcilhennyi,* new species, from Fort Pierce Inlet, Florida, paratype ovigerous ♀ (CL 11.6 mm) USNM 267114: a, Lateral view; b, External surface of right (major) chela. Scale lines indicate 5 mm.

prominence; lacking rostral carina except for slightly raised postrostral area between pairs of postrostral punctae. Cervical groove evident as suture, disjunct at dorsal midline, extending anteroventrally to complex network of sutures in posterior ⅖ of carapace; one branch from this point continued anteriorly as weakly carinate, sinuous, longitudinal suture, of which longest tract terminates anteriorly in antennal notch of carapace margin. Strong, raised hepatic boss in anterior ⅓ of carapace just dorsal to cervical suture. Linea thalassinica strong, parallel to midline of carapace over most of length, diverging slightly posterior of cardiac suture. Cardiac suture well defined, incomplete across dorsal midline of carapace.

Eyestalks dorsally flattened, length equal to or just greater than 2 times width, in dorsal view reaching beyond basal antennal article; mesial surfaces broadly triangular, flattened so eyestalks fit closely together at midline; anterolateral margin of eyestalk arcuate, joining mesial margin anteriorly in narrow, upturned tip; pigmented region in distal ½ of dorsal surface, area of dark pigmentation variable, sometimes exceeding the weakly evident corneal surface; sometimes with 1 or more setose punctae dorsally near midlength of eyestalk. Antennular peduncle shorter than and not so heavy as antennal peduncle; basal article laterally and ventrally inflated to accommodate statocyst, opening to which is occluded by closely set fan of anteromesially directed setae overlain by eyestalk; second article slightly longer than basal article, third article about ⅔ length of second; second and third articles with ventrolateral row of long, ventrally directed setae, continued onto ventral ramus of flagellum; rami of flagellum about equal in length, near 5 times length of third article of peduncle; ventral ramus ventrally setose, line of long setation ventrolaterally and line of slightly shorter setation ventromesially; dorsal ramus primarily with sparse short setae, subterminal articles of dorsal ramus heavier than those of ventral ramus, and endowed with thick line of ventral aesthetascs. Antennal peduncle more than 1.5 times length of antennular peduncle; basal article with dorsolateral carina bearing regular line of fine setae above laterally produced excretory pore; second article with deep, diagonal ventrolateral furrow, distally with field of long setae below ventrolateral suture and another on dorsolateral surface, broad, articulated dorsal scale at joint with third article; third article elongate, slightly longer than fourth or combined lengths of first two.

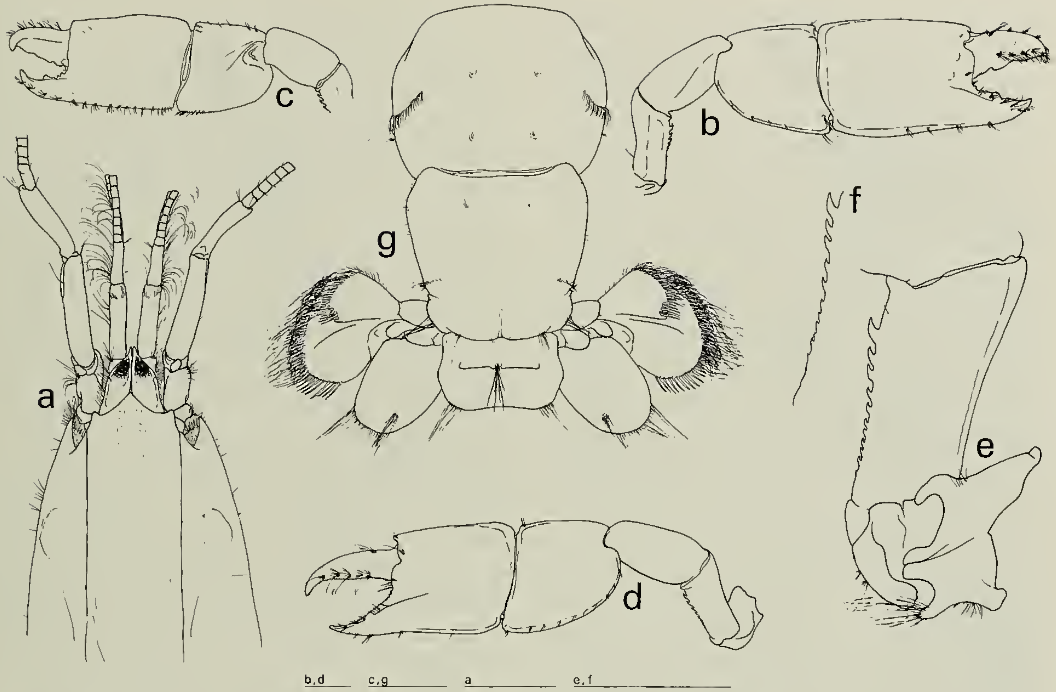

Fig. 2. *Eucalliax mcilhennyi,* new species, from Fort Pierce Inlet, Florida; a–e, g, holotype ♂ (CL 10.1 mm) USNM 267112; f, paratype ♀ (CL 11.6 mm) USNM 267114: a, Anterior carapace, eyestalks, and antennae, dorsal view; b, Right (major) cheliped, external surface; c, Right (major) cheliped internal surface; d, Left (minor) cheliped, external surface; e, Ischium of right (major) cheliped of ♂, internal surface; f, Ischial dentition, right (major) cheliped of ♀, internal surface; g, Posterior abdomen, telson, uropods, dorsal surface. Scale lines indicate 2 mm.

proximolaterally with unfused condylar process articulated to distolateral extreme of second article; fourth article narrower than third; flagellum sparsely setose and more than 4 times length of antennular flagella.

Mandibles set below the produced, rounded, median lobe of epistome; mandible (Fig. 3a) with large, terminally setose, 3-segmented palp, elongated third article of palp terminally rounded; incisor process with well-defined teeth on cutting margin, field of 3–4 large distal teeth separated from large proximal tooth by line of subpectinate lower teeth, internal surface with lip giving rise to molar process proximal to incisor teeth; paragnath (not figured) uncalcified, set against proximal surface of molar process, distolateral corner slightly produced and opposing teeth of molar process. First maxilla (Fig. 3b) with endopodal palp long, narrow, terminal article deflected proximally at articulation; proximal endite densely setose on concave margin, terminally with dense field of complex setae; distal endite elongate, terminally truncate and armed with stiff bristles; exopodite low, rounded. Second maxilla (Fig. 3c) with endopod narrowed abruptly at distal end, terminus directed mesially, first and second endites each longitudinally subdivided, exopod forming large, broad, scaphognathite. First maxilliped (Fig. 3d) with proximal endite triangular, marginal setation including stronger, curved setae at distal corner; distal endite elongate, ovoid, mesial half of external surface and all margins heavily setose, internal surface concave; exopod triangular, divided by transverse suture; distal part broader and with longer marginal setation at its mesial end, proximal part with field of mesially directed setae near mesial end; epipod large, broad, weakly subdivided by transverse suture, its anterior end tapered, angular. Second maxilliped (Fig. 3e) with long, narrow endopod; endopodal merus arcuate, slightly heavier in proximal half than in distal, flexor margin with dense fringe of long, close-set setae; carpus short; propodus heavy, weakly arcuate, length equal to or less than 2 times width, equal to or less than ½ length of merus; dactylus short, about ½ length of propodus, extensor margin arcuate; exopod about as long as endopodal merus, marginally fringed by long setae, subdivided by weak transverse suture at ⅓ length; epipod small, with short, rounded proximal lobe and narrow distal lobe. Third maxilliped (Fig. 3f) without exopod; endopod with long, dense setation on mesial margin; endopodal ischium subtriangular, slightly longer than broad, proximomesial lip forming produced lobe or subacute corner, internal surface with low medial, longitudinally oriented elevation bearing well-defined curved row of about 9–11 sharp teeth, usually with 2–3 smaller supplementary teeth trailing ventral to proximal end of primary row; merus subquadrate, slightly broader than long; carpus strongly flexed in proximal third, with setose lobe on flexor margin, internal surface faceted, superior facet glaborous except for marginal setae, and inferior facets setose; propodus large, subtriangular, about as broad as long, proximal ⅔ of inferior margin forming large, rounded, densely setose lobe; dactylus broad terminally, slightly longer than broad, fringed with very dense field of close-set, stiff setae on broad terminal margin.

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 with major and minor cheliped strongly developed (Fig. 1a), near equal in size but dissimilar in shape of propodus and dentition of fingers, especially in males; major cheliped located on either right or left side of body. Major cheliped of mature male (Fig. 2b, c) massive and strongly calcified; ischium slender, superior margin sinuous, inferior (flexor) margin with row of small, distinctly hooked denticles; merus unarmed, about 1.8 times longer than broad; carpus broad, increasing in breadth distally, inferior margin arcuate, superior and inferior margins keeled, terminated distally in blunt corners; propodus heavy, length (including fixed finger) about 1.7 times height, inner surface of palm smooth, without swollen proximal boss; weak unarmed furrow extending posteriorly from just below gape of fingers on outer face of palm; superior and inferior propodal margins keeled, keel of inferior becoming ill-defined beyond midlength and absent on fixed finger; fixed finger thick, heavily calcified, prehensile margin armed with 2 small well-separated triangular teeth in proximal ⅓ and broad, microserrated tooth just proximal to midlength, with distal half of margin unarmed and terminated at subacute upturned tip; dactylus with subacute, hooked tip, external shoulder of superior margin with setose punctum abutted against low tubercle in proximal ¼ of length in addition to line of about 6 setose punctae on internal side of superior margin, inferior (prehensile) margin with low, sinuously margined tooth encompassing distal ½ and separated from tooth on proximal ½ by rounded gap, proximal tooth with weakly bicarinate margin bearing scant small tubercles or microserration, proximal tooth separated from proximal end of inferior margin by rounded gap. Major cheliped of female also massive (Fig. 1a, b) but less heavily calcified and slightly different in sculpture than that of typical mature males; teeth of dactylus usually of slightly lower profile than in males, those of fixed finger usually centered more proxi-

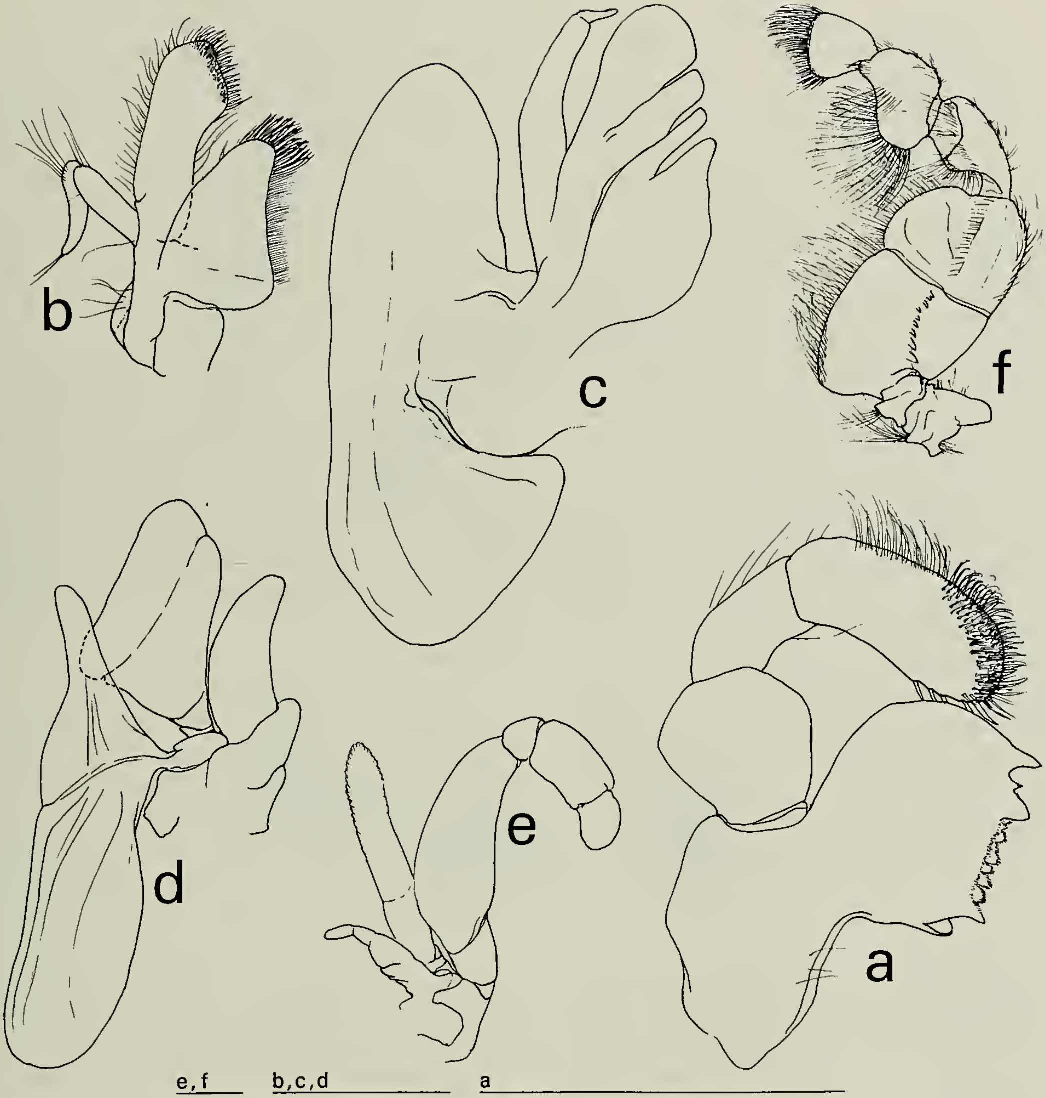

Fig. 3. *Eucalliax mcilhennyi,* holotype ♂ (CL 10.1 mm), from Fort Pierce Inlet, Florida, USNM 267112, right appendages; a–e, external surface; f, internal surface: a, Mandible, excluding paragnath; b, First maxilla; c, Second maxilla, setae not shown; d, First maxilliped, setae not shown; e, Second maxilliped, setae not shown; f, Third maxilliped. Scale lines indicate 1 mm.

mally than in males, both fingers relatively less massive, more narrow, sometimes more acutely tipped, than in males; propodus not as long relative to height, and with margins more arched, than in males.

Minor cheliped (Fig. 2d) slightly lighter, less armed than major, inferior (flexor) margin of ischium with line of distinct hooked spinules; merus unarmed; carpus with blunt distal corners; propodus with distinct unarmed furrow extending posteriorly from just below gape of fingers on outer surface, fixed finger tapered to very narrow acute or subacute tip, prehensile margin proximally serrate; propodus less elongate, relative to height, in females (Fig. 1a) and juvenile males than in mature males; dactylus narrow, with subacute tip, unarmed on prehensile margin.

Second pereopod (Fig. 4a) chelate, most of flexor margins of ischium and merus lined with evenly spaced long setae, similar setae patchy and restricted primarily to distal patches on flexor margin in carpus, inferior margin of propodus with similar setal patches which are long 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, microserration terminating proximally at small corneous tooth and terminating distally in thickened corneous tips of fingers; superior margin of dactylus slightly sinuous, with patches of stiff, arched bristles becoming increasingly reduced in length, close-set and more arched distally. Third pereopod (Fig. 4b) merus length about 2 times width, flexor margin weakly sinuous, typically with 2 small prominences bearing tufts of setae; carpus broadly flared distally to produce strong inferior lobe, width at this point about ¾ length, inferior lobe terminally with field of long arched setae, diminishing in length toward articulation with propodus; propodus with strong proximally directed lobe on inferior margin, lobe terminally with field of long arched setae diminished distally along margin to close-set shorter bristles that become slightly longer at distal extreme, superior margin with tufts of long arched setae, patterned tufts of lighter setae on outer face of article; dactylus tear-shaped, length about 1.4 times width, terminating in narrow corneous tip hooked toward external side, inferior margin sinuous, outer (external) face crossed by fields of short, slightly hooked setae in which longest setae are near superior margin, with separate, dense field of slightly heavier short weakly hooked setae along lower extreme of external face and inferior margin. Fourth pereopod (Figs. 1a, 4c) not subchelate, inferodistal corner of propodus rounded without evidence of fixed finger; dense setation on outer surface of both propodus and tear-shaped dactylus divided into upper and lower fields, setae slightly stronger in lower fields of both, densest on dactylus, especially on and near inferior margin; internal surface of propodus distally with single large very long seta originating from near superior margin and reaching distally well beyond tip of dactyl; dactyl terminated in narrow corneous tip hooked toward external side. Fifth pereopod (Figs. 1a, 4d) 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 finely divided into arched row of close-set denticles.

Texture of abdominal somites (Figs. 1a, 5a, b) smooth dorsally, glabrous, typically with setae limited to isolated pairs of setose punctae on first tergite, strongest of which are in posterior half; second tergite with posterolateral crescentic line of small, lightly setose granules, anterior to which is short oblique line and posterior of which are several small fields of similar granules and punctae, posterolateral-most of which bears long setae; third to fifth tergites each with a distinct, lateral, transverse field of long soft setae, posterior to each of which lies a small field of long stiff setae on the lateral margin; sixth tergite (Figs. 1a, 2g) with lateral, longitudinal finely setose lines of small granules, primary line turning to transverse and directed toward midline in posterior half on lateral lobe of tergite, posteriorly with strong tuft of long stiff setae at each posterolateral corner, similar tuft on posterior margin overlying each anterolateral corner of telson. Shape of first abdominal tergite narrowed anteriorly, anterior ¼ offset by lateral notch and subquadrate (most striking in mature males); second tergite elongate, at least 1.6 times median length of third; third

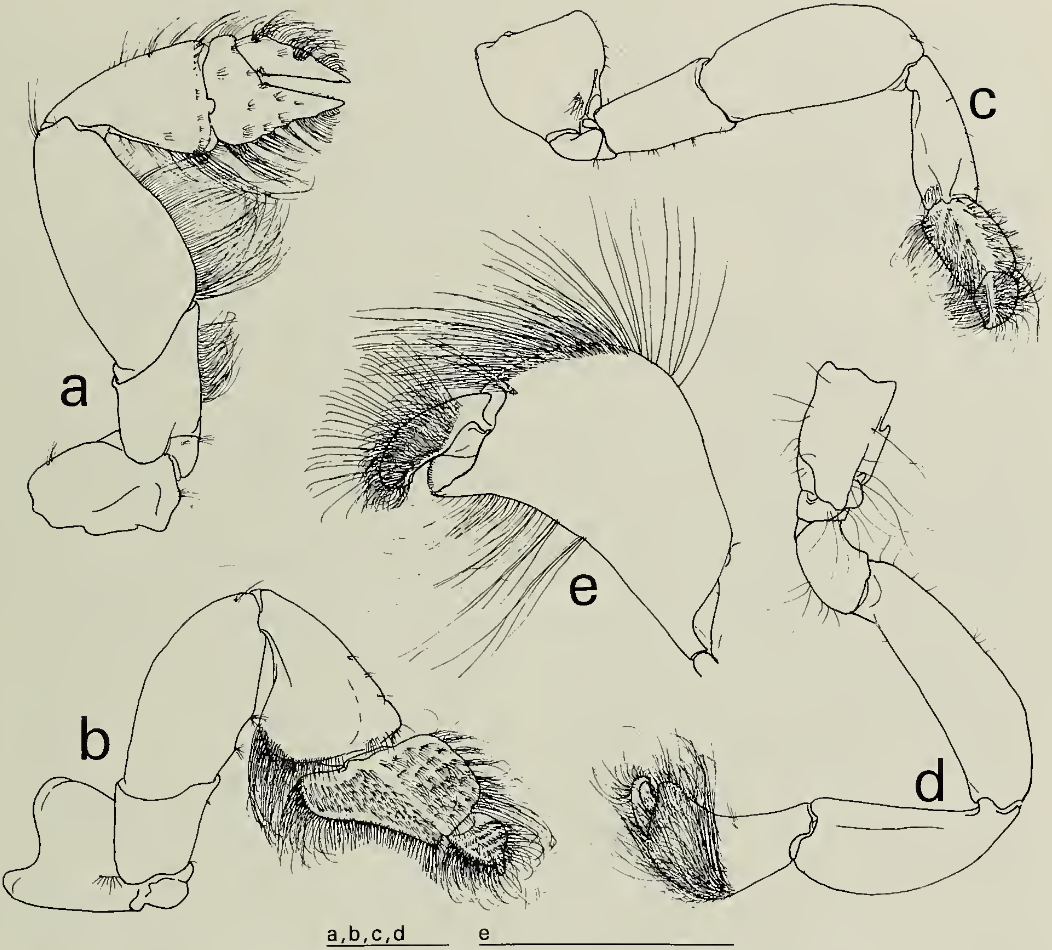

Fig. 4. *Eucalliax mcilhennyi*, new species, from Fort Pierce Inlet, Florida; a–c, holotype ♂ (CL 10.1 mm) USNM 267112; d–e, paratype ♀ (CL 11.6 mm), USNM 267114: a, Right second pereopod, external surface; b, Right third pereopod, external surface; c, Right fourth pereopod, external surface; d, Right fifth pereopod, posteromesial surface; e, Enlarged terminus of fifth pereopod. Scale lines indicate 2 mm.

tergite with deep, elongate anterolateral sulcus extending across anterior ⅓ of each side. Anterior ½ of first abdominal somite wrapped ventrally by girdle of thickened, leathery integument, girdle rounded laterally and transversely bisected by a furrowed suture, posterior half of somite ventrally with pair of conspicuous ovoid plates comprised of similar thickened integument, each of which (in males and females) articulates to first pleopod at its posterior extreme; medial posterior margin of first abdominal somite marked a triangular or rounded, anteriorly extended plate of thickened, leathery integument continuous with massive continuous covering of leathery integument that forms articular membrane between first and second abdominal somites and that covers entire ventral surface of second abdominal somite; similar leathery integument largely covering ventral surfaces of remaining abdominal somites.

First pleopod of male and female uniramous, composed of 2 articles; in male (Fig. 6a, b), total length about ⅔ that of second pleopod, distal article about equal in length

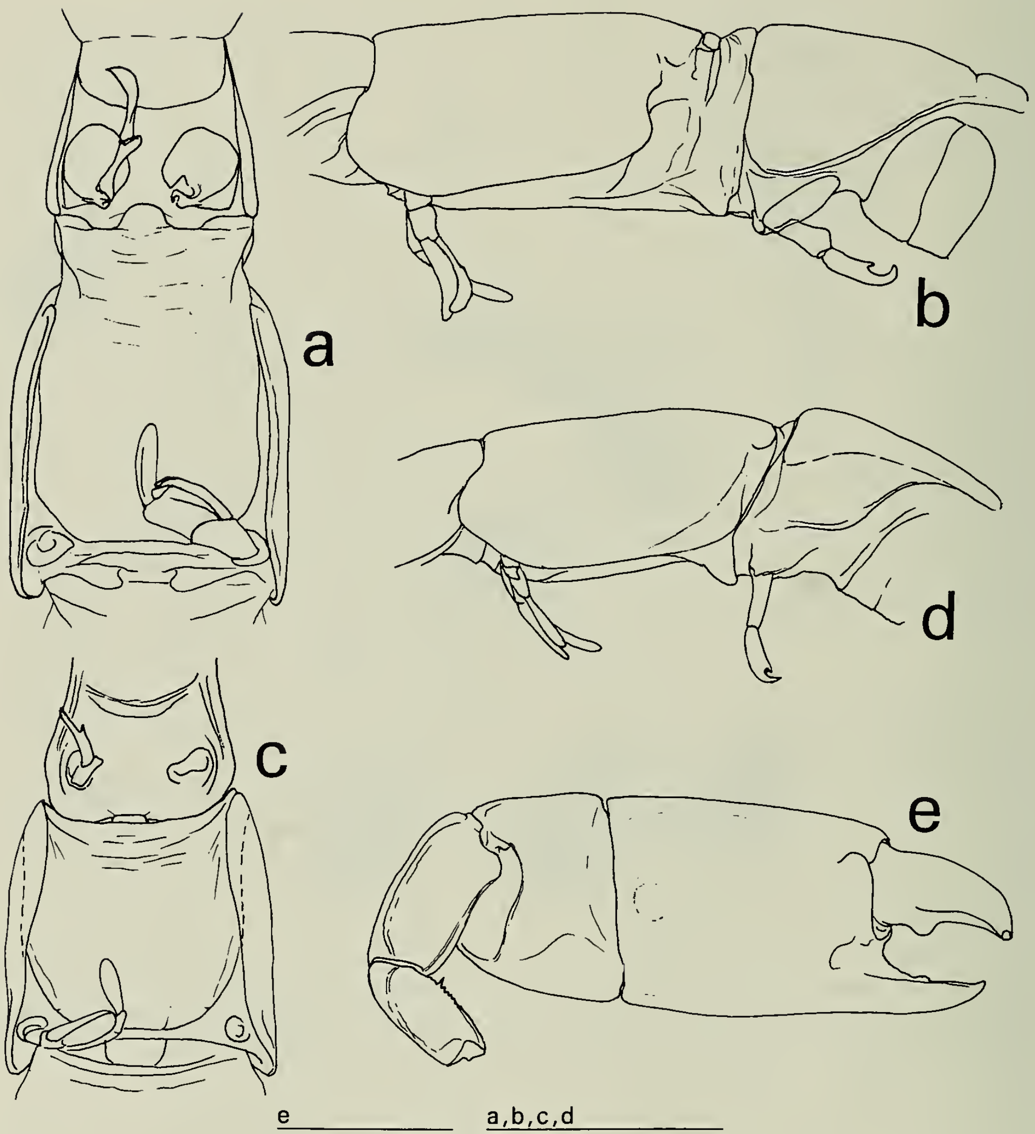

Fig. 5. *Eucalliax mcilhennyi,* new species, holotype ♂ (CL 10.1 mm) from Fort Pierce Inlet, Florida, USNM 267112: a, First and second abdominal segments, ventral surface, setae not shown; b, First and second abdominal segments, right lateral surface, setae not shown. *Eucalliax jonesi* (Heard 1989) from Bimini Harbor, Bahamas; c, d, paratype ♂ (CL 9.6 mm) GCRL 1136; e, holotype ♂ (CL 9.8 mm) USNM 221861: c, First and second abdominal segments, ventral surface, setae not shown; d, First and second abdominal segments, right lateral surface, setae not shown; e, Left (major) chela, internal surface, setae not shown. Scale lines indicate 5 mm.

to proximal and bifurcate at about ⅔ length, with acute tip of spooned terminal end directed laterally; in female (Fig. 6c) total length subequal to that of second pleopod, proximal article about ⅗ length of terminal article, terminal article with longest setae on broad shoulder just beyond midlength. Second pleopod of male and female biramous, with appendix interna on endopod; in male (Fig. 6d), dense setation largely restricted to distal extreme of exopod, distal lobe of endopod and appendix masculina, appendix masculina markedly overreaching distal lobe of endopod and with small appendix interna at its base; in female (Fig. 3e), both rami with long setae, appendix interna small and constricted distally. Third to fifth pleopod pairs (Figs. 1a, 6f) forming large, posteriorly cupped fans when cross-linked by hooked setae of appendices internae on opposed margins of endopods; endopod of each subtriangular, appendices internae finger-like, movably articulated to mesial margin of endopod. Telson (Fig. 2g) broader than long, subrectangular, broadest at lateral lobes in posterior half, posterior margin weakly bilobate; dorsal surface with medial tuft of large setae separating two halves of strong, transverse carina; lateral margins sinuous, without setae; posterior margin with tuft of setae on each of the weak lateral lobes. Uropod (Fig. 2g) with heavy, blunt, posterolaterally directed tooth on protopod, tooth over-reaching anterolateral margin of endopod; endopod broad, suboval, slightly longer than broad, dorsal surface with tuft of long setae on posterior ⅓, setae of posterior margin longest posterolaterally; 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 and long stiff, spiniform setae at posterodistal corner of plate, distal margin of exopod with dense fringe of setation grading to large spiniform setae of posterodistal margin.

Size.—Among the materials examined, the largest male is the holotype (CL 10.1 mm) and the largest female is an ovigerous paratype (CL 11.6 mm). Egg size (max. diameter) on this ovigerous specimen ranged from 0.76–0.96 mm, prior to preservation.

Color (from notes and color photographs of live specimens).—Overall whitish opaque to very faint rosy pink; may lack color pattern or sometimes have very faint dorsal patterning of pink on carapace, abdominal segments, and uropods; when present, pattern usually strongest on posteriormost abdominal segments and telson; carapace sometimes with small median square of reddish pigment just posterior to cervical groove. Chelipeds usually opaque white; sometimes with slight evidence of pale yellow at articulations of chelipeds and on uropods.

Known range and habitat.—Known from intertidal burrows in the immediate vicinity of the type locality on the Atlantic coast of Florida, U.S.A. The type locality is a tidally exposed sandflat sparsely vegetated with sea grass, located on the south margin of Fort Pierce Inlet, Florida. A single specimen was taken from a second site a few hundred meters distant, on the lower intertidal reaches of a well-packed sand beach on Coon Island, which forms a northern margin on this same inlet. All of these fossorial specimens were extracted from their burrows with yabby pumps. The burrow of at least one specimen appeared to also harbor a small commensal crab of the genus *Pinnixa.*

Etymology.—This species is named for Mr. John S. McIlhenny of Avery Island and Baton Rouge, Louisiana. True to tradition in his family, Mr. McIlhenny has melded his passion for Tabasco® pepper sauce with an equal enthusiasm for nature and studies in natural history. The financial support that he has contributed to a number of research biologists through his Coypu Foundation, has furthered research in many subdisciplines, including crustacean biology.

Remarks.—Of the four species of the genus, *Eucalliax mcilhennyi,* new species, *E. jonesi* (Heard 1989) from the Bahamas, and *E. cearaensis* Rodrigues & Manning, 1992 from Brazil, all lack the acutely projecting armature that characterizes distal corners of the carpus in the chelipeds of *E. quadracuta* (Biffar 1970) from Venezuela. While each of these corners has typically developed a doublet of spines in *E. quadracuta,* they are instead weakly produced to a single subacute or rounded corner in the other afore-

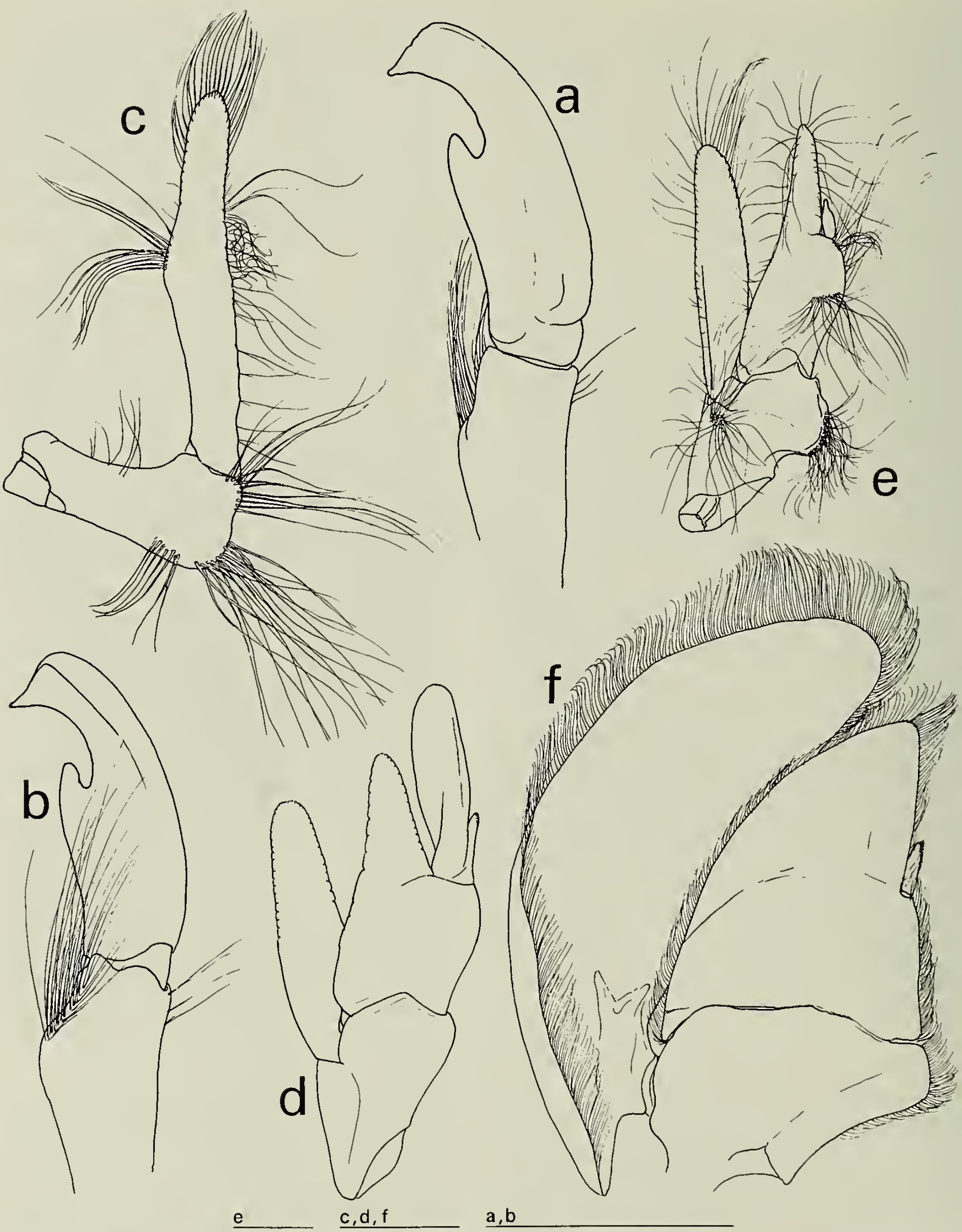

Fig. 6. *Eucalliax mcilhennyi,* new species, from Fort Pierce Inlet, Florida; a–b, d, f, holotype ♂ (CL 10.1 mm) USNM 267112; c, e, paratype ♀ (CL 11.6 mm) USNM 267114: a, Right first pleopod of ♂, external surface; b, Right first pleopod of ♂, internal surface; c, Right first pleopod of ♀, external surface; d, Right second pleopod of ♂, posterior surface; e, Right second pleopod of ♀, posterior surface; f, Right third pleopod, posterior surface. Scale lines indicate 1 mm.

mentioned speices. Materials from Florida that were assigned to *E. quadracuta* by Biffar (1970, 1971) and subsequently destroyed, as well as some materials that we have collected from Fort Pierce Inlet, also have characteristic "*quadracuta*" armature of the chelipeds, but we prefer to recognize them only as members of the "*E. quadracuta* complex" until such time as we can complete a careful comparison with the Venezuelan species. Such caution seems warranted given what appears to be a tendency for restricted distribution in species of this genus. As in *E. mcilhennyi,* the '*E. quadracuta*-complex' materials from Florida include ovigerous females with large eggs (1.1–1.3 mm), a characteristic that may reflect an overall tendency toward abbreviated development and reduced larval dispersal in the genus. This also appears to favor regional endemization in other callianassid populations with such eggs (see Felder & Rodrigues 1993). Owing to this possibility, and in the absence of voucher materials, we must reserve judgment on a report of *Eucalliax jonesi* from the British Virgin Islands (Murphy & Kremer 1992), at least until such time as materials from that locality can be carefully compared to existing types.

In addition to the marked difference in cheliped armature, the strong dorsal ridges present on the carapace in the *E. quadracuta* complex will also serve to readily separate this group from *E. mcilhennyi* and other members of the genus which lack them. Likewise, in mature individuals, size will readily distinguish *E. mcilhennyi* and other members of the genus from the *E. quadracuta* complex. Biffar (1970) reported total lengths of 68–75 mm for the type materials of *E. quadracuta* from Venezuela, with a carapace length of 17 mm in the smallest individual which was the mature holotype male. Our materials of this complex from Florida are even larger with total lengths of 85–91 mm and carapace lengths of 21–22 mm. By contrast, the other known members of the genus are much smaller, with carapace lengths of mature specimens ranging from 10.1–11.6 mm in *E. mcilhennyi,* 9.6–9.8 mm in *E. jonesi,* and 6.0–7.2 mm in *E. cearaensis.*

Among the many characters that can serve to separate *E. mcilhennyi* from both *E. jonesi* and *E. cearaensis* are shape of the rostrum, armature of the cheliped ischium, relative lengths of the antennular and antennal peduncles, shape of the male first pleopod, and ventral plating of the first and second abdominal somites. *Eucalliax cearaensis* differs from both the other species in that its antennular and antennal peduncles are subequal in length, and in that the male first pleopod is not bifurcate and instead terminates in a single hook. In both *E. mcilhennyi* and *E. jonesi* the antennal peduncles markedly overreach the antennular peduncles, and the male first pleopods are bifurcate along their length, producing a short subapical process. *Eucalliax mcilhennyi* can in turn be separated from *E. jonesi* by several characters that are not usually subject to striking sexual dimorphism in this group, and should therefore apply equally well in males and females (despite the fact that female specimens of *E. jonesi* have yet to be described). In comparison to *E. jonesi, E. mcilhennyi* has (i) a much broader and less produced rostrum, (ii) hooked rather than straight spinules lining the ischium of the cheliped, and (iii) a unique pattern of leathery plates (Fig. 5a, b, c, d) on ventral surfaces of the first two abdominal somites. The unique pattern in the ventral integument of the first and second abdominal somites in *E. mcilhennyi* consists not only of the distinct ovoid plates from which the first pleopods originate (Fig. 5a), but also a unique shape in the leathery integument at the posterior margin of the first abdominal somite and the anterior margin of the second abdominal somite. In *E. jonesi,* the median posterior margin of the first abdominal somite is marked ventrally by a short, subquadrate extension of the thick leathery covering on the intersegmental joint and second abdominal somite (Fig. 5c); immediately posterior to this, the leathery integument is deflected ventrally (Fig. 5d). In *E. mcilhennyi,* the median extension on the posterior margin of the first abdominal somite is anteriorly rounded (Fig. 5a) or subtriangular in shape, and the leathery integument posterior to this structure is not markedly deflected to the ventral side (Fig. 5b). In addition, mature males of *E. mcilhennyi* have first pleopods with an entire rather than bifid subapical lobe and with a more spatulate and laterally directed apical lobe. Our reexamination of the *E. jonesi* holotype also revealed a prominent proximal boss on the internal surface of the major palm in this male (Fig. 5e), and this feature is lacking in both sexes of *E. mcilhennyi.*

In the course of examining morphology in *E. mcilhennyi,* several features were noted which may be of particular significance in phylogenetic placement of the genus. The male second pleopod, previously thought to lack an appendix masculina (see Manning & Felder 1989), does appear to have a large terminal article that may be homologous to structures termed the appendix masculina in various ctenochelid genera. If so interpreted, the presence or absence of an appendix masculina must be dropped as a character to distinguish members of the Callianassidae from members of the Ctenochelidae. Also, a uniquely enlarged and elongate, singular seta was found to occur on the internal superodistal corner of the propodus on the fourth pereopod. This unique seta, which is directed distally and overreaches the tip of the dactyl, was also evident in the type materials of *E. jonesi* (GCRL 1136, USNM 221861) and *E. cearaensis* (USNM 252546) that we have subsequently examined, and was manifest as a distinct elongate pair of setae in materials of the *E. quadracuta* complex from Venezuela (MCZ 760) and Florida. Given their location, these setae appear to serve a specialized cleaning function. We also note that such a pair of setae occurs in the Mediterranean species, *Calliax punica* (Saint Laurent & Manning 1982) (USNM 172356), which represents a genus closely allied to *Eucalliax* within the Eucalliinae Manning & Felder, 1991. As a character, they may be unique to the Eucalliinae or perhaps may define some larger taxocene within the Callianassidae.

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PINNIXA SCAMIT, A NEW SPECIES OF PINNOTHERID CRAB (DECAPODA: BRACHYURA) FROM THE CONTINENTAL SLOPE OFF CALIFORNIA

Joel W. Martin and Deborah L. Zmarzly

Abstract.—A new species of the pinnotherid crab genus *Pinnixa, P. scamit*, is described. Collected off the coast of Pt. Arguello, California, U.S.A., at 311 m, the new species belongs to the *Pinnixa occidentalis* complex, species of which are characterized by a highly sculptured carapace, well developed cardiac ridge, and deflexed fixed fingers on the chelae. *Pinnixa scamit* differs from *P. occidentalis* in having a well developed but granular (rather than acute) cardiac ridge, and larger, more acute, slightly curved teeth along the anterolateral margin of the carapace. The most salient difference between the two species is the length of the propodus of the third walking leg (pereiopod 4), which is at least 2.5 times its width in the new species.

In a recent review of crabs in the genus *Pinnixa* White, 1846, known from California, Zmarzly (1992) redescribed 11 previously recognized species and described two new species, *P. forficulimanus* and *P. minuscula*, bringing the number of species of this genus known from California waters to 13. Several of the species treated by Zmarzly were described as exhibiting significant morphological variation. In particular, Zmarzly (1992) reiterated Hart's (1982) comment that the species *Pinnixa occidentalis* Rathbun, 1893, in part because of its variability and in part because of its wide geographic and bathymetric distribution, may represent a species complex rather than a single morphologically variable species.

While examining several decapod crustacean specimens collected as part of a faunal survey of the Santa Maria Basin and western Santa Barbara Channel, conducted by the Minerals Management Service (MMS) of the U.S. Department of the Interior, we noticed two specimens that shared certain features with *Pinnixa occidentalis* Rathbun, 1893, but that did not entirely agree with the original description or Zmarzly's (1992) redescription of this species. Subsequent examination and comparison with true *P. occidentalis* has convinced us that the differences are sufficient to warrant the erection of a new species of *Pinnixa*, which is described below. The holotype and sole paratype are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Pinnixa scamit, new species
Figs. 1, 2

Material examined.—Holotype female, USNM 267500, carapace width 7.4 mm, carapace length 3.7 mm; 29 Nov 1983; MMS station data 071-BSS-01-TX, 34°29.040′N, 120°44.013′W, western Santa Barbara Channel, just seaward of, and SSW of, Pt. Arguello, California; single core replicate; 1020 feet (311 m); 1 mm screen. Paratype juvenile, USNM 267501 (sex indeterminate), carapace width 3.4 mm, carapace length 2.1 mm, same collecting data as for holotype.

Diagnosis.—Carapace highly sculptured, with anterolateral ridge bearing pronounced and slightly anteriorly-curved teeth; frontal margin with deep median cleft; cardiac ridge

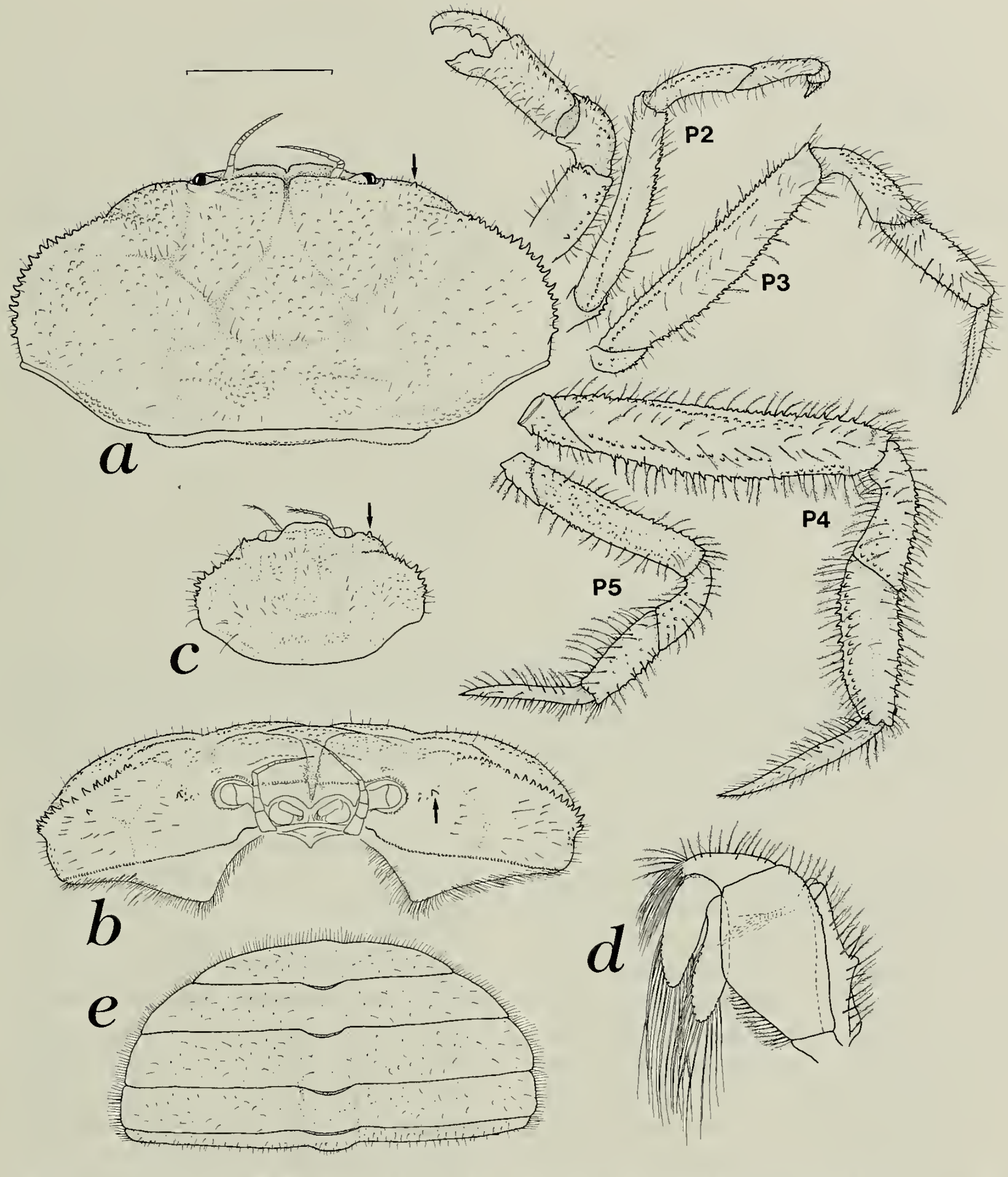

Fig. 1. *Pinnixa scamit,* female holotype, USNM 267500, and juvenile paratype, USNM 267501 (c only), western Santa Barbara Channel, California. a, female holotype, dorsal view of carapace and right side appendages, pereiopods 1–3 drawn in situ, pereiopods 4 and 5 removed and figured separately (to assure correct proportions); b, same specimen, frontal view showing sculpturing of carapace and subhepatic tooth (arrow); c, dorsal view of immature paratype; note that subhepatic tooth (arrow) and acute serrations along anterolateral margin are already present at this size; d, third maxilliped of holotype, left side, outer view; e, abdomen of holotype, ventral view illustrated in situ (first two segments not visible, and segment 3 shortened due to curvature of abdomen). Scale bar = 2.0 mm for a–c, e; 1.0 mm for d.

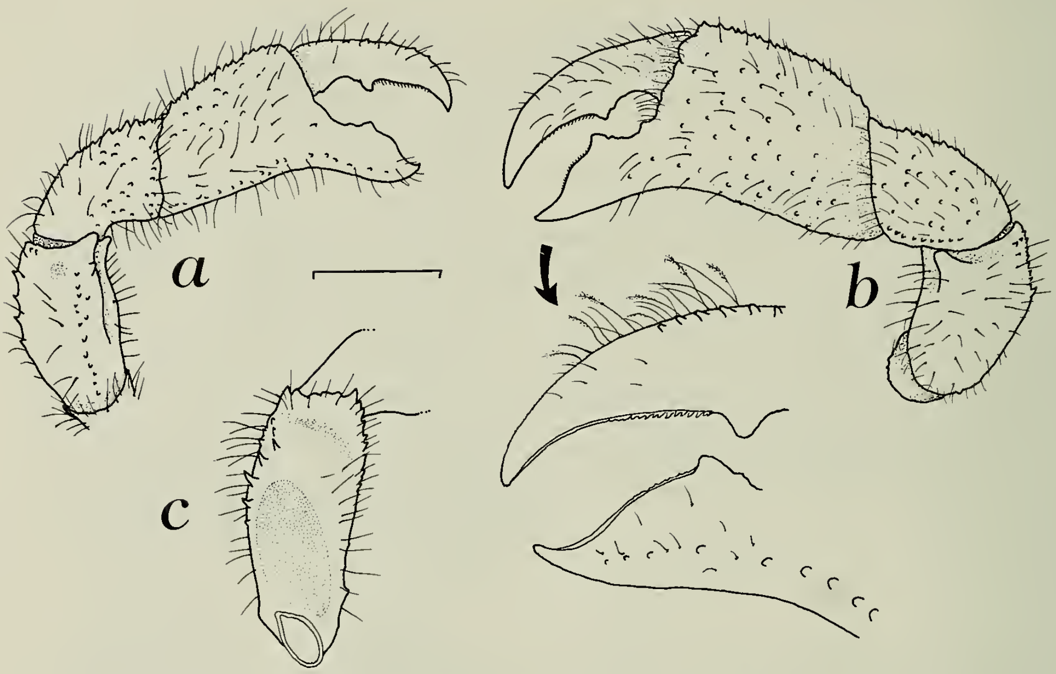

Fig. 2. *Pinnixa scamit,* female holotype, USNM 267500, chelipeds. a, right (minor) cheliped, outer view; b, left (major) cheliped, outer view, with fingers enlarged below (arrow) to show minute teeth along cutting border; length of merus and basi-ischium distorted (overly shortened) in both a and b because of orientation of illustration; c, merus of left cheliped, dorsal view, with carpus toward top of figure. Scale bar = 1.0 mm for all figures except for enlargement of b (which is not to scale).

present, granular, not sharp. Fixed finger or major cheliped slightly deflexed; both fingers of major cheliped with single stout tooth located almost at midlength on inner margin. All ambulatory pereiopods with markedly serrate and setose dorsal and especially ventral margins. Propodus of pereiopod 4 at least 2.5 times longer than wide.

Description of holotype.—Carapace (Fig. 1a, b) two times wider than long, surface with numerous granules and scattered, short setae. Carapace highly sculptured, with areolations distinct and defined by deep grooves. Frontal margin with deep median cleft. Anterolateral margins broadly arcuate, with pronounced ridge bearing well developed acute teeth, each tooth curved slightly to anterior. Subhepatic region of carapace just lateral to orbits bearing small but obvious tooth (arrow, Fig. 1a; more pronounced in juvenile paratype, Fig. 1c). Gastric depression deep. Cardiac ridge well developed but granular, obtuse, not acute, slightly bilobed.

Chelipeds (Figs. 1a, 2) slightly dimorphic, left larger. Fixed finger slightly deflexed, nearly ½ length of palm. Opposing borders of dactylus and fixed finger of each cheliped with pronounced tooth at approximately midlength and with row of small transparent teeth merging distally into thin sharp ridge along cutting edges (Fig. 2b). Palm with scattered short setae and granules on outer surface and serrate ridge on dorsal border. Carpus and merus (Fig. 2c) with well developed acute teeth on dorsolateral and dorsodistal surfaces.

Ambulatory pereiopods (Fig. 1a, where ambulatory pereiopods are denoted by P2–P5) long and relatively slender compared to those in most other species of genus. Each leg with well developed row of teeth along dorsal and ventral borders of merus, carpus, and propodus, less obvious on carpus. Dactylus of each ambulatory leg more or less straight, slightly bent to flexor side on pereiopods 2 through 4, to extensor side on pereiopod 5. All articles with combination of scattered short plumose and simple setae. Pereiopod 4 (third walking leg) longest, with propodus 2.6 times longer than wide. Propodus of pereiopod 4 with ventral margin bicarinate, each carina serrate. Dactylus of pereiopod 4 slightly longer than propodus. Tip of dactylus on each walking leg not strongly curved.

Third maxilliped as figured (Fig. 1d), typical of genus. Endopod with short distally plumose setae on merus and carpus and with long smooth or sparsely setulose setae on distal half of dactylus and propodus; distal border of carpus with thick, brush-like tuft of setae. Proximal article of exopod with obvious lateral protrusion at approximately midlength and plumose setae along lateral border.

Abdomen (Fig. 1e) broadly rounded, well developed, setose, consisting of 7 free segments, only distalmost 5 visible in ventral view (Fig. 1e). Pleopods mature, well developed, and setose.

Male unknown.

Juvenile paratype (Fig. 1c).—Similar to holotype in the serrate anterolateral border and possession of subhepatic tooth. Ambulatory pereiopods also similar to those of holotype. Paratype differs from holotype in having a slightly reduced carapace width : length ratio (a difference that we attribute to normal ontogenetic changes), a slightly more produced front, and a slightly more pronounced subhepatic tooth relative to carapace size (arrow, Fig. 1c).

Type locality.—Western Santa Barbara Channel, SSW of Pt. Arguello, California, 34°29.040′N, 120°44.013′W, 311 m, soft bottom.

Distribution.—Known only from the type locality.

Etymology.—The species name originates from an acronym being used as a noun in apposition. We are pleased to take the name of this species from SCAMIT, the acronym for the Southern California Association of Marine Invertebrate Taxonomists, a largely unheralded organization of professional biologists that has done much to further our knowledge of marine invertebrates in southern California.

Remarks.—Most California species of *Pinnixa* White, 1846, have a ridge, which may be granular to tuberculate, along the anterolateral margin of the carapace. Exceptions include *P. faba* (Dana 1851), *P. longipes* (Lockington 1876), *P. tubicola* Holmes, 1894, and *P. weymouthi* Rathbun, 1918, where an anterolateral ridge is either absent or at best very weakly developed; and *P. forficulimanus* Zmarzly, 1992, *P. minuscula* Zmarzly, 1992, and *P. littoralis* Holmes, 1894, where it is absent (Zmarzly 1992). In the remaining California species of *Pinnixa,* this ridge is obvious in dorsal view, and is sometimes as pronounced as in *P. scamit.* However, in none of the adults of these species are the individual anterolateral teeth as sharp or as anteriorly curved as in *P. scamit.* Juvenile stages of two species, *P. occidentalis* Rathbun, 1893, and *P. franciscana* Rathbun, 1918, sometimes exhibit acute teeth on the anterolateral ridge; however, this feature changes dramatically between the juvenile and adult stages. In addition, *P. scamit* has relatively slender legs with acute marginal serrations as an adult, which is also characteristic only of juvenile stages in *P. occidentalis* and *P. franciscana.* Thus *P. scamit* appears to have retained several "juvenile" characters in the adult stage.

All other California species are easily distinguished from *P. scamit* by the length : width ratio of the propodus of pereiopod 4. In true *P. occidentalis* Rathbun, the species to which *P. scamit* appears to be most closely allied, the propodus of P4 is distinctly broader, nearly as broad as long. In contrast, in *P. scamit* the propodus of pereiopod 4 is approximately 2.6 times longer than wide.

The geographic range is of little help in determining species affinities; the collecting locality of *P. scamit* is within the range of nearly all of the 13 California species of *Pinnixa* listed by Zmarzly (1992, fig. 1), including the wide ranging *Pinnixa occidentalis.* It is unfortunate that we do not have a male specimen, as gonopod morphology would undoubtedly help clarify the relationship between *P. scamit* and other California species. The species also shares certain morphological similarities with *Pinnixa affinis* Rathbun, 1898, known only from 26 fm (47.5 m) in Panama Bay (see Rathbun 1918: 168), but can be distinguished by the more deflexed major chela in *P. affinis* (see Rathbun 1918: fig. 106).

The extent to which some systematically important morphological characters vary in California species of *Pinnixa* is not known. A detailed knowledge of such characters as the morphology of the orbits, eyes, epistome, antennae, and mouthparts, apparently useful in resolving placement within pinnotherid species complexes in other geographic areas, is at present lacking. In-depth study of these features may resolve some of the questions of relationships within the *P. occidentalis* complex.

If the key to California species of *Pinnixa* given by Zmarzly (1992: 678) is employed, then the new species would key to *P. occidentalis.* For separation of the species, we suggest insertion of the following couplet, to replace couplet 8 in Zmarzly's key.

8. Fixed finger of chela straight or curving upward, not deflexed . . . . 9 (as in original key)
– Fixed finger of chela deflexed, angled obliquely downward relative to line delineated by ventral margin of palm (deflection stronger in males than in females) 8A
8A. Length of propodus of pereiopod 4 at least 2.5 times width . . . . *P. scamit,* new species
– Length of propodus of pereiopod 4 approximately 1.5–2.0 times width *P. occidentalis* Rathbun, 1893

Acknowledgments

This manuscript resulted from a 1993 meeting of the Southern California Association of Marine Invertebrate Taxonomists (SCAMIT). We are grateful to the members of that organization for their assistance and for their consistent dedication to marine invertebrate systematics. We also thank Dr. George C. Steyskal for his invaluable help and advice concerning our choice of a specific epithet.

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STUDIES OF NEOTROPICAL CADDISFLIES, L: THE DESCRIPTION OF *CERASMATRICHIA,* NEW GENUS, A RELATIVE OF *ALISOTRICHIA,* WITH DESCRIPTIONS OF NEW AND OLD SPECIES AND THE LARVA (TRICHOPTERA: HYDROPTILIDAE)

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Abstract.—*Cerasmatrichia,* new genus (type species *C. trinitatis*), is established and defined in the adult and larval stage. *Alisotrichia dominicensis* Flint, *A. wirthi* Flint and *A. adunca* Flint are transferred thereto, and their males and females redescribed. *Cerasmatrichia spinosa* (Venezuela), *C. argylensis* (Tobago, Trinidad), *C. trinitatis* (Trinidad), are newly described in the male and female sexes; the larva of the first is firmly established by metamorphotypes, and therefore used as the basis for the generic level description of the larva (modified if necessary to include the larvae of species A–E). Larvae and females of an additional six species serve to extend the range of the genus to Costa Rica, south to Peru, east through Venezuela and north in the Lesser Antilles to Guadeloupe.

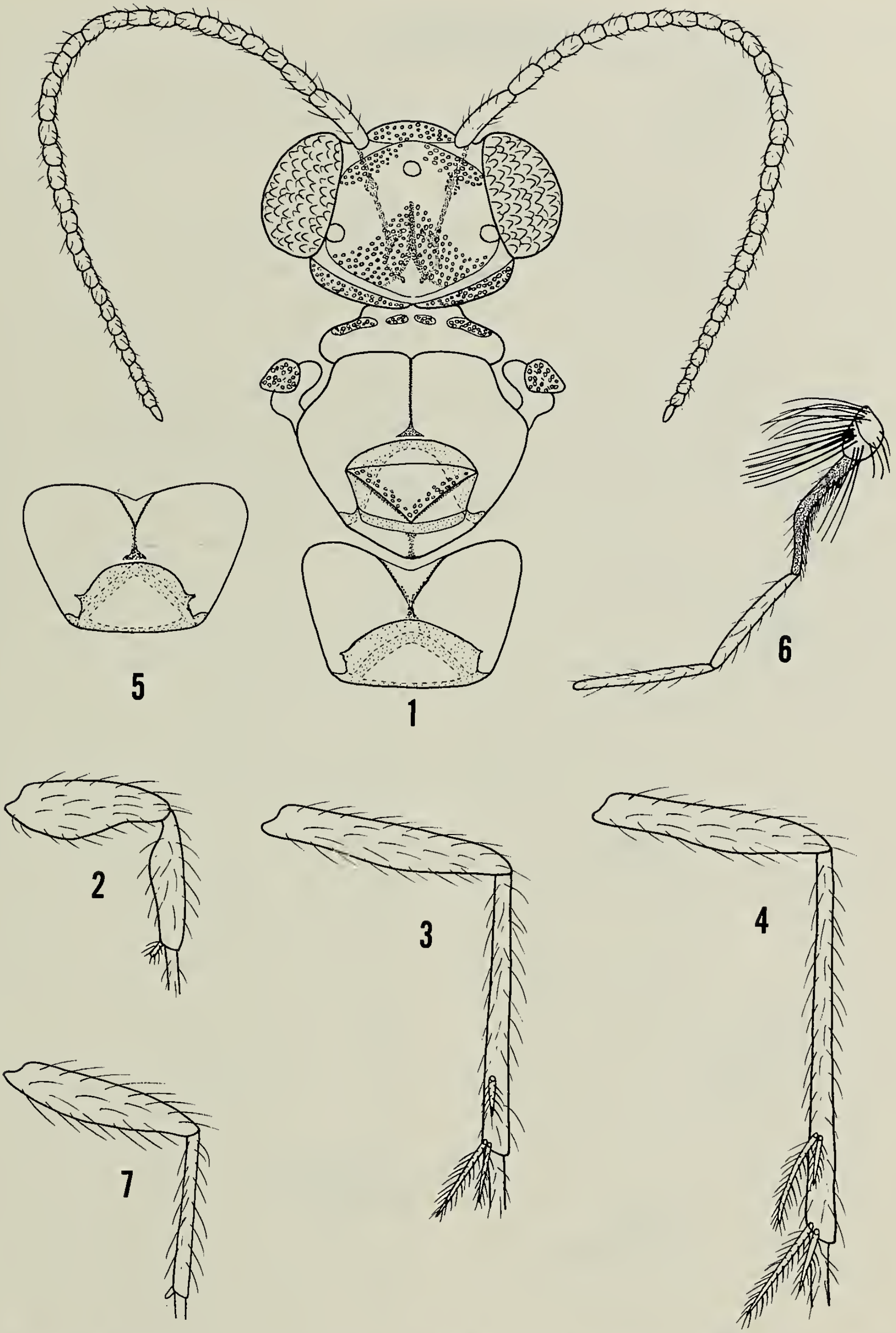
Since the genus *Alisotrichia* was described in 1964 for a Puerto Rican species, the genus has grown to 32 species and become very heterogeneous. As part of studies by the first two authors on the definition and limits of the tribe Stactobiini in the New World, we have been attempting to define natural groups in this melange, and when warranted, establish new genera for them (e.g., Harris & Holzenthal 1993, Harris & Bueno 1994). One of the most obvious groups centers around *A. dominicensis* Flint, which is the focus of this study. The recent discovery of several undescribed species by the third author, and the firm association of the larval stage has confirmed the distinctiveness of this assemblage of species. We are here establishing the new genus *Cerasmatrichia,* redescribing three species transferred thereto, describing three newly discovered species, and the larval stage.

Material is deposited in several museums as indicated by the following acronyms: IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels; NMNH, National Museum of Natural History, Washington D.C.; IZAM, Instituto de Zoologia Agricola, Maracay, Venezuela; UWI, Department of Zoology, University of the West Indies, St. Augustine, Trinidad; ZMUA, Zoölogisch Museum, Universiteit van Amsterdam, Amsterdam.

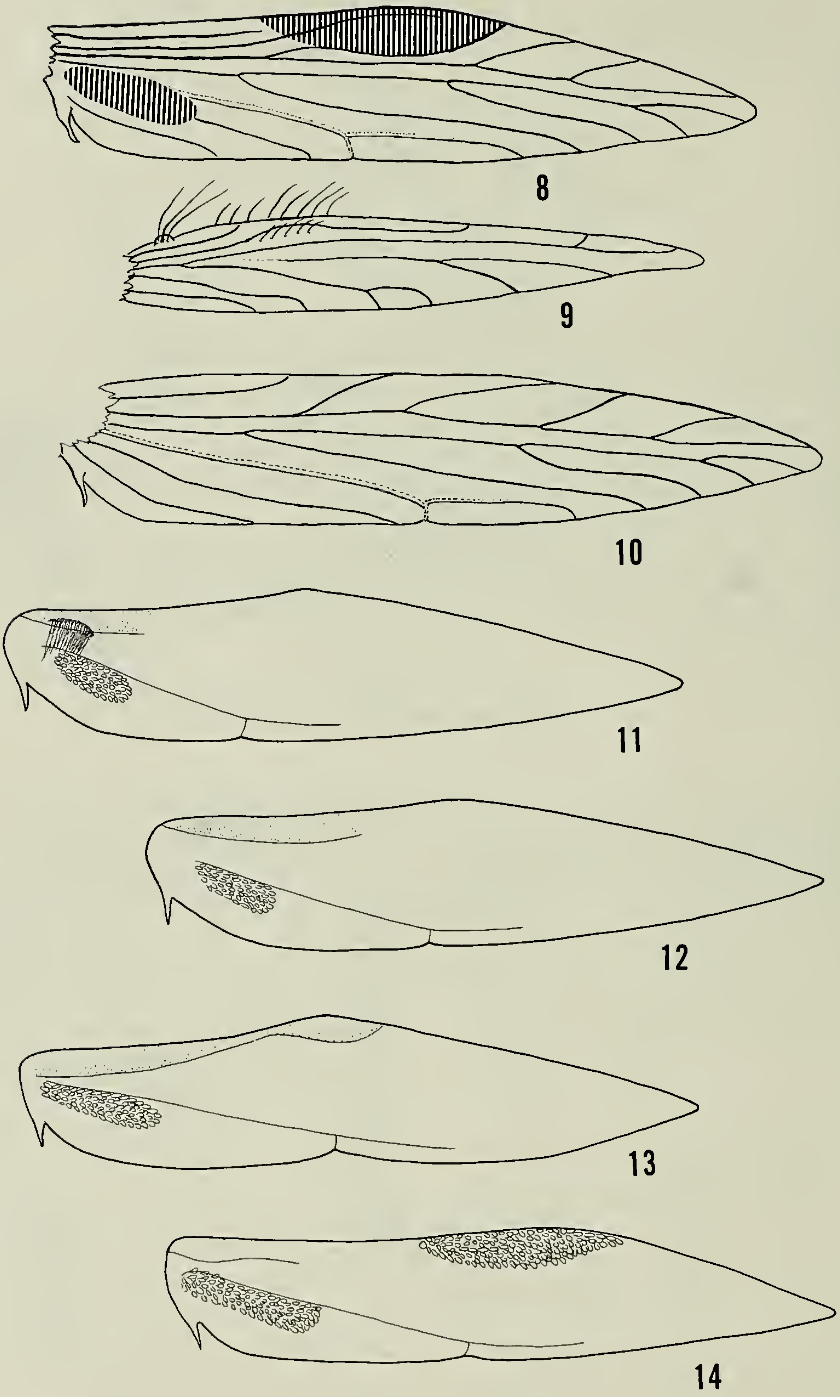
Genus *Cerasmatrichia,* New Genus

Type Species.—*Cerasmatrichia trinitatis* new species.

Adult (Figs. 1–14).—Of moderate size, forewing length 2–3 mm; color generally fuscous, sometimes with indistinct whitish maculae. Head with 3 ocelli. Antennae simple, scape elongate, with 25–35 segments in male, 22–26 in female. Maxillary palpus with 5 segments: 2 basal segments very small, globular, 3 remaining segments of equal length, each 3–4 times as long as basal



Figs. 1–7. 1–4, *Cerasmatrichia trinitatis,* adult. 1, head and thorax, dorsal; 2, fore femur and tibia; 3, mid femur and tibia; 4, hind femur and tibia. 5–7, *C. wirthi,* adult. 5, metanotum, dorsal; 6, maxillary palpus; 7, fore femur and tibia.

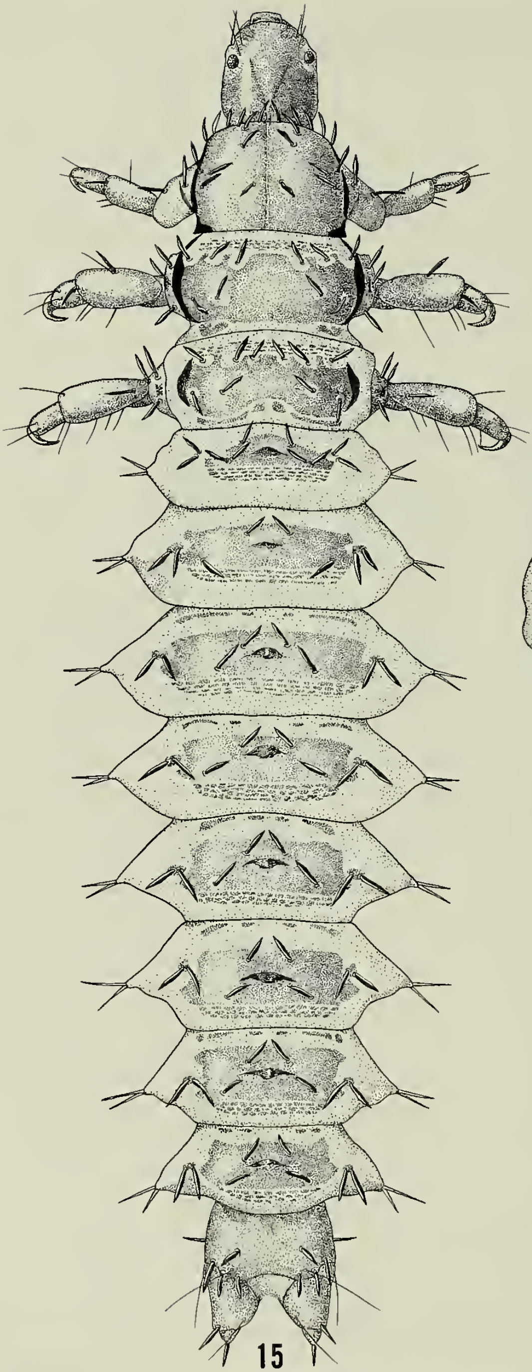


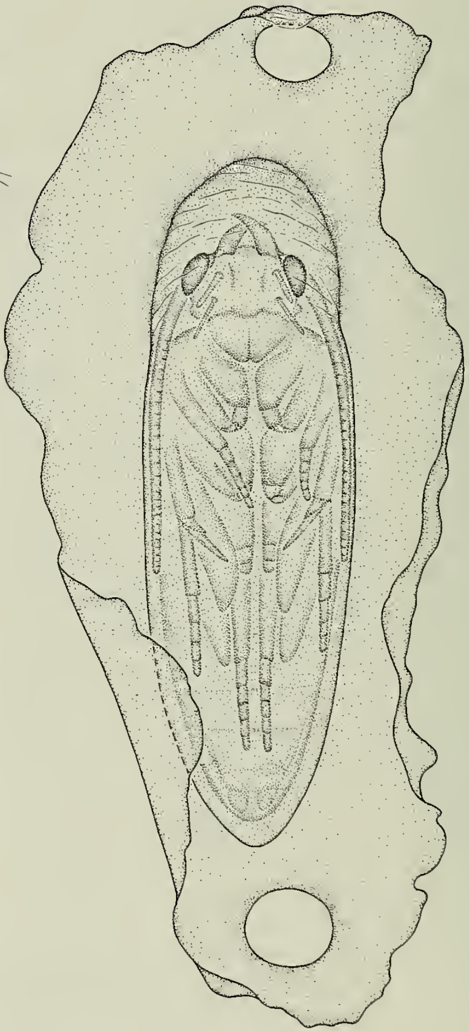
Figs. 8–14. 8–10, *Cerasmatrichia trinitatis,* wings. 8, forewing venation, male; 9, hindwing venation, male; 10, forewing venation, female. 11, *C. wirthi,* male forewing schematic showing modified areas. 12, same of *C. dominicensis.* 13, same of *C. argylensis.* 14, same of *C. trinitatis.*

2; labial palpus 3-segmented. Tentorial bridge divided mesally. Wings with reduced venation; forewing with small, pointed basal lobe, CuP (?) with pale, fracture-like line bordering its anterior side in both male and female; forewing in male with leathery, modified posterobasal and often costal areas bearing specialized setae; hindwing narrow, attenuate. Mesoscutellum with transverse suture; metascutellum with anterior margin strongly convex, truncate laterally. Spur on foreleg very short and lightly sclerotized, smaller in female than male (often unobservable except under highest magnification); 3 spurs on midleg; 4 on hindleg. Seventh sternum in most males with short, fat lobe; females rarely with small point on sixth sternum. Males have eighth sternum large, projecting posteroventrally, with small spines posteroventrally; tergum smaller, roughly quadrate. Ninth segment produced anterolaterally, thus mostly open dorsally and ventrally, sometimes with ventrolateral lobate process. Tenth tergum variously formed, with paired lateral sclerites, spines, or single mesal process. Inferior appendages usually divided into two arms: one more slender and arising and curving ventrolaterally, other usually broader and directed dorsomesally. Subgenital plate strong, projecting posteriad. Phallus with narrow basal section and broader, tubular apical portion; with rather simple, internal, tubular ejaculatory duct. Female genitalia with simple, conical seventh sternum; tergum produced into pair of posterolateral, darkened, hirsute lobes. Eighth segment simple, tubular, rarely somewhat ornamented, or with posterolateral lobes dorsally, with long, slender anterolateral apodemes and ring of stout setae along posterior margin. Ninth segment slender, elongate, sclerotized laterally, with long, slender, anterolateral apodemes. Tenth segment small, lightly sclerotized, narrowed apically with pair of slender apicolateral papillae. Vaginal sclerites complex, with small, spherical sclerite pierced by central opening, sometimes with strong anterior plate with projecting teeth, often with only membranous sacs variously sclerotized in certain species.

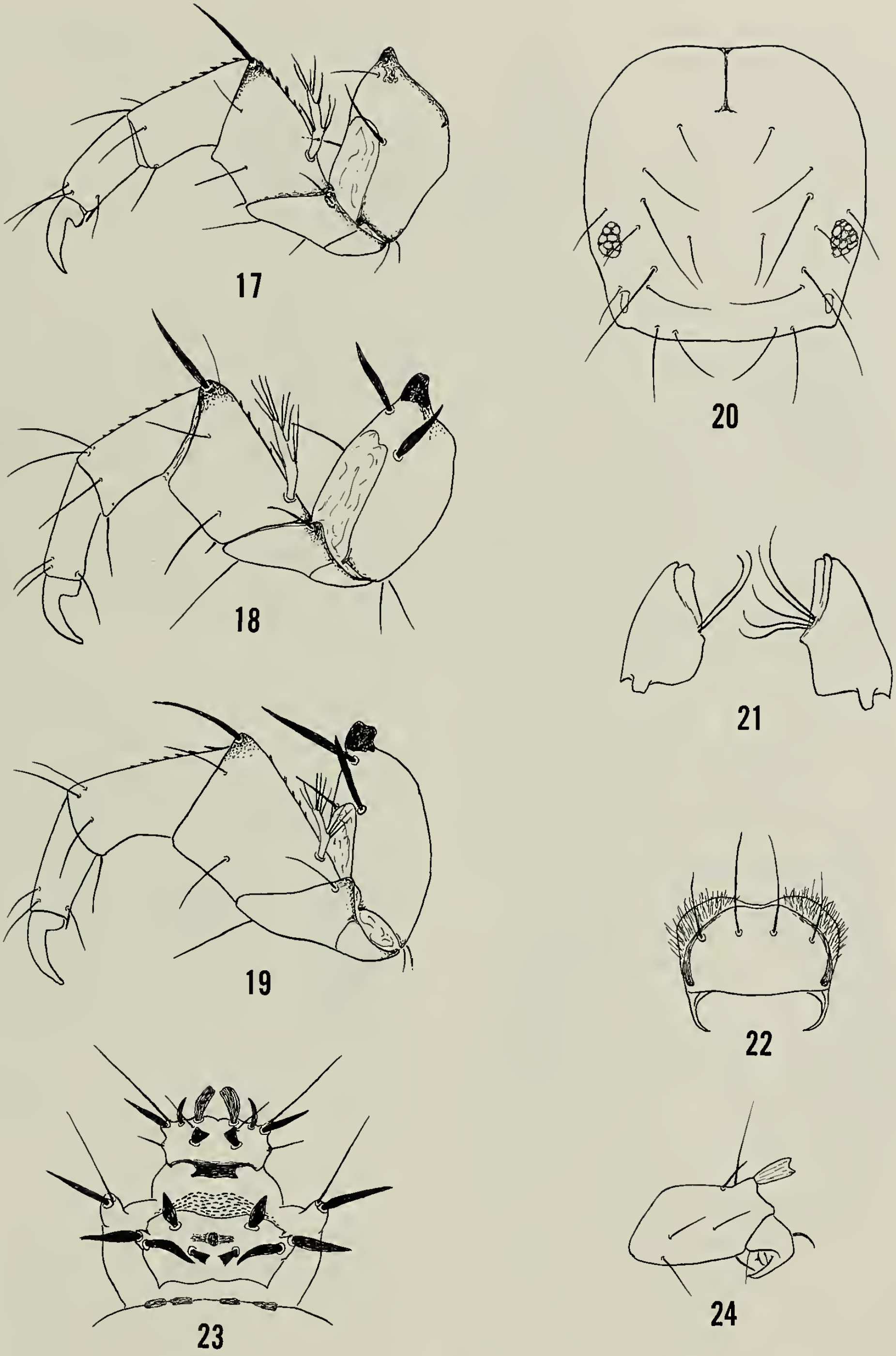
Larva (Figs. 15–24).—Length, 3.5–5 mm. Head pale brown, unpigmented around eye and ventrally, slightly elongate, coronal suture weak, other sutures lacking. Head with several setae quite prominent, especially anteriorly; antenna elongate. Labrum about twice as wide as long, with anterolateral membranous lobe, densely hairy, 2 pair of major setae clearly visible dorsally. Mandibles short, broad, slightly concave apicomesally with 2 or 3 weak cusps; each with median brush of several long setae. Pronotum divided longitudinally, meso- and metanota entire; all with many small, dark points; bearing numerous, enlarged setae arising from large pale cuticular spots. Meso- and metanota each with small, secondary sclerites along posterior margin and region of rugosities along anterior margin. Meso- and metapleura each with 2 of these large setae arising from short protuberance; propleuron with only posterior seta, trochantin small, pale, conical with small seta. All legs short, stout, virtually identical; middorsal seta of each femur enlarged, feathered; dorsal surfaces of femora and tibiae roughened (in some species each point is seen to bear small seta); claw without evident seta. First to ninth abdominal terga with large sclerites, those on one to eight each with transverse, central, dark area and several, large, dark setae. Row of small sclerites between tergites and row of rugosities along posterior margin. First to eighth segments each with conical lobe laterally capped by small sclerite bearing pair of large setae, one dark, other smaller and pale; ninth tergum with large shield-like sclerite bearing number of setae. Anal prolegs short, each with several slender setae and large apicomesal, pale blade; claw hooked sharply ventrad.

Distribution.—Examples are known from about 10°N in Costa Rica south along the mountains to 13°S in Peru, and east across northern South America to south-central





Figs. 15–16. 15, *Cerasmatrichia* species B, larva, dorsal. 16, *C. spinosa,* pupa and case, ventral.



Figs. 17–24. *Cerasmatrichia spinosa,* larva. 17, foreleg; 18, midleg; 19, hindleg; 20, head; 21, mandibles; 22, labrum; 23, eighth and ninth terga; 24, anal proleg.

Venezuela (Puerto Ayacucho), and north along the Lesser Antilles to Guadeloupe.

Biology.—All species are rheophilous, with larvae found either near the waterline on boulders in fast flowing rivers and small streams or on the rocks in madicolous habitats. Adults have rarely been taken at ultraviolet light at night in large numbers, usually they are taken in rather small numbers at light or by net in the day.

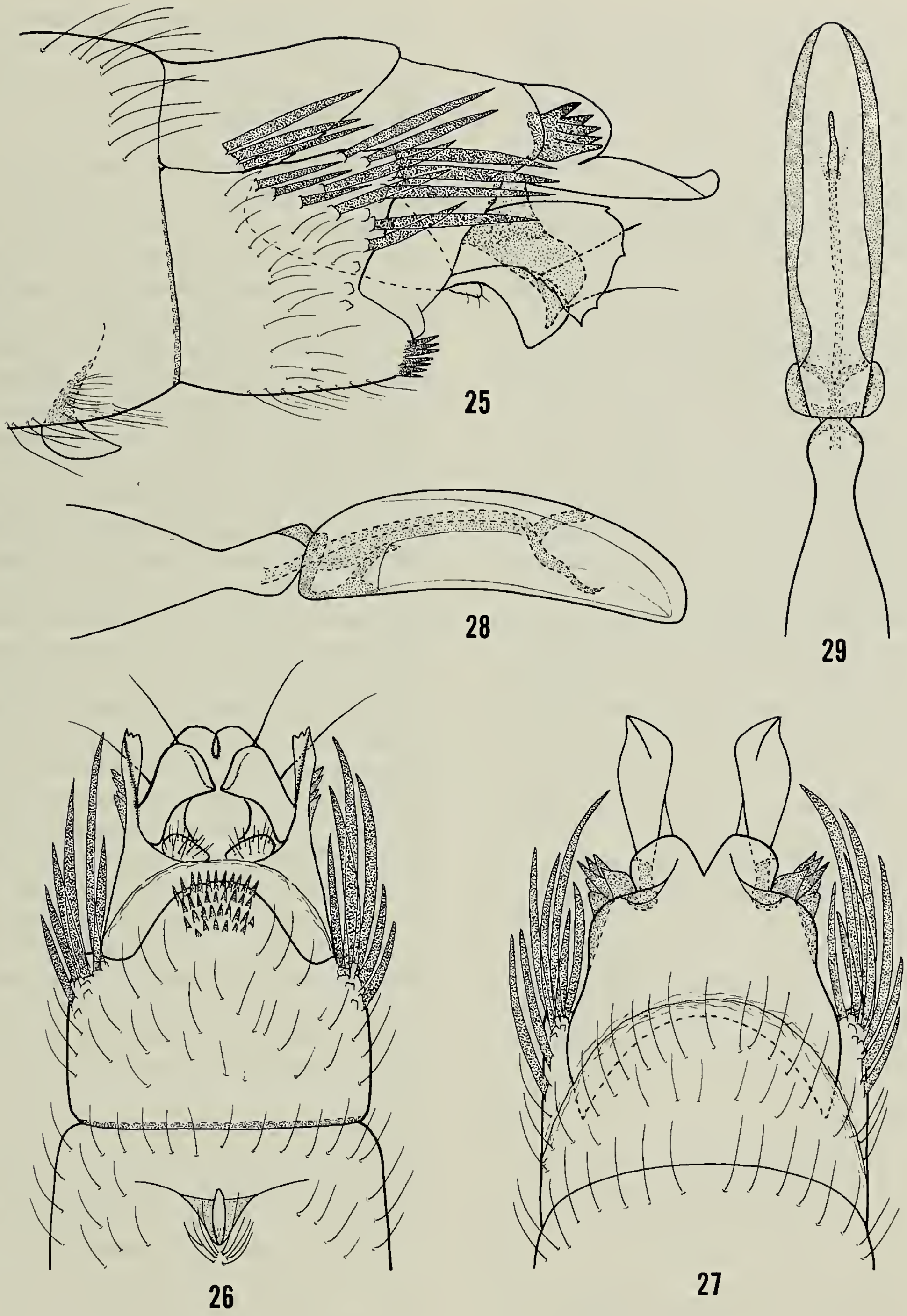
The larvae are free-living until near pupation time. The pupae and their shelters of the two available collections are nearly identical. There is a thin, dorsal, sheetlike covering, beneath which (next to the substrate) is an oval, firmly spun cocoon within which is found the pupa (Fig. 16). Strangely, the dorsal covering is pierced both anteriorly and posteriorly by a large circular opening; this dorsal sheet is thus like the covering of the final instar larvae of the Leucotrichiini. The inner cocoon is attached along the middorsal line to the dorsal sheet, except at the head end where it is broadly attached. When the pharate adult emerges it uses its mandibles to cut a circular opening dorsally, the silken flap is left attached by a small strap left uncut on the posterior side.

Remarks.—A preliminary cladistic analysis of the species originally placed in *Alisotrichia* is presented by Harris & Holzenthal (1993). In it the *dominicensis* group was clearly defined and separated from the other recognizable groups in *Alisotrichia* s.l. The retention in the group of the plesiomorphic state of tibial spur present on foreleg serves to distinguish the group from the sister lineage in which this spur is lost. As shown herein, this spur is greatly reduced and well on the way to total loss even in *Cerasmatrichia.* However, they did propose 3 synapomorphies to define the group which still seem valid: female seventh tergum (mistakenly called VIII tergum) with paired setal patches, male eight sternum with patch of heavy spine posteromesally, and ejaculatory duct of phallus protruding ventrally. Probably many of the larval structures mentioned above are synapomorphic, but it would be premature to infer phylogeny based on them while evidence is still lacking from larvae of many other groups. However, considering what is known of this stage in other species, it is suggested that some (or all) of the following are likely larval synapomorphies: elongate, fusiform shape; the presence of enlarged, swordlike setae on the thorax and abdomen; a large, dorsal, fimbriate seta on each femur; and the large, conical lateral protuberances on the abdomen which are capped by a sclerite bearing two large setae. In addition, the presence of 3 ocelli, unmodified antennae, spur count of 1 (but virtually lost), 3, 4, and modified forewing structure in the males will help differentiate the species from various other groups in *Alisotrichia* s.l.

Warning should be given concerning some of the differences apparent in the illustrations of the female genitalia. The seventh tergum appears to show small differences in shape between the various species. The comparative widths and lengths are greatly dependant on the degree of flattening, rotation and orientation of the specimen. It is presently deemed unwise to use this segment alone to identify the species. Likewise the apparent differences in the transverse, rake-like bar of *C. wirthi* and *C. adunca* are due to orientation. This plate can be artificially rotated in either species to produce the aspect shown in the figure of the other.

Key to Described Species

1. Males with process from seventh sternum, hooked in lateral aspect (Fig. 25). Female vaginal apparatus consisting of a spherical sclerite and possibly other sclerites more posterior (Fig. 40) (*dominicensis* group) 2
   Males lacking process from seventh



Figs. 25–29. *Cerasmatrichia spinosa,* male genitalia. 25, lateral; 26, ventral; 27, dorsal; 28, phallus, lateral; 29, phallus, dorsal.

sternum (Fig. 57). Female vaginal apparatus consisting of spherical sclerite and a more anterior, transverse, rake-like sclerite (Fig. 40) (*wirthi* group) 5

2. Male tenth tergal area without spines, with a long, central strap-like sclerite (Fig. 32). Female vagina with only a spherical sclerite (Fig. 37). . ... *dominicensis*

   Male tenth tergal area bearing either a pair of divergent pointed processes (Fig. 43) or clusters of spines (Fig. 27). Female vagina with a spherical sclerite (Fig. 56), and often a more posterior, complex sclerite (Fig. 40) 3

3. Male tenth tergum consisting of a pair of divergent, pointed processes (Fig. 43). Female vagina with only a spherical sclerite (Fig. 56) *argylensis*

   Male tenth tergum with many spine-like processes (Fig. 27). Female vagina with both spherical sclerite and a more posterior sclerite (Fig. 40) 4

4. Male tenth tergum basolaterally with a cluster of short spines (Fig. 27); eighth sternum laterally with many, enlarged setae (Figs. 25, 26, 27). Female eighth sternum lightly sclerotized and longitudinally striate (Fig. 38) .... *spinosa*

   Male tenth tergum consisting of 6 pairs of long, slender spines (Fig. 48). Female eighth sternum with ventral, lateral and dorsal sclerotized areas distinct and not striate (Fig. 51) .... *trinitatis*

5. Male tenth tergum consisting of pair of diverging, tapering sclerites whose apices end in sharp point (Fig. 57). Female indistinguishable from following species .... *wirthi*

   Male tenth tergum consisting of pair of broadly oval sclerites whose apices are narrowed and compressed (Fig. 63). Female similar to preceding species .... *adunca*

Cerasmatrichia spinosa, new species

Figs. 16–29, 38–40

Alisotrichia wirthi Flint.—Flint, 1981:26 [misidentification, in part].

This is a readily identifiable species in both the male and female. The male of no other species bears a cluster of short, fat setae basolaterally on the tenth tergum, which is then continued as a pair of lateral, rodlike plates, nor does any other species have the cluster of enlarged setae dorsolaterally from the eighth sternum. The female genitalia show a lightly striate surface to the eighth segment, and the posterior vaginal apparatus is distinctively sclerotized.

Adult.—Length of forewing 2.3 mm. Coloration in alcohol, mottled brown (probably mottled fuscous in life). Male with apparent sexual modifications: 3rd segment of maxillary palpus bearing modified setae mesally; fore coxa with patch of modified setae basolaterally, femur slightly inflated basally, otherwise unmodified; forewing with large basal pocket and marginal cell of scale-like hairs (as in Fig. 8). Male seventh sternum with strong process; female sixth sternum bearing small point. Male genitalia. Eighth sternum with dorsolateral corner produced as large angulate lobe and bearing cluster of long, enlarged spines, mesally produced with cluster of small spines. Ninth segment widely open dorsally and ventrally, strongly produced anterolaterally as rounded lobe. Tenth tergum developed on each side as rounded, convoluted basolateral lobe bearing cluster of short, very broad setae from which cluster arises elongate rodlike sclerite with slightly twisted tip. Inferior appendage with large lateral, lightly sclerotized plate (or possibly this is an extension of lateral margin of ninth segment); elongate and broad mesal plate with apex curved slightly ventrad, with small basal, membranous lobe. Subgenital plate long, arising ventrolaterally from basal area of tenth tergum, tip hooked ventrad, appearing as darkened ovoid in ventral aspect. Phallus with tubular basal portion, and enlarged, more membranous, apical portion separated by sharp constriction; apical portion with central ejaculatory and some basal, internal sclerites. Female genitalia. Eighth segment lightly sclerotized, surface striate; posterior row of stout setae. Vagina with anterior spherical sclerite; posterior area with elongate lightly sclerotized region bearing more heavily sclerotized lateral pockets.

Larva.—Length, 4 mm. Head pale brown, unpigmented around eye and ventrally. Pronotum with enlarged setae: anterior margin bearing row of 5–6 each side, behind margin submesal pair, at midlength submesal pair and 3 laterally, with scattered, small, dark points. Meso- and metanota with enlarged setae: anterior margin with 3 each side, midlength with 2 each side, with scattered small, dark points and point free areas. Dorsal surfaces of femora and tibiae roughened without evident seta. First to ninth abdominal terga with large sclerites, those on one to eight each with transverse, central, dark area; first tergum with 3, large, dark setae each side, second through eighth terga with 4 such setae (one extra seta in lateral cluster) each side. Row of small sclerites between tergites and row of rugosities along posterior margin of all segments. Ninth tergum with large shield-like sclerite bearing 3, enlarged, dark setae and 3 slender, pointed setae, each side.

Material examined.—Venezuela, Edo. Aragua, Río El Limón, fish hatchery, Maracay, 16 Feb 1976, C. M. & O. S. Flint, Jr., ♂ holotype, ♀ allotype, 13 ♂, 1 ♀ paratypes (all metamorphotypes), 51 prepupae, pupae and empty cases, 78 larvae (NMNH); same data, except 19–20 May 1975, F. H. Weibezahn, 1 ♂ paratype (IZAM).

Cerasmatrichia dominicensis (Flint), new combination
Figs. 12, 30–37

Alisotrichia dominicensis Flint, 1968:44; 1970:29.—Botosaneanu, 1989:97; 1990: 44 [Martinique].

Ochrotrichia (*O.*) species.—Flint & Sykora, 1993:58 [misidentification, Guadeloupe].

This is a readily identifiable species in the male. The male of no other species bears a single dorsomesal, sclerotized strap on the tenth tergum, which appears to be connected laterally into the subgenital plate which is directed straight down. The female, however, offers no clear-cut differences from that of *C. argylensis.*

Adult.—Length of forewing, 2 mm. Color fuscous; antennae and fore and mid tarsi cream colored, head anteriorly and mesonotum with white hair, forewings with white maculae basally and at midlength. Male with minor sexual modifications: 3rd segment of maxillary palpus seemingly unmodified; fore femur slightly inflated basally, otherwise unmodified; forewing with small midbasal area modified and bulging, costal area from base to midlength with membrane thickened. Male seventh sternum with strong process; female sixth sternum with small point. Male genitalia. Eighth sternum with posterolateral margin produced as large rounded lobe, posteromesally with cluster of small spines. Ninth segment widely open dorsally and ventrally, strongly produced anterolaterally as narrowly angled lobe. Tenth tergum developed as broad, lightly sclerotized region basally, abruptly narrowing into long, parallel-sided, heavily sclerotized, middorsal band with apex slightly hooked dorsad. Inferior appendage with lateral arm short, arising basolaterally from elongate mesal plate which is angulate apically; mesal arm twice as long as lateral arm, tapered to blunt apex in lateral aspect, slightly capitate and lobed in ventral aspect. Subgenital plate long, slender, arising ventrolaterally from basal area of tenth tergum, apex directed ventrad, tip appearing as darkened ovoid in ventral aspect. Phallus with tubular basal portion, and enlarged, more membranous apical portion separated by sharp constriction; apical portion with central ejaculatory and some basal, internal sclerites. Female genitalia. Eighth segment lightly sclerotized ventrally, unornamented; posterior margin with row of stout setae. Vagina with anterior spherical sclerite with small central opening; posterior area completely membranous.

Material examined.—Dominica: 2.2 mi E Pont Casse, 7 May 1964, O. S. Flint, Jr., 1 ♂ holotype (NMNH). 2.5 mi E Pont Casse, 16 Jan 1965, W. W. Wirth, 3 ♀ allotype and paratypes (NMNH). Fond Figues, 25 Jan 1965, W. W. Wirth, 1 ♂ paratype (NMNH). Morne Nicholls, 9 Nov 1964, P. J. Spangler, 1 ♀ paratype (NMNH). Martinique: Rivière Coco at Morne Vert, 14 Feb 1986, L. Botosaneanu, 1 ♂ (ZMUA). Ravine l'Abbé, Morne Vert, 3 Mar 1989, L. Botosaneanu, light, 1 ♂ (ZMUA). Guadeloupe: Basse Terre, Cascade aux Ecrevilles, 9 Apr 1992, L. Botosaneanu, 1 ♂ (ZMUA). Rivière Laurant, near Belleville, 8 Apr 1979, Starmühlner & Therezien, 1 ♀ (NMNH).

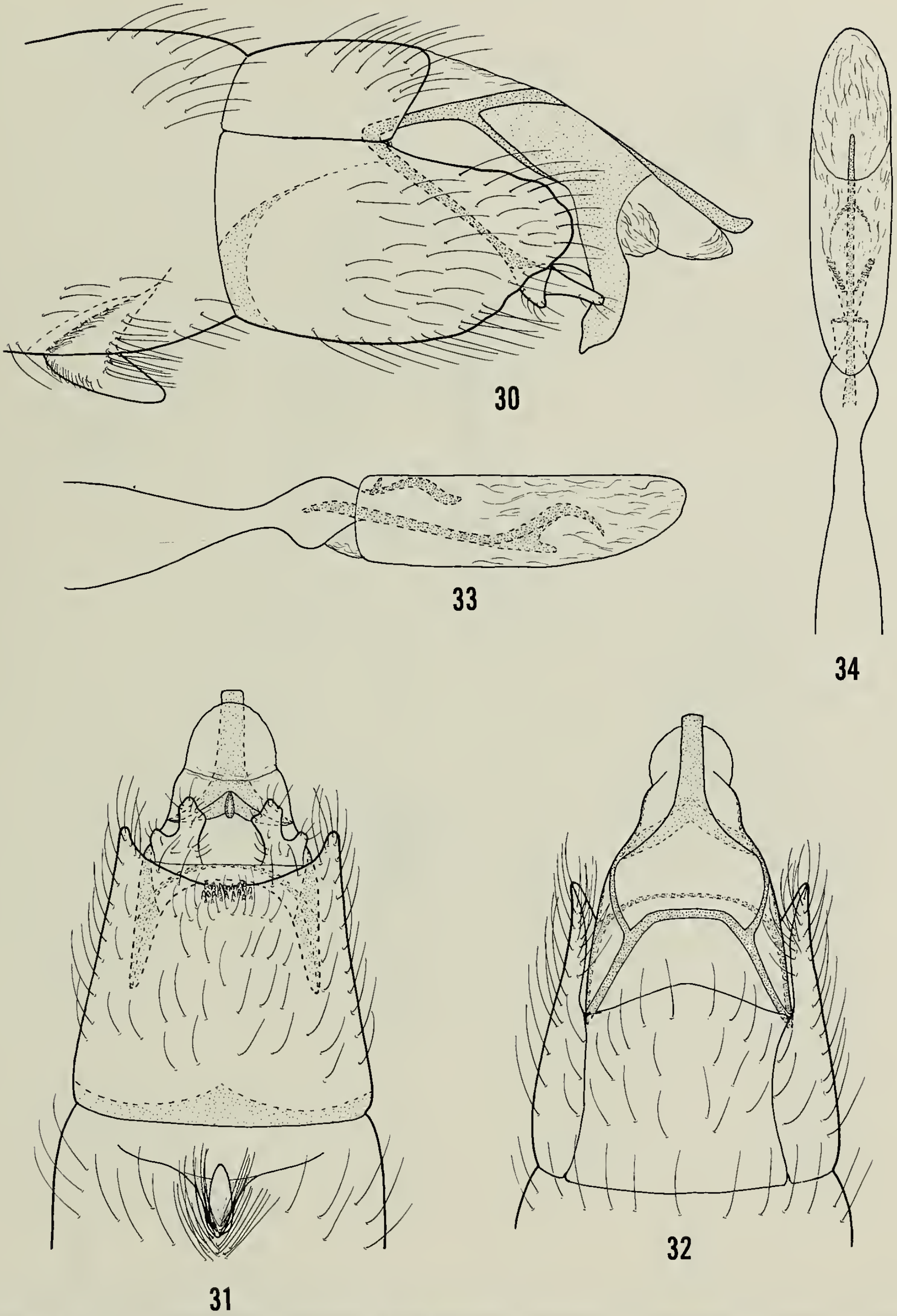
Cerasmatrichia argylensis, new species
Figs. 13, 41–45, 54–56

Hydroptilid genus, sp. 2, Botosaneanu & Sakal, 1992:201.

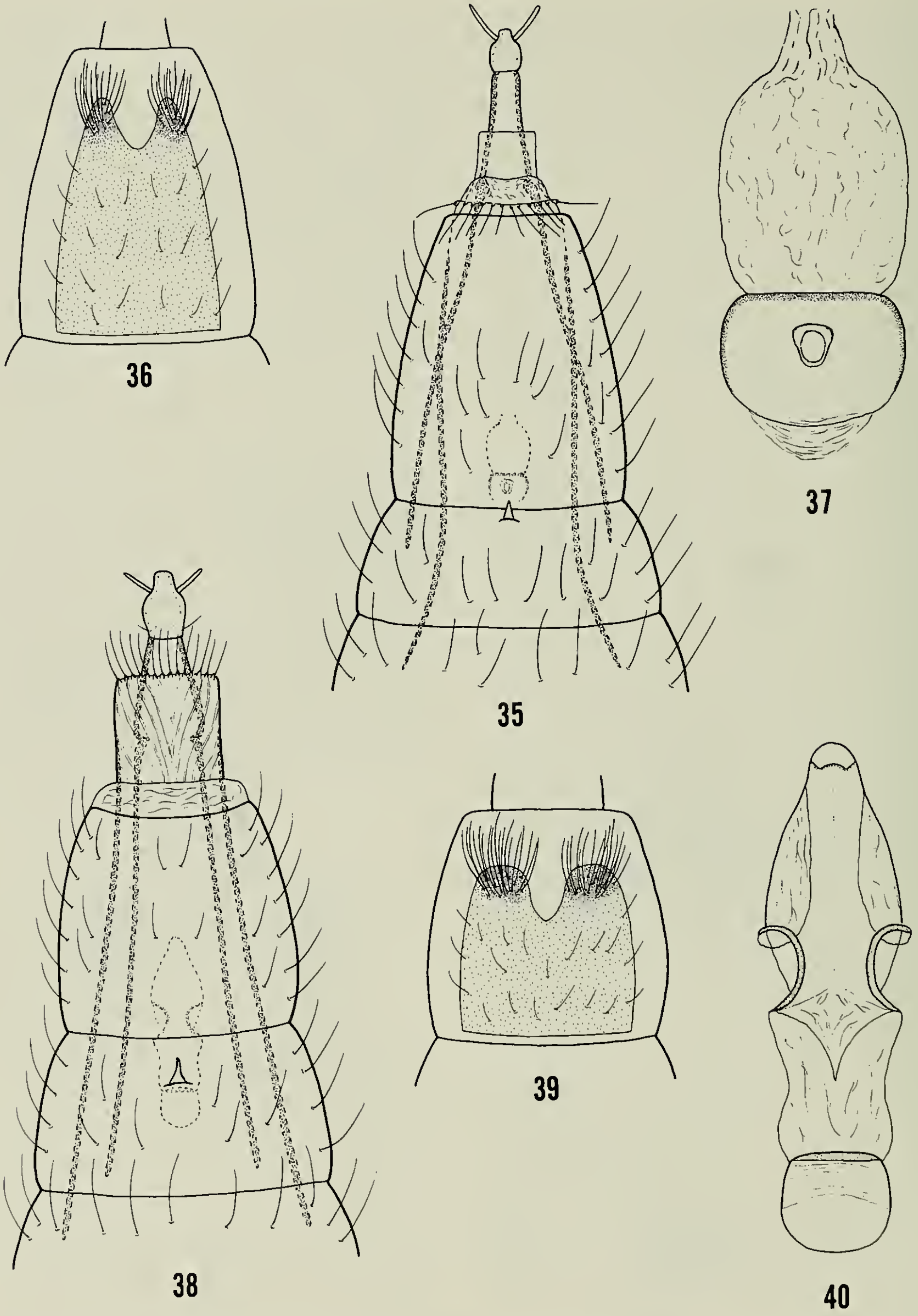
The species is readily recognized in the male sex by the tenth tergum developed into a pair of strong, divergent hooks. The female, however, can not be distinguished with absolute certainty from that of *C. dominicensis.*

Adult.—Length of forewing, 2 mm. Color of female fuscous; antennae and fore and mid tarsi cream colored, head with white hair anteriorly, mesonotum and forewings with indistinct, silvery-white maculae. Male with sexual modifications: 3rd segment of maxillary palpus slightly cupped, with concave face modified and bearing specialized setae; fore femur inflated basally, integument modified and bearing specialized setae; forewing with midbasal area modified and strongly bulging, costal area from base to midlength with membrane thickened. Male seventh sternum with strong process; female sixth sternum bearing small point. Male genitalia. Eighth sternum with posterolateral margin produced as large rounded lobe, posteromesally with cluster of small spines. Ninth segment widely open dorsally and ventrally, strongly produced anterolaterally as narrowly rounded lobe. Tenth tergum developed as pair of heavily sclerotized hooks with apices directed laterad. Inferior appendage with lateral arm terete, directed laterad; mesal arm bilobed and mitten-like in ventral aspect; setate lobe ventrally at junction of two arms. Subgenital plate long, slender, tip enlarged, decurved in lateral aspect, bilobed in ventral aspect. Phallus with tubular basal portion, and enlarged, more membranous apical portion separated by sharp constriction; apical portion with central ejaculatory duct extending through more sclerotized cavity. Female genitalia. Eighth segment lightly sclerotized ventrally, unornamented; posterior row of stout setae. Vagina with anterior spherical sclerite appearing transversely divided at equator; posterior area completely membranous.

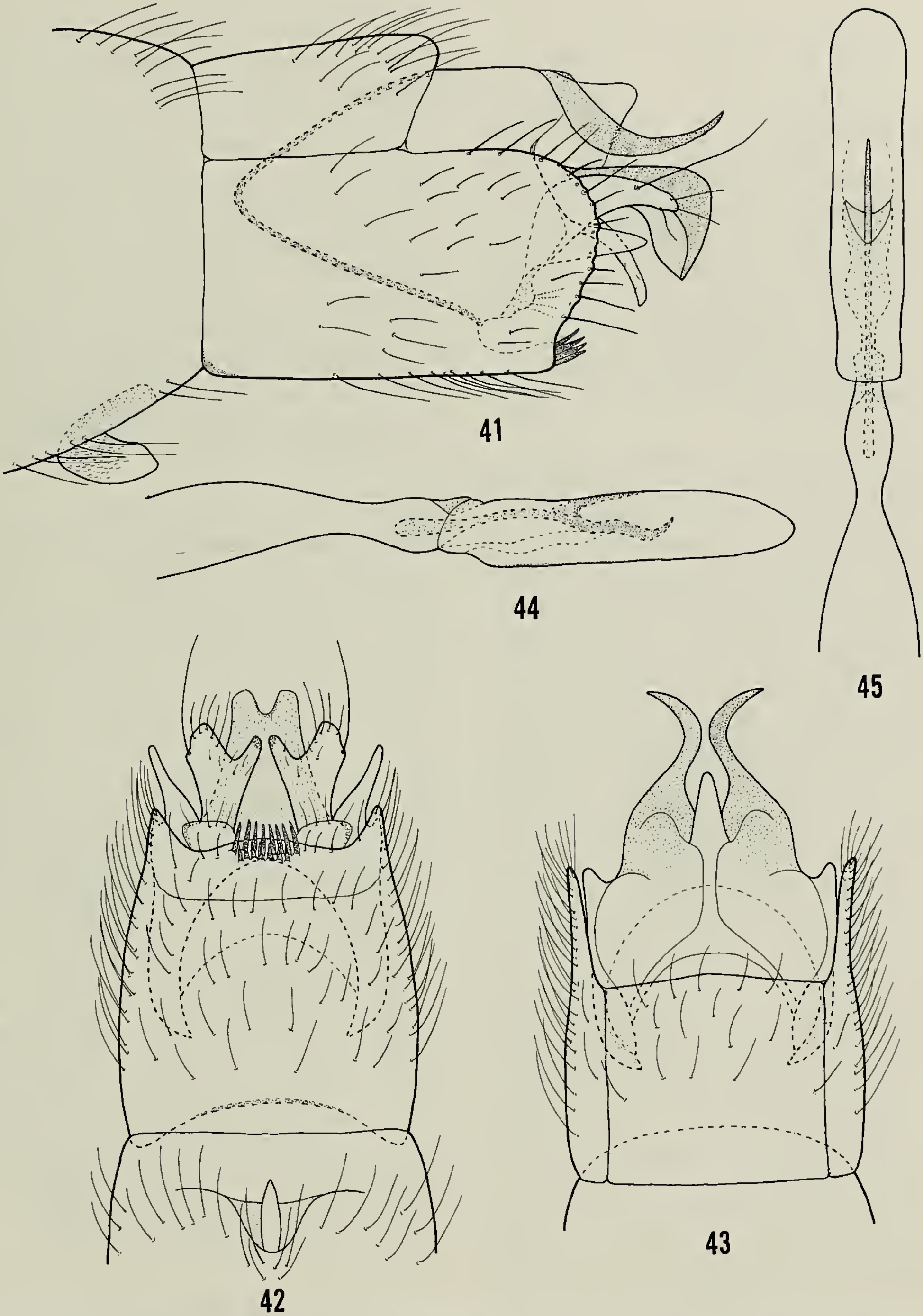
Material examined.—Tobago: [St. Paul Parish], Argyle River at Argyle Waterfall, 22 Apr 1991, L. Botosaneanu, Mary Alkins-Koo, M. Koo, at light: ♂ holotype, ♀ allotype, 1 ♂ paratype (ZMUA), 1 ♂ paratype (NMNH). [St. John Parish], 6.5 km N Roxborough [on Parlatuvier Rd.], B1/5 (11°17'N, 60°35'W), 15–16 Jun 1993, O. S. Flint, Jr., UV light, 1 ♂ paratype (NMNH); same, but 14 Jun 1993, O. S. Flint & W. N. Mathis, by net, 1 ♀ paratype (NMNH). 3 km S Charlotteville, WASA intake stream (11°19'N, 60°33'W), 125 m, O. S. Flint & N. E. Adams, UV light, 1 ♀ paratype (NMNH). Trinidad: [St. George County], Northern Range, below Maracas Waterfall (10°44'N, 61°24'W), 250 m, 18 Jun 1993, N. E. Adams & W. N. Mathis, 1 ♀ (NMNH).



Figs. 30–34. *Cerasmatrichia dominicensis,* male genitalia. 30, lateral; 31, ventral; 32, dorsal; 33, phallus, lateral; 34, phallus, dorsal.



Figs. 35–40. 35–37, *Cerasmatrichia dominicensis*, female genitalia. 35, ventral; 36, seventh tergum, dorsal; 37, vaginal sclerites, ventral. 38–40, *C. spinosa*, female genitalia. 38, ventral; 39, seventh tergum, dorsal; 40, vaginal sclerites, ventral.



Figs. 41–45. *Cerasmatrichia argylensis,* male genitalia. 41, lateral; 42, ventral; 43, dorsal; 44, phallus, lateral; 45, phallus, dorsal.

Cerasmatrichia trinitatis, new species

Figs. 1–4, 8–10, 14, 46–53

Hydroptilid genus, sp. 1, Botosaneanu & Sakal, 1992:201.

The species is readily recognized in the male sex by the very spinose tenth tergum, perhaps *C. argylensis* with its single pair of spines in this area is its closest relative. The female is also readily recognized as no other species has such a highly ornamented eighth segment, nor such a strongly sclerotized and complex posterior portion of the vaginal region.

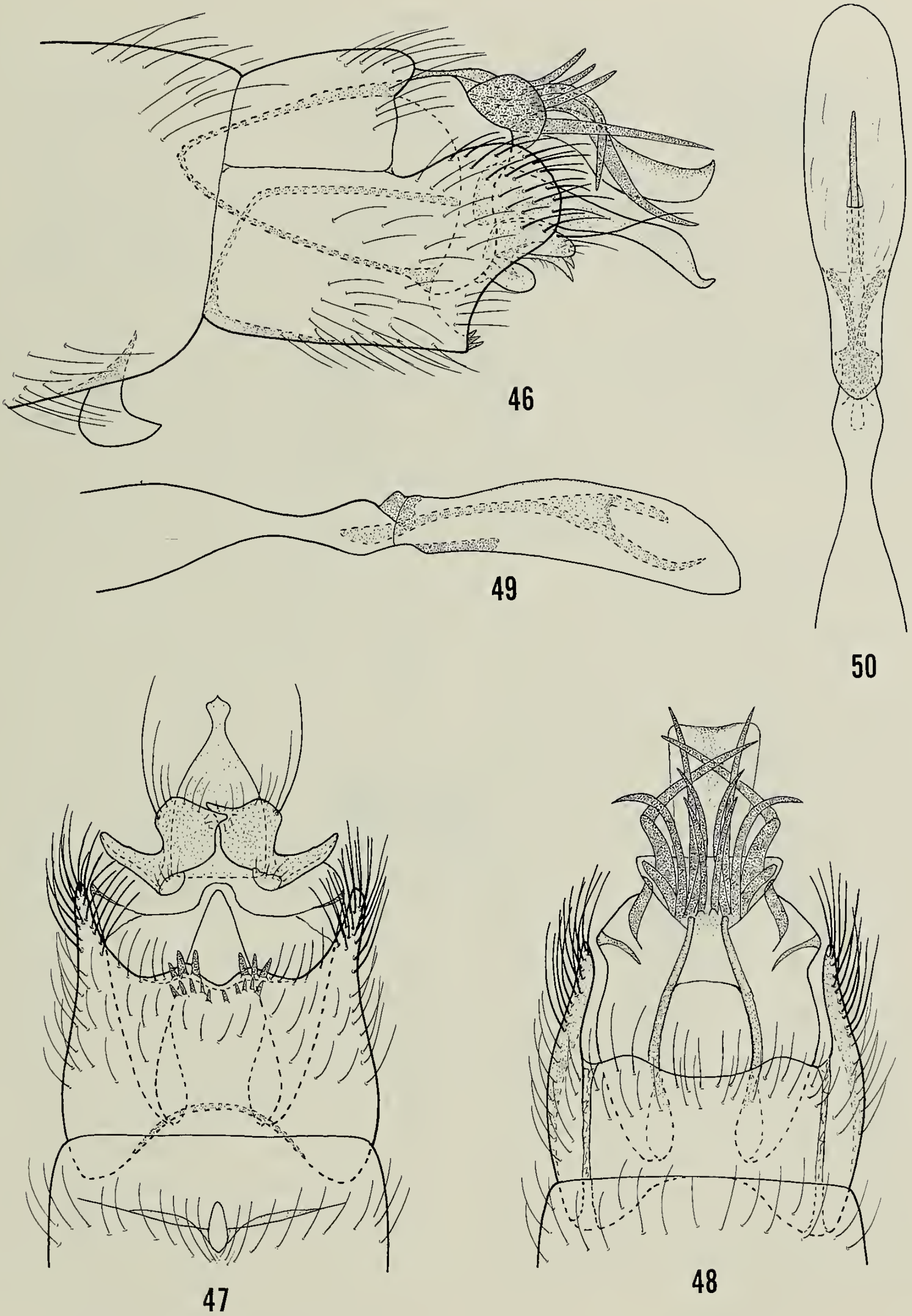
Adult.—Length of forewing, 2.5 mm. Color fuscous; antennae and fore and mid tarsi cream colored, head with white hair anteriorly, mesonotum and forewings with indistinct, silvery-white maculae; female paler overall. Male with sexual modifications: 3rd segment of maxillary palpus slightly cupped, with concave face modified and bearing specialized setae; fore femur inflated basally, integument modified and bearing specialized setae; forewing with mid-basal area modified and strongly bulging, costal area with membrane thickened. Male seventh sternum bearing strong process; female sixth bearing small point. Male genitalia. Eighth sternum with posterolateral margin produced as large rounded lobe, posteromesally with cluster of small spines. Ninth segment widely open dorsally and ventrally, strongly produced anterolaterally as narrowly rounded lobe. Tenth tergum greatly modified, bearing cluster of heavily sclerotized spines basally: 3 pairs mesally, of which ventralmost much the longest, lateral spine long, twisted laterally, then ventrally and mesally, around a shorter spine curved laterad; thin, lightly sclerotized plate beneath these spines and arched dorsomesally. Inferior appendage with lateral arm terete, directed laterad; mesal arm broad in ventral aspect with distinct apicomesal point, small setate lobe ventrally at junction of two arms. Subgenital plate long, slender, tip distinctly narrowed. Phallus with tubular basal portion, and enlarged, more membranous apical portion separated by sharp constriction; apical portion with central ejaculatory duct and few basal sclerites. Female genitalia. Eighth segment with large, bilobed, rugose ventral sclerotized area, divided anteromesally, paired dorsolateral, sclerotized pockets, and pair of oval, dorsal plates; posterior row of stout setae with dorsolateral portion arising from narrow, darkened sclerite. Vagina with anterior spherical sclerite and strongly sclerotized posterior complex, in ventral aspect, with sclerotized lateral surface, sclerotized, projecting, midventral ridge, and small, transverse anterior plate.

Material examined.—Trinidad: [St. George County], Northern Range, Maracas Waterfall (10°44′N, 61°24′W), 270 m, 12 Apr 1991, L. Botosaneanu & D. Sakal, at light: ♂ holotype, ♀ allotype (ZMUA), 25 ♂, 27 ♀ paratypes, (ZMUA,NMNH, UWI, IRSNB); same, but 18 Jun 1993, O. S. Flint, Jr., 44 ♂, 112 ♀ paratypes (ZMUA, NMNH, UWI); same, but below falls, 250 m, N. E. Adams and W. N. Mathis, 1 ♂, 3 ♀ paratypes (NMNH). Northern Range, streamlet at "La Laja" (10°43′N, 61°17′W), Guanapo River catchment, 520 m, N. E. Adams & W. N. Mathis, UV light, 2 ♀ paratypes (NMNH); same, but 1st order stream, 14 Apr 1991, L. Botosaneanu & D. Sakal, at light, 4 ♂, 1 ♀ paratypes (ZMUA); same, but 2nd order stream, 13 Apr 1991, 3 ♂, 1 ♀ paratypes (ZMUA). North Coast Road, hygropetric habitat, west from Maracas Bay, 30 Apr 1991, L. Botosaneanu & D. Sakal, at light, 1 ♂, 5 ♀ paratypes (ZMUA). Blue Basin Waterfall, 17 Apr 1991, L. Botosaneanu & D. Sakal, at light, 23 ♀ (ZMUA, NMNH).

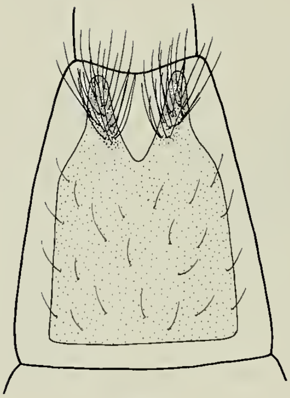
Cerasmatrichia wirthi (Flint), new combination

Figs. 5–7, 11, 57–62, 68–70

Alisotrichia wirthi Flint, 1968:46; 1970:29; 1981:26 [in part].



Figs. 46–50. *Cerasmatrichia trinitatis,* male genitalia. 46, lateral; 47, ventral; 48, dorsal; 49, phallus, lateral; 50, phallus, dorsal.



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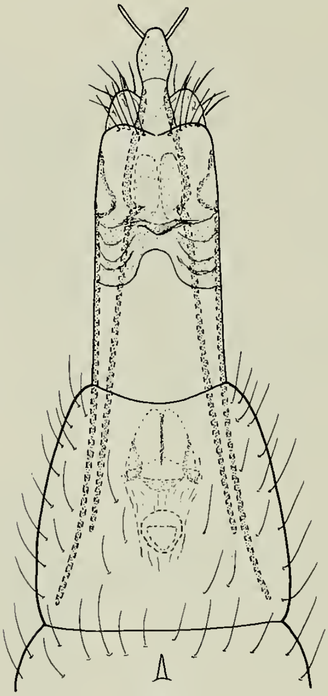

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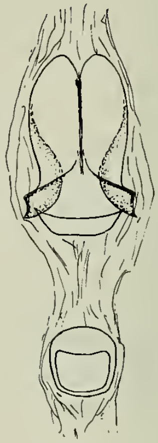

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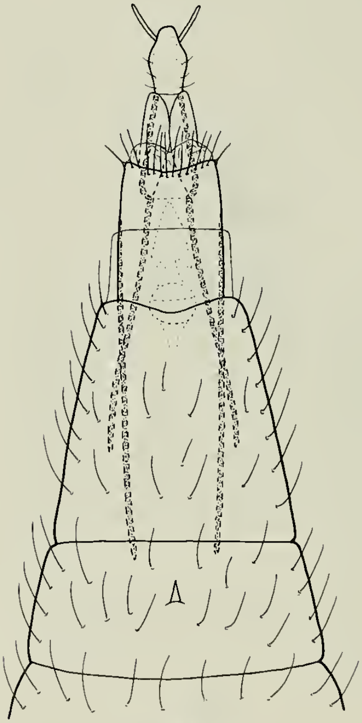

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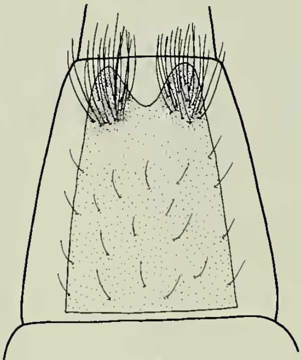

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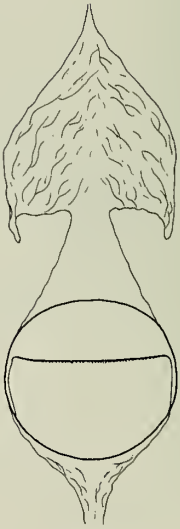

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Figs. 51–56. 51–53, *Cerasmatrichia trinitatis*, female genitalia. 51, ventral; 52, seventh tergum, dorsal; 53, vaginal sclerites, ventral. 54–56, *C. argylensis*, female genitalia. 54, ventral; 55, seventh tergum, dorsal; 56, vaginal sclerites, ventral.

This species is quite similar to its sister, *C. adunca,* in the male and not apparently separable in the female. The two are most easily distinguished in the male by the form of the tenth tergites. In *C. wirthi* they are rather slender and divergent in dorsal aspect with a sharp, upturned tip, but in *C. adunca* they are broad, tapering apicad to a thin, vertical plate that appears as a dark line.

Adult.—Length of forewing, 2–3 mm. Color fuscous; antennae pale brown, fore tarsi and tibia, and mid tarsi cream colored; forewings almost uniformly fuscous. Male with sexual modifications: 3rd segment of maxillary palpus with integument very dark and bearing specialized setae; fore femur unmodified; forewing with bulging, modified midbasal area, costal area for half length of wing with membrane thickened. Male seventh sternum without process, with narrow, transverse, projecting carina; female sixth sternum lacking point. Male genitalia. Eighth tergum and sternum almost completely fused into a cylinder; posteroventral margin almost truncate, produced into pair of small, submesal lobes, with cluster of small spines. Ninth segment widely open dorsally and ventrally, produced ventrolaterally as small lobe over base of its inferior appendage. Tenth tergum developed as pair of elongate, divergent sclerites with pointed, upturned tip. Inferior appendage simple, elongate structure, curved ventrad and enlarged apically with single large seta dorsally at midlength; with elongate, oblique setose lobe basally. Subgenital plate as long as inferior appendages, tip hooked ventrad, appearing as darkened ovoid in ventral aspect. Phallus with tubular basal portion, and enlarged, apical portion separated by sharp constriction; apical portion with outer surface strongly sclerotized (and frequently detaching from phallus if phallus is removed), centrally with ejaculatory duct and some basal, internal sclerites. Female genitalia. Eighth segment lightly sclerotized laterally; posterior row of stout setae. Vagina with spherical sclerite, anteriad to which is strongly sclerotized, transverse bar bearing many long teeth, comblike.

Material examined.—Dominica: Fond Figues River, 13 Mar 1965, W. W. Wirth, ♂ holotype; same data, but 6 Apr 1964, O. S. Flint, Jr., 1 ♂ paratype (NMNH). Pont Casse, 1.5 mi N, 12 Feb 1965, W. W. Wirth, 1 ♀ (NMNH). Venezuela: Edo. Aragua, Dos Riitos, 6 km N Rancho Grande, 4 Feb 1976, C. M. & O. S. Flint, Jr., 1 ♂ (NMNH). Estación Experimental Cataurito, ca. 32 km E Villa de Cura, 1100 m, 1 Feb 1983, O. S. Flint, Jr., 4 ♂, 1 ♀ (NMNH). Edo. Miranda, Santa Cruz de Río Grande, Parque Guatopo, 7 Feb 1976, C. M. & O. S. Flint, Jr., 1 ♂ (NMNH).

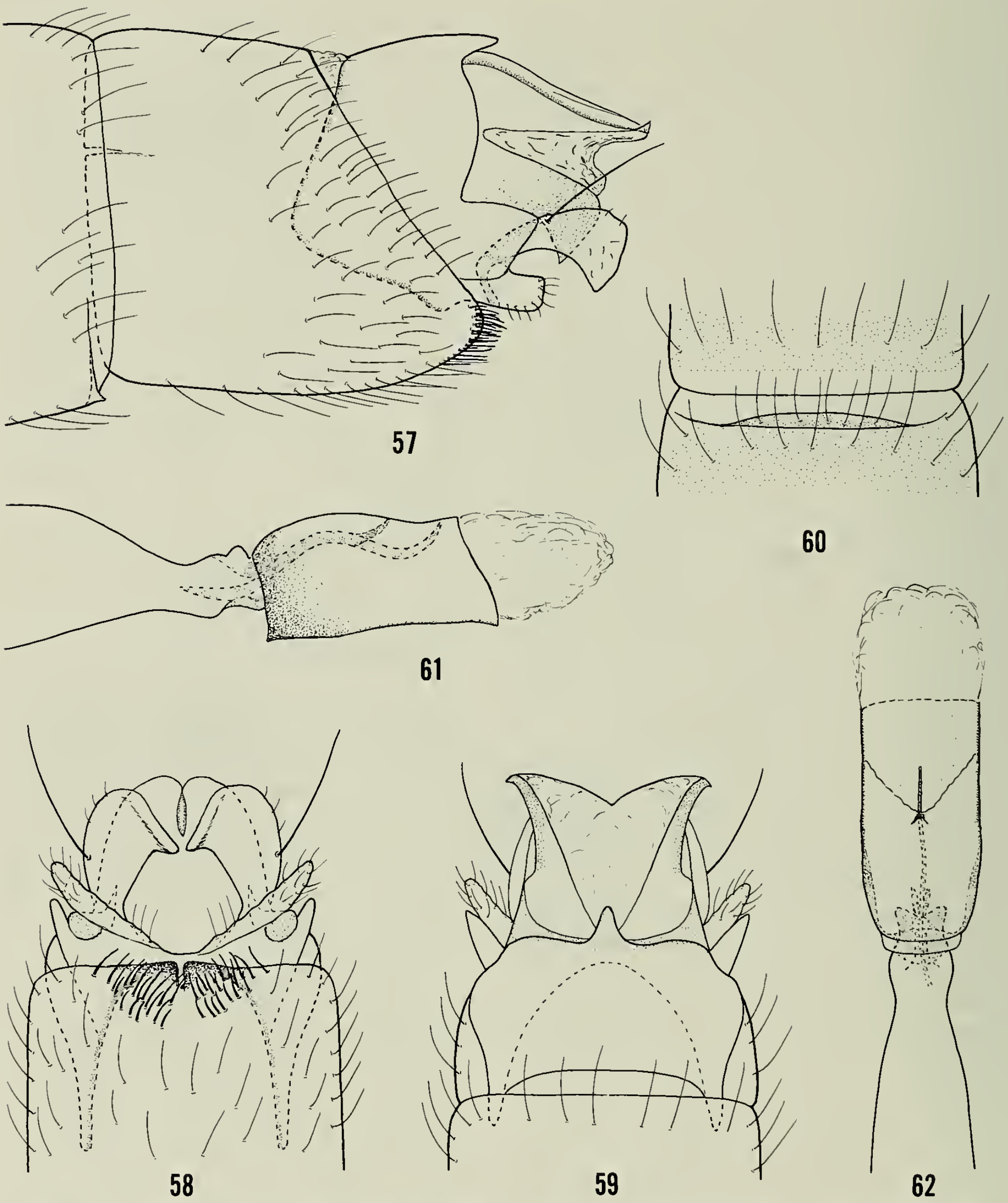
Cerasmatrichia adunca (Flint), new combination

Figs. 63–67, 71–73

Alisotrichia adunca Flint, 1991:44.

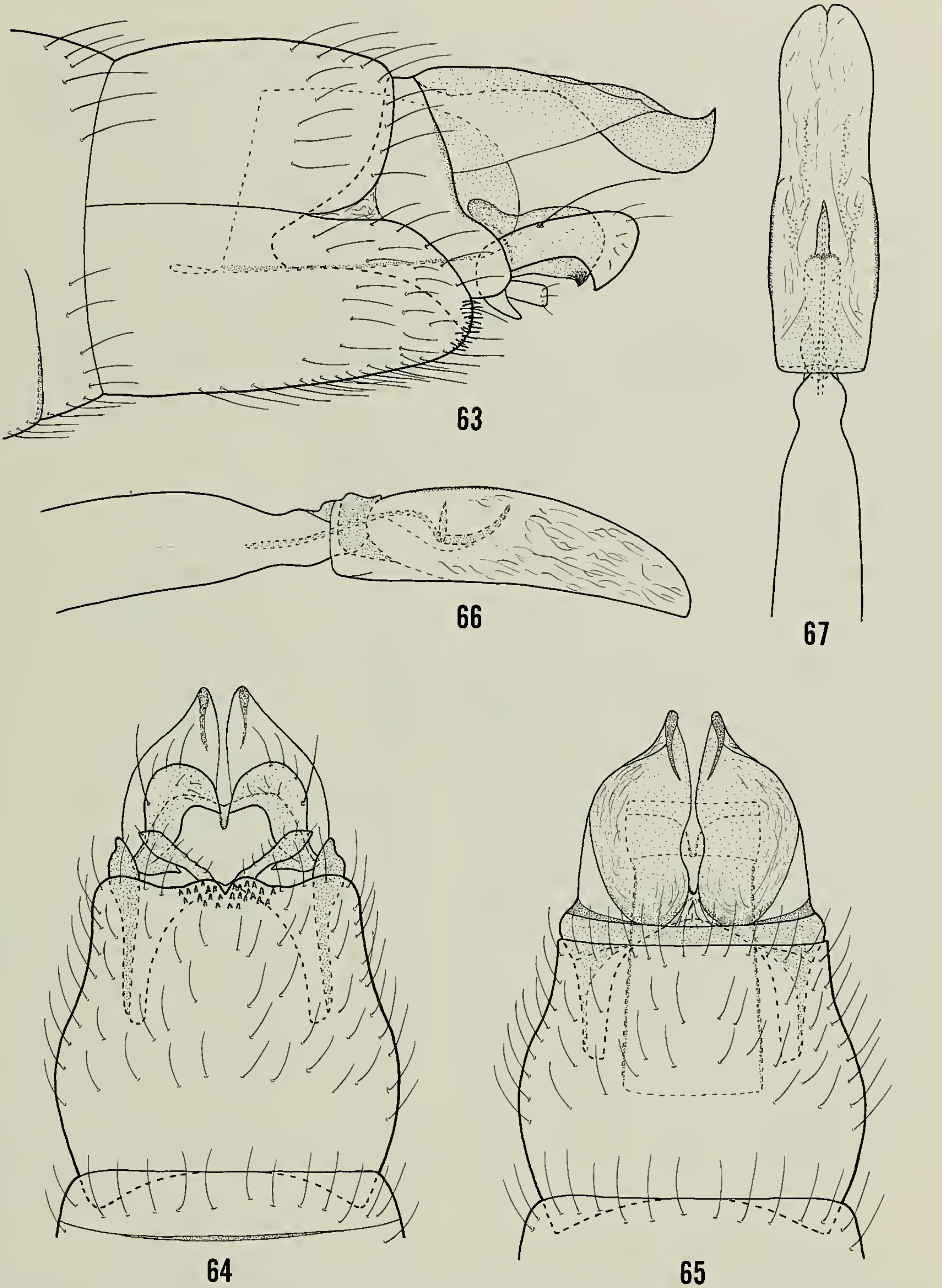
As mentioned under *C. wirthi,* these two species are quite similar and perhaps not separable in the female. The form of the male tenth tergites are the most distinctive. In *C. wirthi* they are rather slender and divergent in dorsal aspect with a sharp, upturned tip, but in *C. adunca* they are broad, tapering apicad to a thin, vertical plate that appears as a dark line.

As in *C. wirthi,* the phallus of the male has a large shield-like sclerite surrounding the apical portion. This shield mimics the "penis-sheath" of the Leucotrichiini and has been a source of confusion. It was clearly shown in the original description of this species (Flint 1991, figs. 106–108) as a large, apically rounded plate in lateral aspect. Careful examination shows it to be distinct from what is here called the subgenital plate, although they are easily confounded as in his figs. 107, 108. This plate often detaches from the phallus if one tries to pull the phallus back through the abdomen (as happened in Fig. 63 herein, where it is shown as the large, rectanguloid structure within segments 8 and 9).



Figs. 57–62. *Cerasmatrichia wirthi,* male genitalia. 57, lateral; 58, ventral; 59, dorsal; 60, seventh and eighth sterna, ventral; 61, phallus, lateral; 62, phallus, dorsal.

Adult. — Length of forewing, 2.5 mm. Color fuscous; frontal hairs of head, antennae, fore tarsi and tibia, and mid tarsi cream colored; forewings fuscous with many small, pale maculae. Male with sexual modifications: 3rd segment of maxillary palpus and fore femur apparently unmodified; forewing with membrane of midbasal area thickened, slightly bulging, but apparently not otherwise modified, costal area for half length of



Figs. 63–67. *Cerasmatrichia adunca,* male genitalia. 63, lateral; 64, ventral; 65, dorsal; 66, phallus, lateral; 67, phallus, dorsal.

wing with membrane thickened. Male seventh sternum without process, with long, narrow, transverse, projecting carina; female sixth sternum lacking point. Male genitalia. Eighth tergum and sternum distinct; posteroventral margin almost truncate, produced into pair of small, submesal lobes, with cluster of small spines. Ninth segment widely open dorsally and ventrally, sharply produced anterolaterally. Tenth tergum developed as pair of broad, ovoid, lateral sclerites each with thin, vertical apex appearing as dark mark in dorsal aspect. Inferior appendage single, elongate structure, curved ventrad and slightly enlarged apically with large seta dorsally at midlength; with elongate, oblique setose lobe basally. Subgenital plate slightly shorter than inferior appendages, tip hooked ventrad, appearing as darkened point in lateral aspect. Phallus with tubular basal portion, and enlarged, apical portion separated by sharp constriction; apical portion with outer surface strongly sclerotized (detached from phallus and shown internally in Figs. 63 and 65, herein), centrally with ejaculatory duct and some basal, internal sclerites. Female genitalia. Eighth segment lightly sclerotized laterally; posterior marginal row of stout setae. Vagina with spherical sclerite, anteriad to which is strongly sclerotized transverse bar bearing many long teeth, comblike.

Material examined.—Colombia: Dpto. Antioquia, 10 km E Medellín, road to Guarne, 7 Feb 1983, O. S. Flint, Jr., ♂ holotype (NMNH). Quebrada El Pozo, 8 km W El Peñol, 9 Feb 1983, O. S. Flint, Jr., 1 ♂, 1 ♀ paratypes (NMNH).

Cerasmatrichia species

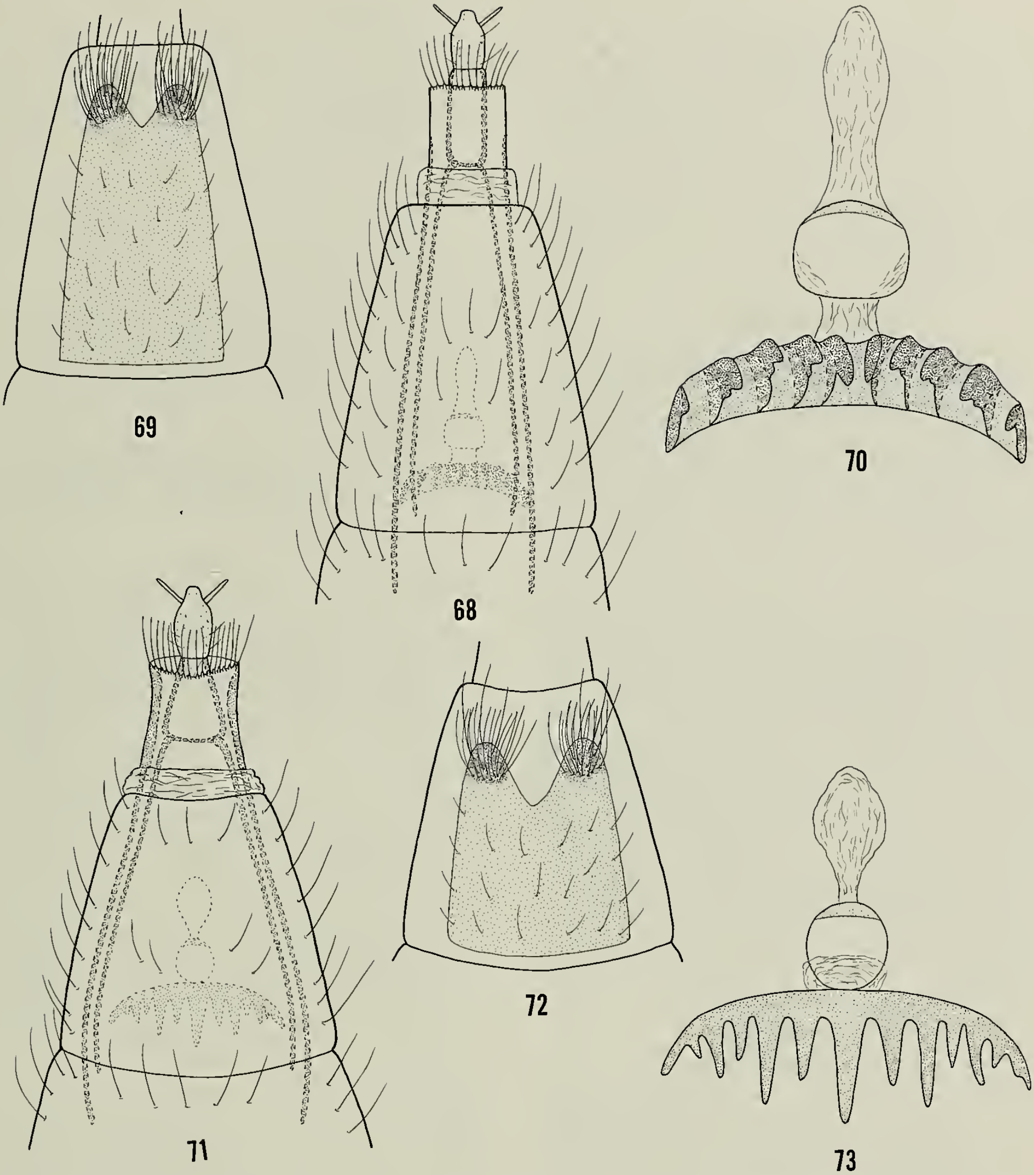
We here record a series of collections, larvae or females, that can not be definitively placed to species. They serve to expand the known range of the genus and give some idea of specific differences to be found in the larvae.

Species A.—This collection of pupae and prepupae contains several nearly mature metamorphotypes, but not in good enough condition to permit description. They do represent an undescribed species of the *C. dominicensis* group. The larva bears an extra row of enlarged setae along the anterior margins of the pro-, meso- and metanota, the points dorsally on the femora and tibiae are very large and clearly setate, and the membranous surface of the abdomen dorsally is covered with dark spicules. Material: Venezuela, Edo. Merida, Mucujun Valley, 11 km NE Merida, 21 Feb 1976, C. M. & O. S. Flint, Jr., 1 ♂, 4 ♀ metamorphotypes, 13 pupae, 2 prepupae, 2 empty cases (NMNH).

Species B.—These are the larvae shown in Fig. 15. They probably are those of *C. dominicensis,* whose adults were taken close to larger rivers such as those from which these larvae came. Material: Dominica, Laurent River [at Bells], 21 Jul 1963, O. S. Flint, Jr., 1 larva (NMNH). Geneva Estate, 9 Dec 1964, Paul J. Spangler, 1 larva (NMNH). Fond Figues River, 9 Feb 1965, W. W. Wirth, rocks in river, 1 larva (NMNH). Martinique, Rivière Blanche, near l'Alma, 19 Apr 1979, Starmühlner, 2 larvae (ZMUA).

Species C.—This single larva is damaged in the prothoracic region and is somewhat shriveled and thus not fully distended, therefore telescoping the segments. It appears to be virtually identical to the larva of Species B although the enlarged setae seem exceptionally long and dark. Material: Costa Rica, Cartago Prov., Reserva Tapantí, Río Dos Amigos, ca. 6 km (road) NW tunnel, 9.704°N, 83.783°W, elev. 1500 m, 9–10 Jun 1988, C. M. & O. S. Flint, Jr., Holzenthal, 1 larva (NMNH).

Species D.—This larva agrees, again, with the basic structure, but its entire dorsal surface (sclerites and membrane) is covered with dark points, the points on the tibiae are produced into a comblike row of clear projections, and the abdominal terga lack the posterior band of rugosities. Material:



Figs. 68–73. 68–70, *Cerasmatrichia wirthi,* female genitalia. 68, ventral; 69, seventh tergum, dorsal; 70, vaginal sclerites, ventral. 71–73, *C. adunca,* female genitalia. 71, ventral; 72, seventh tergum, dorsal; 73, vaginal sclerites, ventral.

Peru, Dept. Cuzco, San Pedro (at km 152 & 2 km east), 13°09′S, 71°26′W, 1430 m, 31 Aug 1989, R. A. Faitoute (colln. 11), 1 larva (NMNH).

Species E.—This is another larva that is very similar to those of *C. spinosa.* It differs in lacking the posterior bands of rugosities on the abdominal terga, but has the membrane darkened and with dark points laterad, and the femora and tibiae seem smooth dorsally. Material: Venezuela, T.F. Amazonas, 40 km S Puerto Ayacucho at Tobogan, 24 Feb 1986, leaf packs, P. J. Spangler (colln. 12), 1 larva (NMNH).

Species F.—A single female, unassociated with any male has been found in the collections. The genitalia are identical to the species of the *C. wirthi* group. Material: Ecuador, Tungurahua Prov., 13 km E Baños, 15 Sep 1990, O. S. Flint, Jr., 1 ♀ (NMNH).

Acknowledgments

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A NEW HEMICHORDATE, *SACCOGLOSSUS BROMOPHENOLOSUS* (HEMICHORDATA: ENTEROPNEUSTA: HARRIMANIIDAE), FROM NORTH AMERICA

Gary M. King, Cem Giray, and Irv Kornfield

Abstract.—A new species, *S. bromophenolosus,* is distinguished from its congener, *S. kowalevskii* (Agassiz 1873), on the basis of the following morphological, biochemical, and genetic criteria: placement of gill pores; prominence of the dorsal ridge; structure of the proboscis skeleton; presence of bromophenols or bromopyrroles; relative electrophoretic mobility of allozymes (e.g., superoxide dismutase); molecular weights of fragments from restriction endonuclease digestion of mitochondrial DNA. *S. bromophenolosus* occurs from southern Maine, U.S.A., to Nova Scotia, Canada, with an additional record from Willapa Bay, Washington, U.S.A.

Three families of enteropneusts (Hemichordata: Enteropneusta: Harrimaniidae, Ptychoderidae, and Spengeliidae) occur along the coasts of North America (Milne & Milne 1973, Bullock 1975, Ruppert & Fox 1988). The best known species belong to the genus *Saccoglossus* (Harrimaniidae), which occurs on both the Atlantic and Pacific coasts (Milne & Milne 1973, Bullock 1975). Of the several saccoglossids, *S. kowalevskii* (Agassiz 1873) has been described in greatest detail. Various aspects of its distribution, biology and ecology have been reported subsequent to Agassiz's (1873) initial description (e.g., Bateson 1886, Bullock 1940, Tweedell 1961, Colwin & Colwin 1962, Barrington 1965, King 1986, Woodin et al. 1987, Balser & Ruppert 1990, Carey & Mayer 1990). *S. kowalevskii* has been considered the only member of its genus on the Atlantic coast of North America, and has been noted in intertidal collections from Nova Scotia to Georgia (Dörjes 1972, Bromley 1979). Although there are certain characteristics common to all saccoglossids along this range, a comparison of biochemical attributes reported for populations from Maine and South Carolina has raised questions about the taxonomic status of the species (King 1986, Woodin et al. 1987). Specifically, animals collected in Maine and northward typically accumulate high concentrations of two secondary products, 2,4-dibromophenol and a dibromoindole (King 1986, unpubl. data), while animals from other locales accumulate 2,3,4-tribromopyrrole (King, unpubl. data, Woodin et al. 1987). The differential accumulation of these haloaromatics does not appear to correlate with any major environmental variables or gradients. Further, the presence of a given haloaromatic phenotype appears to be a fixed trait associated with populations from specific regions.

We now report that the genus *Saccoglossus* consists of at least two distinct species along the Atlantic coast of North America. These two species are readily differentiated by gross external morphological characters, the accumulation of halogenated aromatic compounds, morphology of the proboscis skeleton, electrophoretic mobilities of several enzymes, and the sequence composition of the mitochondrial DNAs (mtDNA). We propose the name *S. bromophenolosus* for the new species occurring from southern

Maine northward and possessing features as detailed below. *S. kowalevskii* occurs from southern Maine southward, as noted by Verrill (1873) and Gosner (1979).

Materials and Methods

Saccoglossids were collected from the intertidal zones of sites ranging from Halifax, Nova Scotia, to Georgetown, South Carolina, by excavating sediments to a depth of about 10 cm at low tide. The proboscis, collar and anterior portions of the trunk were obtained readily by removing the animals directly from the substrate, but complete specimens were difficult to collect due to the fragility of the posterior region of the trunk. Specimens were examined in the field for external morphological characteristics (see below) and then placed individually in small vials (20 ml) containing local seawater; the animals were subsequently transported to Walpole, Maine, for further processing. MtDNA was extracted from live animals using procedures modified from Lansman et al. (1981) within 24–48 h of return to the laboratory. A minimum of 10 live animals from Lowes Cove and York, Maine (69°34′N, 43°56′W; 43°09′N, 70°39′W) and from Portsmouth, New Hampshire (43°06′N, 70°42′W) were also homogenized for electrophoretic analyses of enzymes at the following loci using standard methods (Murphy et al. 1990): glucose phosphate isomerase (GPI; E.C. 5.3.1.9), malate dehydrogenase (MDH; E.C. 1.1.1.37), phosphoglucomutase (PGM; E.C. 2.7.5.1), and superoxide dismutase (SOD; E.C. 1.15.1.1). Analyses of haloorganic contents utilized extracts of animals that were extracted with hexane immediately after collection and removal of adhering sediment. In addition, animals used for mtDNA and allozyme analyses were "halotyped" by collecting 1–2-μl samples of the seawater immediately adjacent to the proboscis with a 10-μl gas chromatography syringe (Hamilton Inc., Reno, Nevada). The epidermis of the proboscides was irritated with the syringe needle prior to sample collection in order to stimulate mucus and haloorganic excretion. The samples were analyzed by direct injection into a gas chromatograph. Details of the extraction and analytical procedures have been reported elsewhere (King 1986, 1988). The proboscideal skeletons of 5 individuals from Lowes Cove and York, Maine, were examined after dissection of live animals.

Saccoglossus bromophenolosus, new species

Figs. 1–4, Table 1

Saccoglossus sp. Bullock 1975, p. 619; Kozloff 1987, p. 478.

Saccoglossus kowalevskii.—Milne & Milne 1973, (p.p.): 230; Bromley 1979, p. 533.

Saccoglossus kowalewskyi.—Brinkhurst et al., 1976, p. 156.

Saccoglossus kowalevskyi.—King, 1986, p. 257.

Saccoglossus kowalewskii.—Linkletter et al. 1977, (p.p.): 42, Gosner 1979, p. 265; Meinkoth, 1981, (p.p.): 726; Carey & Mayer, 1990, p. 79.

Diagnosis.—*Saccoglossus bromophenolosus* attains a length up to 20 cm. It has an elongate proboscis that extends 1.5–2 cm in narcotized specimens. The proboscis has a shallow dorsal groove and a single pore at the base of the proboscis. Concretions fill the primary shaft of the proboscis skeleton. Hexane extracts of the proboscis contain 2,4-dibromophenol and a dibromoindole; these compounds account for the characteristic "bromoform" odor of live specimens. The collar is differentiated into 4–5 zones, and is generally rectangular from above with an aspect ratio of about 3:5 (width : length). The trunk is differentiated into distinct branchial and hepatic-genital regions. Dorsolaterally placed gill pores appear ellipsoid in relaxed and ventilating specimens, with the major axis oriented vertically; the gill pores do not occur in folds and vary from about

60–110 pair per individual. Esophageal pores, which occur slightly posterior to the gill pores vary from about 4–8 pair in number. Gonads begin at the terminus of the branchial region in both sexes, and are dorsolateral in placement.

Material examined.—Holotype (USNM 168049) and 3 paratypes (USNM 168050-168052) from Lowes Cove, Maine (69°34′N, 43°56′W), collected by G.M. King 20 October, 1993.

Description.—The holotype is a sexually immature female with the following characteristics observed while the animal was relaxed in a solution of 7% $MgCl_2$. The incomplete specimen was 82 mm in length; an additional 60–70 mm of the posterior-most region of the trunk was lost unavoidably during collection. The posterior-most section of the trunk was extremely thin and fragile; in color and diameter, it resembled the fecal coils present at the sediment surface. The relaxed and extended proboscis was creamy white in color with a shallow dorsal groove running from the base to the proboscis tip. Striations perpendicular to the major axis of the proboscis were observed at low power on a dissecting microscope. The proboscis was 16 mm in length and 3 mm at the base. The basal-most region was a rust orange in color. The orange collar was 5 mm in length and 2.5 and 3 mm in diameter at the anterior and posterior ends, respectively. Both ends of the collar were distinctly thickened, with a prominent lighter-colored ridge circling the posterior of the collar. The branchial region of the trunk was about 2.5 mm in diameter where it joined the posterior of the collar. A prominent, raised dorsal ridge began immediately posterior to the collar and ran the length of the branchial region, terminating just anterior to the esophageal pores. Near the collar, the dorsal ridge was about 1 mm in width with a central groove about 0.5 mm in width. This region of the trunk was pinkish-orange to orange and about 14 mm in length. A total of 61 pairs of gill pores were located dorsolaterally, beginning at the junction of collar and trunk. Slightly posterior to the terminal gill pores, 4 pairs of dorsal esophageal pores were observed; they formed an angle of about 30° opening toward the trunk. The hepatic-genital region of the trunk extended about 23 mm, measured from the termination of the gill pores to a point where genital structures were not observable. Nascent grayish egg masses were visible dorsolaterally just beneath the epidermis. The hepatic-genital region was grayish-brown dorsally and yellowish-brown laterally. The posterior-most region of the trunk was 34 mm in length, yellowish-brown in color and characterized by pairs of carmine-colored spots located dorsally.

General dimensions for 3 male paratypes with maturing gonads were similar to those of the holotype. However, gill pore numbers ranged between 68–101 and esophageal pores numbered 4–6. The sperm sacs were dorsolateral and pink in color.

Remarks.—Although the range of body size, coloration, location and appearance of the gonads, and external features of the collar and proboscis of *S. bromophenolosus* and *S. kowalevskii* are very similar, gill pore placement and the morphology of the dorsal ridge allow discrimination of the species by visual inspection in the laboratory or field (Fig. 1, 2). In contrast to *S. bromophenolosus,* the dorsal ridge of *S. kowalevskii* is relatively broad and flattened immediately posterior to the collar, covering >50% of the dorsal area. The dorsolateral gill pores of *S. kowalevskii* occur within lateral grooves that can be closed, thereby obscuring them from view (Fig. 2). This state is typical of specimens preserved without prior relaxation. In addition to external morphology, *S. bromophenolosus* and *S. kowalevskii* can be distinguished by other diagnostic characteristics requiring dissection or various laboratory analyses (Fig. 3, Table 1). Collections to date indicate that *S. kowalevskii* and *S. bromophenolosus* exist sympatrically only within a narrow range around the mouth of

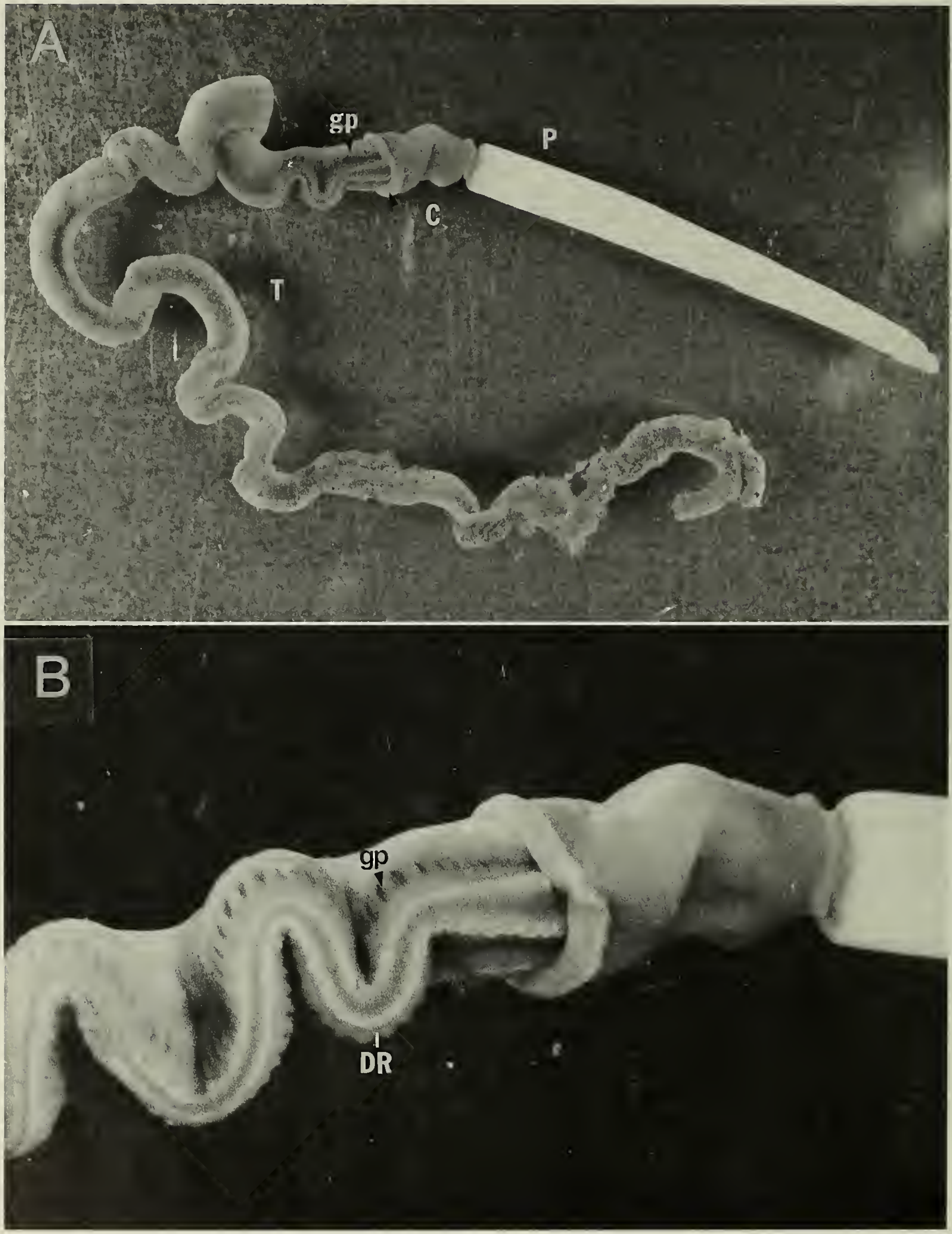


Fig. 1. A. Dorsolateral view of relaxed, sexually immature female of *S. bromophenolosus,* new species illustrating superficial features of the proboscis (P), collar (C, limits indicated by arrows) and trunk (T); gill pores (gp, indicated by arrow) are evident immediately posterior to the collar. B. Detailed view of the posterior proboscis, collar, and anterior of the trunk, illustrating the prominent, raised dorsal ridge (DR) and gill pores.

Fig. 2. Anterior portion of *S. kowalevskii* showing the broad, flattened dorsal ridge (DR), collar (C) and proboscis (P); gill pores are obscured by lateral folds (F, indicated by arrow). The "sole" (S) occurs ventrally.

the Piscataqua River, New Hampshire (43°06′N, 70°42′W); *S. kowalevskii* has not been observed north of York, Maine, while *S. bromophenolosus* has not been found south of Portsmouth, New Hampshire.

Allozyme analyses indicated substantial divergence between *S. bromophenolosus* and *S. kowalevskii* since GPI, MDH, and PGM were fixed for alternative, diagnostic alleles within each taxon; SOD was represented at 2 monomorphic loci in *S. bromophenolosus,* and by a single, different monomorphic locus in *S. kowalevskii.* MtDNA analyses also revealed substantial divergence (Fig. 4).

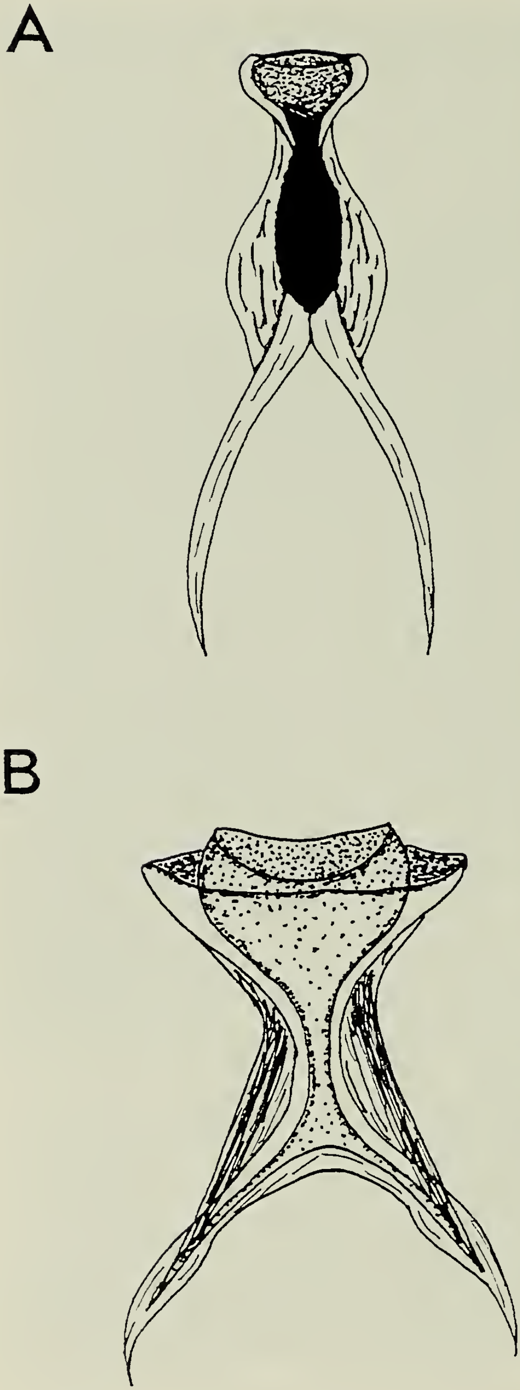
Table 1.—Diagnostic characters that distinguish among 3 species of North Atlantic saccoglossids.

	S. bromophenolosus	*S. kowalevskii*	*S. ruber*
Characteristic			
Dorsal ridge	raised, narrow	broad, flattened	raised, narrow
Gill pore placement	central	lateral	central
Coloration[1] (proboscis-collar-trunk)	W/P-O/R-O	W/P-O/R-O	P/R/R-O
Halotype[2]	DBP/DBI	TBPy	DBP/TBP
Proboscis skeleton[3]	narrow curve-co	broad curve-no co	narrow curve-co

[1] Color code: W/R, ranges from white to pale pink; O/R, ranges from orange to red; O, orange; P/R, pale pink to pale red.

[2] Compound code: DBP = 2,4-dibromophenol; DBI = dibromoindole (positions of bromine atoms uncertain); TBP = 2,4,6-tribromophenol; TBPy = 2,3,4-tribromopyrrole.

[3] Co refers to concretions within the proboscis skeleton.



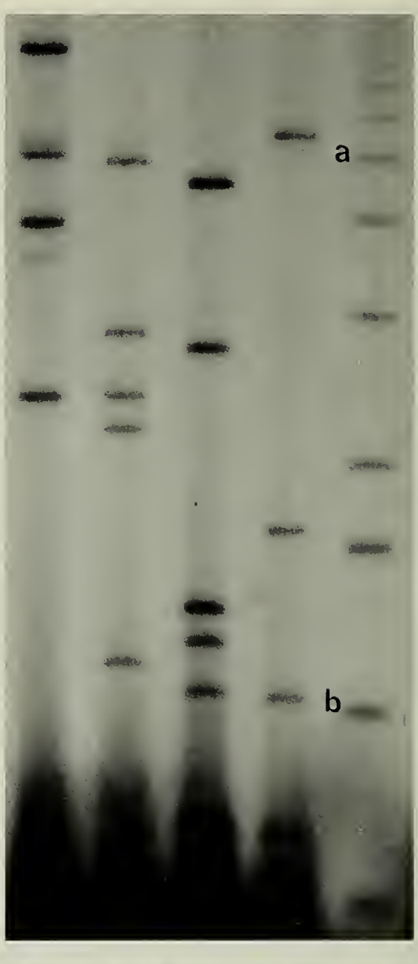


Fig. 4. Autoradiogram of fragments from the digestion of pooled mtDNA from specimens of *S. bromophenolosus*, new species (lanes 1, 3) or *S. kowalevskii* (lanes 2, 4) with the restriction endonucleases *Hind* III (lanes 1, 2) or *Sty* I (lanes 3, 4). Fragments were separated after digestion by agarose gel electrophoresis and radiolabelled with ^{35}S using a nick translation procedure. Lane 5 contains a molecular weight standard (1 kb ladder, BRL); "a" and "b" indicate 5090 and 1018 base pair fragments, respectively.

←

Fig. 3. A. Diagram of the proboscideal skeleton of *S. bromophenolosus*, new species; dark central region consists of concretions as described for *S. ruber* (Burdon-Jones & Patil 1960). B. Diagram of the proboscis skeleton of *S. kowalevskii*; note absence of central concretions and more deeply curved skeletal arms.

No common DNA fragments were found in comparisons of restriction endonuclease digests of the mtDNA of the two taxa based on *Hind* III, *Xba* I, *Nde* I, *Sty* I, *Stu* I, *Dra* I or *Ava* I. In contrast, mtDNA haplotypes for populations of each taxon were homogenous. For example, an *Xba* I digest yielded the following approximate fragment molecular weights: *S. bromophenolosus*—8750, 1075, 925, and 625, *S. kowalevskii*—5000, 3225, 2275, 1875, and 1000.

Etymology.—The species name is derived from its characteristic haloorganic content, 2,4-dibromophenol, and the Latin suffix,-*osus*; thus *S. bromophenolosus, Saccoglossus* "with bromophenol."

Distribution.—On the east coast of North America, the range of *S. bromophenolosus* extends north from the mouth of the Piscataqua River separating Maine and New Hampshire to at least Halifax, Nova Scotia. *S. bromophenolosus* is found in silty sands throughout the intertidal zone in this range. It is often distributed in patches, with densities from about 10–>100 individuals m^{-2}. In addition, a sub-tidal form has been recorded from the Damariscotta River (69°34′N, 43°56′W) at a depth of 10–20 m. Specimens obtained from Willapa Bay, Washington (46°37′N, 124°00′W) have very similar mtDNA haplotypes and 16S ribosomal DNA sequences (pers. observations); in addition, the external morphologies and haloorganic contents of these organisms are indistinguishable from *S. bromophenolosus* (K. Woodwick, in litt.). Since these northwestern Pacific saccoglossids represent a previously unnamed species (Kozloff 1987), we incorporate them as trans-Arctic representatives of *S. bromophenolosus.* The range of the western North American populations is uncertain, but appears to include Oregon and Washington (Bullock 1975, Kozloff 1987).

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ADVERTISEMENT CALLS AND RELATIONSHIPS OF CHILEAN FROGS *EUPSOPHUS CONTULMOENSIS* AND *E. INSULARIS* (AMPHIBIA: ANURA: LEPTODACTYLIDAE)

J. Ramón Formas and Lila Brieva

Abstract.—Advertisement calls of *E. contulmoensis* and *E. insularis* are described. The calls of both species consist of a single short note. Call data, together with chromosomal information, indicate that *E. contulmoensis,* and *E. insularis, E. roseus, E. calcaratus* and *E. migueli* comprise a related group distinct from *E. vertebralis* and *E. emiliopugini.*

Calls of frogs can be useful in revealing evolutionary relationships at the species level. In general, closely related species have some acoustic characteristics in common (Blair 1958, Barrio 1965, Mecham 1971, Martin 1972, Schiøtz 1973, Kuramoto 1974, Ryan 1988, Straughan & Heyer 1971). In order to establish evolutionary trends related to the diversification of the genus *Eupsophus,* we analyzed the advertisement calls of *E. contulmoensis* and *E. insularis.* Both calls are compared with those other members of the genus that were previously described by Formas & Vera (1980), Formas (1985, 1989), and Penna & Veloso (1990).

Eupsophus is the most speciose taxon of the rather reduced anuran fauna of the *Nothofagus* forests of southern Chile and Argentina. Seven species have been described: *E. roseus, E. calcaratus, E. migueli, E. contulmoensis, E. insularis, E. vertebralis* and *E. emiliopugini.*

E. contulmoensis has been collected in the type locality of Contulmo (37°52′S, 73°12′W), Nahuelbuta Range (Ortiz et al. 1989), and *E. insularis* is endemic to Mocha Island (38°22′S, 73°56′S; 38 km W of the coast of Arauco Province) (Formas & Vera 1982).

Methods and Materials

Field recordings were made at 19 cm/sec on an Uher 4000 Report-IC portable tape-recorder and an Uher 517 microphone. Call durations, number of notes per call, and note duration were analyzed with a storage oscilloscope Tektronix 5113. Audiospectrograms were made with a Kay Elemetric audiospectrograph model 675, using 85–8000 Hz frequency scale and narrow (45 Hz) band filter. Call repetition rates were measured in the field by counting consecutive calls over one minute. Water temperature, location and behavior of the individuals used in the analysis were taken at the time of recording. Specimens and tapes were deposited in the collection of Amphibians of the Institute of Zoology, Universidad Austral de Chile (IZUA), Valdivia.

Eupsophus contulmoensis Ortiz, Ibarra-Vidal, & Formas, 1989

The advertisement call of *E. contulmoensis* was recorded at the type locality (Natural Monument of Contulmo, Malleco Province). Description is based on 25 calls from seven specimens recorded at 11.8°C (water temperature) during November 1990. Males

Table 1.—Call characteristic (mean and range) of *Eupsophus* species (S, short call; L, long call)

Species	Call type	Notes per call	Call length sec	Repetition rate	Dominant frequency (Hz)
E. contulmoensis		1	0.18 (0.15–0.20)	23.3 (15–34)	(1100–2000)
E. insularis		1	0.16 (0.14–0.18)	7.8 (4–12)	(1500–2100)
E. roseus †	S	1	0.20 (0.19–0.21)	64.0 (60–72)	(1600–2900)
**	S	1	0.10 (0.07–0.16)	25.1 (11.1–60)	(1250–1350)
**	L	32.1 (8–47)	2.73 (0.65–40.0)	10.2 (93–112)	(1220–1470)
E. migueli ††	S	1	0.24 (0.20–0.35)	6.0 (3–8)	(1500–2500)
**	S	1	0.20 (0.16–0.26)	4.2 (2.4–6.6)	(1170–1820)
††	L	24.0 (19–33)	3.40 (3.30–4.40)	6.0 (5–8)	(900–1500)
**	L	12.3 (4–23)	1.07 (0.30–2.16)	5.4 (2.4–8.4)	(1210–2000)
E. calcaratus ††		1	0.19 (0.15–0.21)	19.0 (16–25)	(1100–2700)
E. vertebralis †		5.0 (4–6)	0.60 (0.40–0.80)	4.0 (2–10)	(1100–2500)
**		5.6 (3.8)	0.64 (0.40–0.88)	27.8 (18.6–36.6)	(700–1110)
E. emiliopugini *		2	0.50	—	(729–1320)

† From Formas & Vera (1980); †† Formas (1985); * Formas (1989); ** Penna & Veloso (1990).

were observed and collected while they were calling from cavities in the ground at the border of a stream close to the forest. Individuals were organized into duets and trios spaced apart by 40–180 cm. Generally males called in alternation. The advertisement call of *E. contulmoensis* is composed of only one note (Fig. 1a, d; Table 1) that lasts 0.15–0.18 seconds. The dominant frequency is spread between 1100–2000 Hz and the repetition rate is 15–34 calls/minute. All calls showed modulation and defined harmonics are present at about 500 Hz intervals.

Eupsophus insularis (Philippi)

Description is based on 18 calls recorded from three individuals at Isla Mocha, during December 1989. Calls were recorded at a water temperature of 12°C. Males were observed and captured while they were calling from cavities in the ground close to a stream at the border of the forest. The individuals call isolated and neither duets nor trios were detected. Calls consist of a single note (Fig. 1b, e; Table 1) lasting 0.14–0.18 seconds. The call is modulated and defined harmonics are present at about 500 Hz intervals. Maximum energy is spread over a frequency range of 1500–2100 Hz.

E. roseus (Dumeril & Bibron), *E. migueli* Formas, *E. calcaratus* (Günther), *E. vertebralis* Grandison, and *E. emiliopugini* Formas

Call characteristics of the above cited species were described previously (Formas & Vera 1980; Formas 1985, 1989; Penna & Veloso 1990) and are depicted in Table 1.

Discussion

It is noteworthy that all *Eupsophus* species call during the spring-time from cavities along margins of small streams in the forest (Formas & Vera 1980; Formas 1985, 1989; Penna & Veloso 1990). Among the anuran fauna of the temperate *Nothofagus* forest of South America, males of *Eupsophus* species are unique in calling from flooded underground cavities near streams.

Based only on temporal parameters (call length and notes per call) of advertisement calls, Formas (1985) established two clusters of species within the genus *Eupsophus.* The first group contains *E. roseus, E. migueli* and *e. calcaratus,* whose calls consist of only one note lasting 0.10 to 0.20 seconds (Table 1). Calls of *E. contulmoensis* and *E. insularis* (a single note lasting 0.14 to 0.18 seconds) provide good evidence for group-

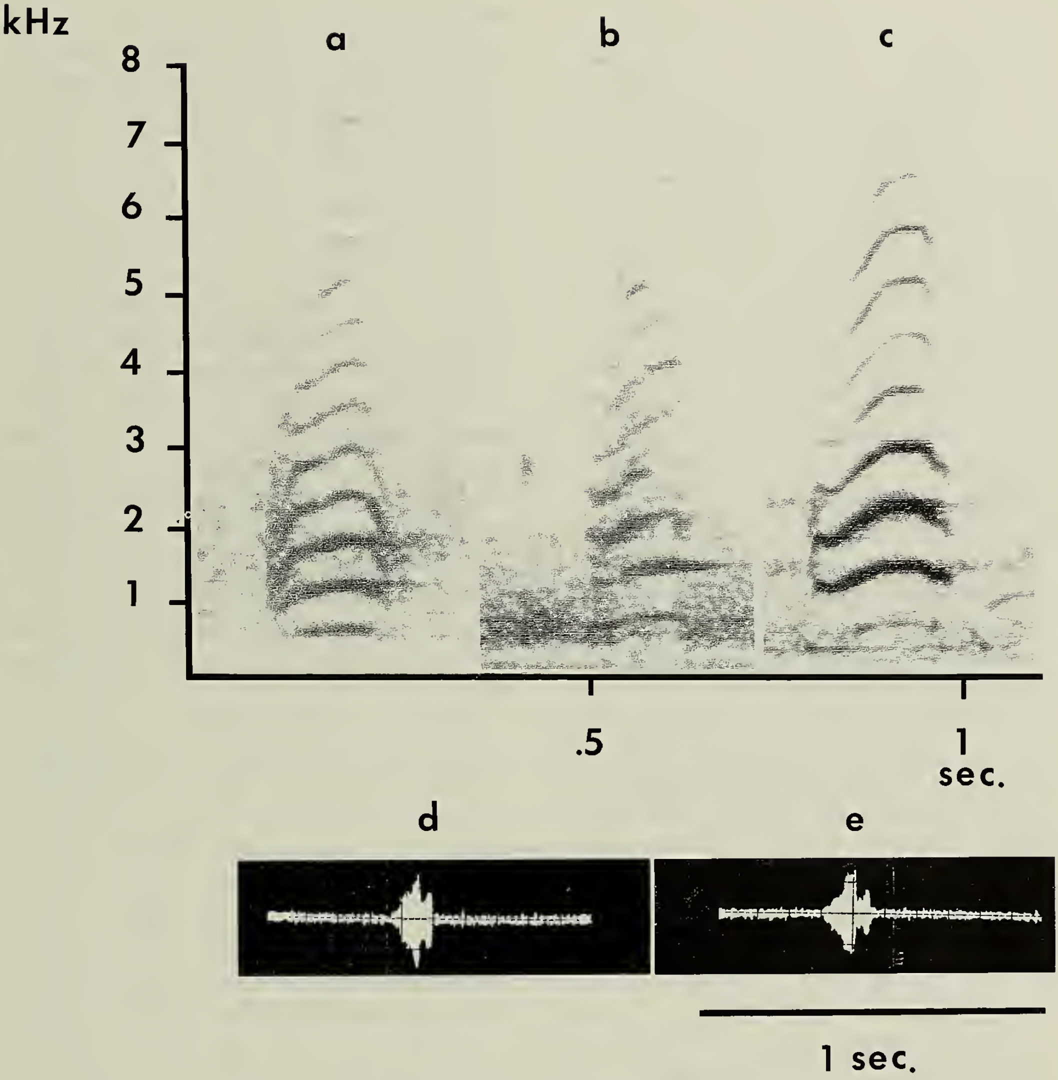

Fig. 1. Audiospectrograms of the advertisement call of *Eupsophus contulmoensis* (a), *E. insularis* (b), and *E. roseus* (c), band filter 45 Hz. Oscillograms of the advertisement call of *E. contulmoensis* (d) and *E. insularis* (e).

ing both of these species within this species group. The second group includes *E. vertebralis,* whose call contains 4–6 notes lasting 0.09 seconds. The advertisement call of *E. emiliopugini* shows that this species emits two notes lasting 0.20 seconds. Based on this information, we consider that *E. emiliopugini* should be grouped with *E. vertebralis,* rather than the *roseus* group.

Both species groups (i.e., *roseus* and *vertebralis*) are also supported when spectral parameters of the calls are considered. Members of the *vertebralis* group show lower mean values of dominant frequencies (1024–1350 Hz) than do members of the *roseus* group (1550–1900 Hz) (Table 1). On the other hand, members of the *vertebralis* group exhibit marked pulsed calls (11–34

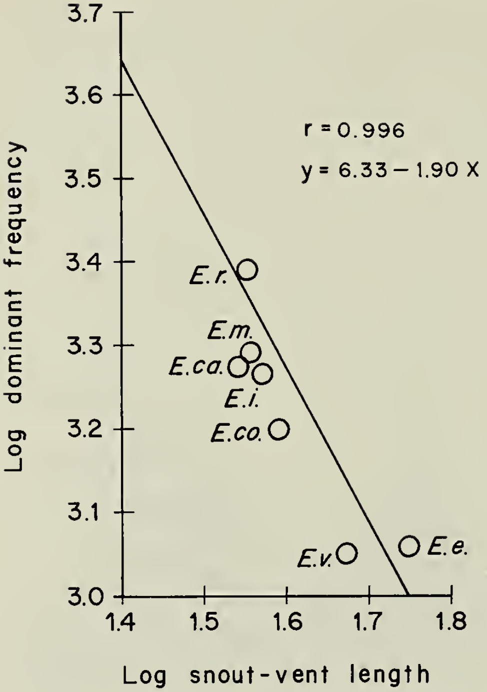

Fig. 2. Relation between mean snout–vent length and mean dominant frequency of the calls of *Eupsophus* species. Snout–vent length measurements correspond to samples of males from localities where recordings were made. Abbreviations (sample size in parentheses): E.r., *Eupsophus roseus* (12), E.m., *Eupsophus migueli* (7), E.ca., *E. calcaratus* (6), E.i., *E. insularis* (5), E.co., *E. contulmoensis* (7), E.v., *E. vertebralis* (14), E.e., *E. emiliopugini* (17).

pulses per note), while the *roseus* group species show calls poor in pulsations.

As indicated earlier, different authors have suggested that calls of frogs are useful in revealing systematic and evolutionary relationships. Temporal and spectral parameters of the advertisement calls of *Eupsophus* species may also reveal information concerning the evolutionary history of these species. Spectral components of the call (dominant frequencies) show wide overlap within *Eupsophus* (Table 1). The frequency range (700–2900 Hz) at which these species call is also shared by other frogs of the temperate *Nothofagus* forest (Penna & Veloso 1990), and thus cannot be related to particular physical features of the call sites of these frogs. When the mean dominant frequencies of *Eupsophus* species are compared, *E. emiliopugini* and *E. vertebralis* show lower values (1024–1350 Hz) than those presented by *E. contulmoensis, E. insularis, E. roseus, E. calcaratus* and *E. migueli* (1550–1900 Hz) (Table 1). The relationship between the mean dominant frequency of the call varies inversely with the logarithm of animal size ($r = -0.996$) (Fig. 2). The advertisement calls of *E. emiliopugini* and *E. vertebralis* have been described as conspicuously pulsed (Formas 1989). The former species emits 25.45 (17–34) pulses per note and the latter 15.90 (11–23) pulses per note. In contrast, calls of *E. roseus, E. migueli, E. contulmoensis, E. insularis* and *E. calcaratus* are poor in pulsation; however the "B" call (or long call) of *E. migueli* is markedly pulsed; 6–9 pulses per note (Formas 1985).

Eupsophus species exhibit considerable variation in calls, especially in the number of notes and their durations. Extremes are the single note (short call) of *E. roseus, E. migueli, E. calcaratus, E. contulmoensis,* and *E. insularis* (0.10–0.20 seconds), and the complex trilled calls (long call) with more than 40 notes of *E. roseus* and *E. migueli* (3.3–4.4 seconds). This latter vocalization has been interpreted as a territorial call (Formas 1985, Penna & Veloso 1990). Between these extremes are the advertisement calls of *E. emiliopugini* (2 notes) and *E. vertebralis* (4–6 notes lasting 0.40 to 0.80 seconds). If the length of each individual note is considered, the individual notes of the call of *E. emiliopugini* lasts 0.20 (0.19–0.23) seconds in duration, a value similar to the single notes of the advertisement calls of *E. roseus, E. calcaratus, E. migueli, E. contolmoensis,* and *E. insularis* ($\bar{X} = 0.18$; range 0.14–0.26 seconds). On the other hand, individual notes of the advertisement call of *E. vertebralis* have a duration ($\bar{X} = 0.089$; range 0.062–0.187) similar to the individual notes of the long call of *E. migueli* ($\bar{X} =$

0.083; range 0.051–0.092). In spite of this similarity, both calls are different in the number of pulses per note ($\bar{X} = 15.90$ in *E. vertebralis;* $\bar{X} = 7.5$ in *E. migueli*), number of notes per call (4–6 in *E. vertebralis*; more than 40 notes in *E. migueli*), and duration of the call ($\bar{X} = 0.6$; range 0.4–0.8 seconds in *E. vertebralis* and $\bar{X} = 3.4$; range 3.3–4.4 seconds in *E. migueli*).

Although members of the *roseus* group exhibit some similar patterns in advertisement calls, differences can be found when intervals among harmonics are examined. Calls of *E. contulmoensis* and *E. insularis* have harmonics at about 500 Hz intervals, while *E. calcaratus, E. migueli* and *E. roseus* show harmonics at about 1000 Hz intervals. A comparison among the calls of *E. roseus, E. contulmoensis* and *E. insularis* is shown in Fig. 1. In the case of the *vertebralis* species group, both members (*E. vertebralis* and *E. emiliopugini*) have harmonics at about 250 Hz intervals (Formas 1989).

Recognizing two species groups within the genus *Eupsophus* based on some temporal (call length and notes per call) and spectral (mean dominant frequencies and pulses) characteristics of advertisement calls agrees with the same proposal based on chromosomal data (Formas 1980). Members of the *vertebralis* group (*E. vertebralis* and *E. emiliopugini*) share a 28-chromosome karyotype (Formas 1991), while members of the *roseus* group have a 30-chromosome karyotype (Formas 1980, Iturra & Veloso 1981, 1989). Cuevas (personal communication) found that *E. insularis* and *E. contulmoensis* have a 30-chromosome karyotype, as occurs in *E. roseus, E. migueli,* and *E. calcaratus.*

Members of the *Eupsophus roseus* species group (*E. roseus, E. calcaratus, E. insularis, E. contulmoensis,* and *E. migueli*) are allopatric species; however, *E. roseus* and *E. migueli* are sympatric but not syntopic at the locality of Mehuín (39°26′S, 73°10′W) (Iturra & Veloso 1981). Members of the *E. vertebralis* species group (*E. vertebralis* and *E. emiliopugini*) are also allopatric. In spite of the fact that species of each group (*roseus* and *vertebralis*) are allopatric, it is possible to find members of the two different species groups in sympatry. For example, at the locality of Mehuín, *E. vertebralis* and *E. migueli* were observed while calling from cavities separated by two or three meters (Brieva, personal observation). A similar case of sympatry between members of the two different species group was observed at Cuesta de Soto (7 km by road from Valdivia city) between *E. roseus* and *E. vertebralis.* In three localities from southern Chile (La Picada, 42°07′S, 73°49′W; Río Rollizo, 41°27′S, 72°27′W; and Puntra, 42°07′S, 73°49′W) *E. emiliopugini* and *E. calcaratus* were observed calling from cavities separated by 25–50 cm (Formas 1989). Finally, *E. vertebralis* and *E. contulmoensis* were observed while calling from cavities separated by two to four meters at the locality of Contulmo (Natural Monument of Contulmo) (Formas, personal observation).

The four pairs of *Eupsophus* species recorded to occur in sympatry (*E. migueli* and *E. vertebralis*; *E. roseus* and *E. vertebralis*; *E. calcaratus* and *E. emiliopugini*; *E. vertebralis* and *E. contulmoensis*) are members of the two different species groups. These pairs of sympatric species exhibit a strong divergence among their advertisement calls. Passmore (1981) found that sympatric species of the African frog genus *Ptychadena* show remarkable differences in temporal and spectral components of their calls. In order to explain the origin of this phenomenon he used the notion of the Specific Mate Recognition System (SMRS) (Paterson 1978, 1982). According to this view, interspecific differences in signals do not agree with the traditional hypothesis that call divergence among closely related species develops due to selection for increasing reproductive isolation upon re-encounter of previously isolated populations (Dobzhansky 1970). Passmore's (1981) explanation for *Ptychadena* species is that the "pattern of vocal divergence probably resulted from independent evolutionary histories, and concomitant with the development of their respective acoustical recognition mechanism, rather than from selective pressure for increasing reproductive isolation" (Penna & Veloso 1990).

In light of the SMRS concept we propose a hypothesis addressing the divergence of vocal patterns and the evolutionary history of the genus *Eupsophus.* As shown above (Table 1) the *vertebralis* group (*E. vertebralis* and *E. emiliopugini*) exhibits two different advertisement calls. Both members of this species group occur allopatrically (Formas 1989) and their karyotypes show differences in relation to chromosome pair No. 14 (telocentric in *E. vertebralis* and metacentric in *E. emiliopugini*; Formas 1991). From an evolutionary point of view, the genus *Eupsophus* has a long history, with early generic differentiation documented by fossil records dating back to the Oligocene (Schaeffer 1949, Baez & Gasparini 1979). Conditions for further acoustical and chromosomal diversification within these species existed during Pleistocene glaciations, during which reduced areas free of ice provided scattered refugia for the survival of flora and fauna (Vuilleumier 1968, Heusser 1974, Ashworth et al. 1991). Since the present geographical ranges of *E. vertebralis* and *E. emiliopugini* (especially the southermost part) are in an area that was affected by glaciations, we hypothesize that ice-free areas were the appropriate scenarios where acoustical and chromosomal differentiation took place. Frogs of the *roseus* group (*E. roseus, E. migueli, E. calcaratus, E. contulmoensis,* and *E. insularis*) are allopatric species sharing a similar one note advertisement call; however, *E. contulmoensis* and *E. insularis* have harmonics at about 500 Hz intervals while *E. roseus, E. migueli* and *E. calcaratus* have harmonics at about 1000 Hz intervals. Vocal differences among these allopatric species suggest that these species represent a recent stage of speciation. All members of the *roseus* group have the same chromosomal formula (2N = 30), although differences have been found among the karyotypes of some species. For example, the karyotypes of *E. roseus* and *E. migueli* (Iturra & Veloso 1989) exhibit marked similarities, but sex chromosomes differ. In these two species, the Y chromosome is a small metacentric one without paracentromeric heterochromatin, and corresponds to pair No. 14. In *E. roseus,* the sex chromosomes have the same metacentric morphology, but in *E. migueli* the X chromosome is telocentric. This example of chromosomal divergence between two members of the *roseus* group (which share the same temporal and spectral characteristic of the advertisement calls) suggests that chromosomal differentiation has played a more important role in the diversification of some members of the *roseus* species group than has the advertisement call. Finally, based on chromosome data, we suggest that vocal differences noted for *Eupsophus* species that occur in sympatry results from the presumed independent evolutionary histories of the taxa involved.

Acknowledgments

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TWO NEW SPECIES OF THE *HYLA SUMICHRASTI* GROUP (AMPHIBIA: ANURA: HYLIDAE) FROM MEXICO

Joseph R. Mendelson III and Jonathan A. Campbell

Abstract.—Two new species belonging to the *Hyla sumichrasti* group of Mexico are described; one is from the cloud forests of the southeastern Oaxacan highlands and the other from the extremely xeric Zapotitlán Valley of Puebla. The new species from Oaxaca can be distinguished from other members of the group based on body proportions and external morphology. The new species from Puebla resembles *H. sumichrasti,* but differs in hand size and morphology, snout shape, and presence of vomerine teeth. A canonical analysis of morphometrics of the four species in the group reveals that *H. sumichrasti* and the new species from Puebla are similar, but distinguishable, whereas *H. smaragdina* and the new species from Oaxaca are distinct from the other members of the group. *Hyla sumichrasti* is reported for the first time from the state of Guerrero.

Resumen.—Se describen dos especies nuevas que pertencen al grupo *Hyla sumichrasti* de México, una del bosque de neblina de las montañas del sureste de Oaxaca y la otra del valle árido de Zapotitlán en Puebla. La especie nueva de Oaxaca se puede distinguir de los otros miembros del grupo sobre la base de sus proporciones corporales y su morfología externa. La especie nueva de Puebla es similar a *H. sumichrasti,* pero tiene manos de forma y tamaño diferentes, hocico de forma diferente y dientes vomerinos. Un análisis canónico de la morfometría de las cuatro especies del grupo revela que *Hyla sumichrasti* y la especie nueva de Puebla son similares, pero se pueden distinguir mientras que *Hyla smaragdina* y la especie nueva de Oaxaca son distintas de los otros miembros del grupo. Se reporta por primera vez una población de *Hyla sumichrasti* para el estado de Guerrero.

Nearly 20 years have passed since the description of any new members of the speciose genus *Hyla* from the vast and geographically complex regions of Mexico (see Caldwell 1974). We examined two enigmatic series of specimens belonging to the *Hyla sumichrasti* group (Duellman 1970), which is endemic to Mexico, and conclude that each represents an undescribed species.

Members of the *Hyla sumichrasti* group (*H. sumichrasti* and *H. smaragdina,* from southern and western Mexico, respectively) have larvae with immense mouths containing three upper and seven lower tooth rows and the adults have distinctively broad, flat heads with a unique combination of cranial characters—viz. massive nasals that are in broad contact medially, a short and broad sphenethmoid, a large frontoparietal fontanelle, and absence of quadratojugals (Duellman 1970). By virtue of these characters, the group is remarkably distinct from other species groups in Middle America (Duellman 1970). Herein we describe two new species which we place in the *H. sumichrasti* group based on the cranial and external characters of the adults.

Materials and Methods

Terminology and measurements follow those described by Duellman (1970) and the descriptions are formatted similarly for ease of comparison. Webbing formulae for hands and feet follow Myers & Duellman (1982). All measurements were taken by the same person (JRM) using digital calipers. Observations were made under a dissecting microscope. The condition of the nasal bones was evaluated by lifting the skin of the snout posteriorly until the bones were exposed. Comparative material examined is listed in Appendix 1; specimens examined are from the collections at The University of Kansas (KU), The University of Texas at Arlington (UTA), and the California Academy of Sciences (CAS). All localities were presented in metric measurements. Localities of type specimens are presented here as they appear in the original catalogues. Small sample sizes limited comparisons and morphometric analysis to male specimens only.

Stepwise discriminant function analysis (DFA) was performed using the BMDP computer program on the following morphometric measurements (all log-transformed): (1) snout–vent length (SVL), (2) tibia length, (3) foot length, (4) head length, (5) head width, (6) anterior margin of tympanum—posterior margin of eye distance, (7) eye–nostril distance, (8) diameter of tympanum, (9) length of first finger, (10) length of third finger, and (11) diameter of disc on third finger.

Systematics

Hyla chimalapa, new species

Figs. 1; 2A; 3A

Holotype.—UTA A-13365 (original number JAC 9324), a male from Colonia Rodulfo Figueroa, 19 km NW Rizo de Oro (Chiapas), 1542 m, Oaxaca, Mexico; obtained on 4 Aug 1983 by J. A. Campbell, D. M. Hillis, and W. W. Lamar.

Paratopotype.—UTA A-13366, a male, other data as for holotype.

Paratypes.—CAS 170121, 170122, 170124, 170125, 170127, 170130, adult males, and CAS 170119, 170120, 170123, 170126, 170128, 170129, adult females, from 5–7 mi NW Rizo de Oro along road to Cerro Baul, Chiapas, Mexico, 3300 feet elev., collected by D. E. Breedlove on 19 Apr 1972; CAS 170114, an adult female from 12 mi W of Rizo de Oro (Chiapas) along ridge south of Cerro Baul, Oaxaca, Mexico, 5000 feet elev., obtained by D. E. Breedlove on 28 Apr 1972.

Referred specimens.—KU 179072, an adult male from 6.5 km (by road) NE Miltepec (=Niltepec), Oaxaca, Mexico, obtained by D. R. Frost and S. Aird on 16 Jun 1977. CAS 163309, an adult female from 1.6 km W Rizo de Oro, crest of ridge between Tapanatepec and Cintalapa Valley, 853 m, Chiapas, Mexico, obtained by D. E. Breedlove on 12 Jun 1965.

Diagnosis.—*Hyla chimalapa* is referred to the *H. sumichrasti* group because of the broad, flat head and large nasals that are in broad contact medially. This species may be distinguished from other members of this group by the following combination of characters: (1) tympanum distinct; (2) snout acutely pointed in dorsal view and protruding, pointed in lateral view; (3) vomerine teeth absent; (4) tongue round; (5) tarsal fold distinct; (6) tibiotarsal articulation extending to snout; (7) fingers long, slender, about half webbed; (8) transverse dermal fold on heel absent; (9) ventral coloration extending from axilla onto dorsomedial surface of upper arm; and (10) row of ulnar tubercles present.

Hyla chimalapa differs from *H. sumichrasti* by having relatively longer legs; a relatively wider head; a distinct tympanum; round tongue; snout protruding and pointed in lateral view (Fig. 3a, c); fingers longer,

Fig. 1. *Hyla chimalapa*, holotype, UTA A-13365, photographed in life.

more slender; distinct tarsal fold present; transverse dermal fold on heel absent; dorsomedial surface of upper arm light; row of ulnar tubercles present; and vomerine teeth absent. *Hyla chimalapa* differs from *H. smaragdina* by being larger, and by having relatively longer legs; a relatively wider head; flecking on dorsum less extensive; dorsomedial surface of upper arm light; snout more pointed in dorsal and lateral view (Fig. 3a, d); tongue round; row of ulnar tubercles present; fingers relatively longer, more slender, about half webbed; transverse dermal fold on heel absent; and vomerine teeth absent. *Hyla chimalapa* differs from *Hyla xera* (described below) by being smaller, and by having relatively longer legs; snout more pointed in profile; fingers longer, more slender, about half webbed; distinct tarsal fold present; row of ulnar tubercles present; palmar tubercle present; transverse dermal fold on heel absent; and dorsomedial surface of upper arm light.

Description of holotype.—Body robust; head as wide as body, slightly wider than long; head width 34.5 percent SVL; head length 33.7 percent SVL; snout acutely pointed in dorsal view, protruding and pointed in profile; distance from eye to nostril equal to diameter of eye; nostril four-fifths distance from eye to tip of snout; top of head flat, smooth; canthus rostralis distinct, rounded; loreal region flat; lips thin, barely flared; interorbital distance about 50 percent greater than width of eyelid; tympanum distinct with raised annulus, diameter about equal to distance from eye to tympanum; supratympanic fold thin, obscuring posterodorsal margin of tympanum, extending posteriorly from orbit, postero-

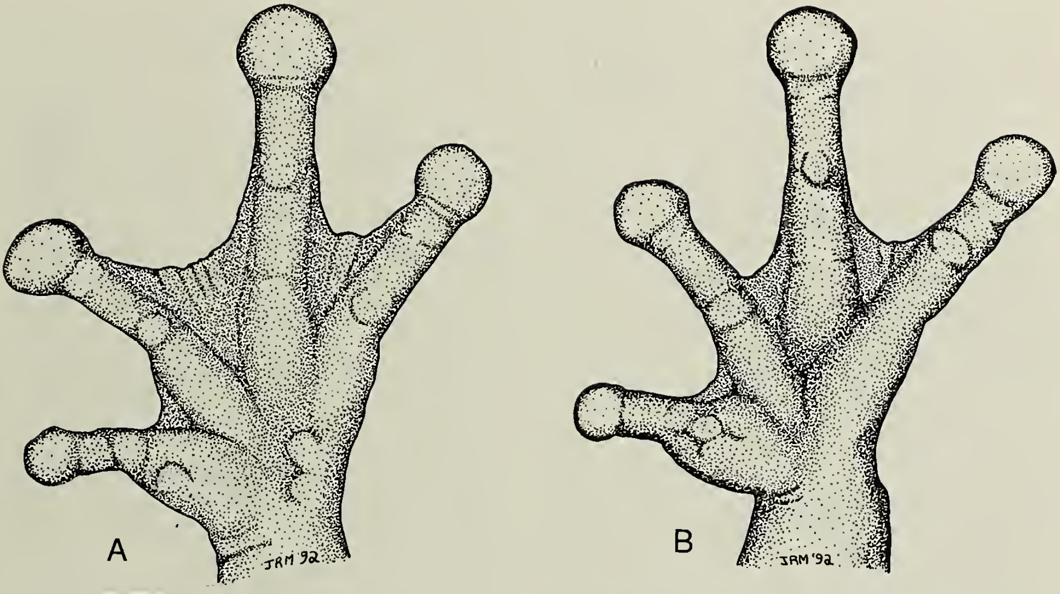

Fig. 2. Ventral aspect of the hand of (A) *Hyla chimalapa,* holotype, UTA A-13365, and (B) *Hyla xera,* holotype, UTA A-13387. Scale bar represents 2 mm.

ventrally from point above tympanum, becoming indistinct at point over the insertion of the arm.

Axillary membrane extending about one-fourth length of upper arm; ulnar tubercles present, weakly defined; dermal fold on wrist distinct; fingers long, slender, bearing expanded, slightly ovoid terminal discs; diameter of disc on third finger slightly larger than diameter of tympanum; relative length of fingers $1 < 4 < 2 < 3$; fingers about half webbed with slight lateral fringe on all fingers except first, and medial surface of second; webbing formula $\mathrm{I}2^{+}-2^{+}\mathrm{II}2^{+}-2^{+}\mathrm{III}2^{+}-2^{-}\mathrm{IV}$; subarticular tubercles indistinct except for round, elevated tubercles on first finger; supernumerary tubercles absent; palmar tubercle small, low, bifid; prepollex barely evident, lacking horny excrescence. Hind limb long; shank robust; tibia length 56.6 percent SVL; foot length 49.4 percent SVL; heels of adpressed limbs overlapping by one third length of shank; tibiotarsal articulation extending to snout; tarsal fold distinct, extending full length of tarsus; transverse dermal fold on heel absent; inner metatarsal tubercle small, oval, low; outer metatarsal tubercle absent; subarticular tubercles round, low, flat; supernumerary tubercles absent; toes long, slender, bearing round discs slightly smaller than those on fingers; toes about three-fourths webbed with lateral fringe except on outer edges of first and fifth toes; webbing formula $\mathrm{I}1-2^{-}\mathrm{II}1-2^{-}\mathrm{III}1-2^{-}\mathrm{IV}2^{-}-1\mathrm{V}$.

Skin on throat and belly granular, other surfaces smooth; cloacal opening directed posteroventrally at midlevel of thighs; cloacal sheath short. Vomerine teeth absent. Choanae small, subcircular, widely spaced. Tongue round, barely free posteriorly. Vocal slits extending from midlateral base of tongue nearly to angle of jaw; vocal sac single, median, subgular.

Measurements (mm): Measurements of the holotype followed by those of the paratopotype in parentheses. SVL 24.9 (23.3), tibia length 14.1 (13.6), foot length 12.3 (11.4), head length 8.4 (7.9), head width 8.6 (8.0), interorbital distance 3.7 (3.2), eyelid

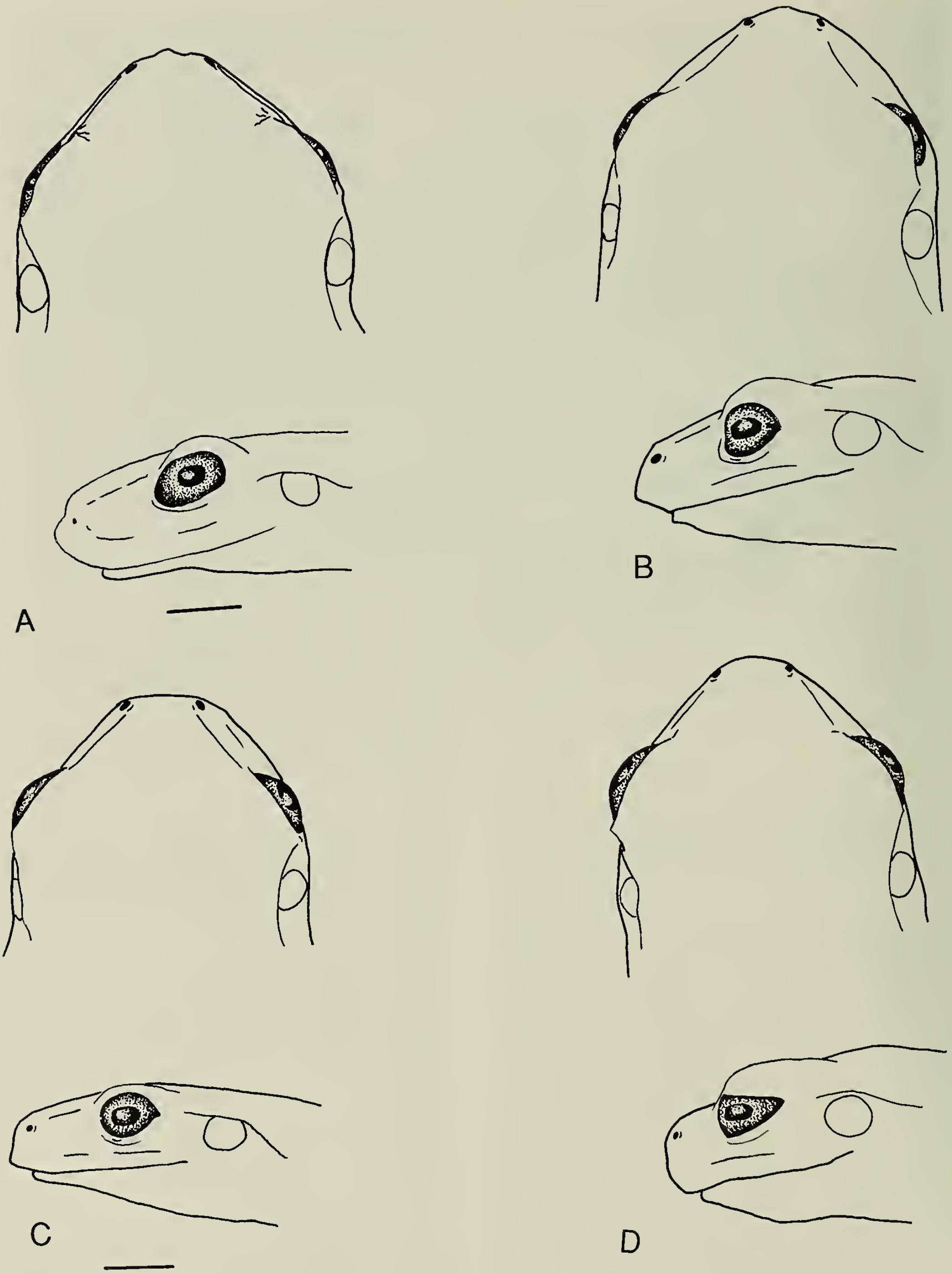

Fig. 3. Dorsal (upper) and lateral (lower) profiles of the snouts of (A) *Hyla chimalapa*, holotype, UTA A-13365, (B) *Hyla xera*, holotype, UTA A-13387, (C) *Hyla sumichrasti*, KU 100941, and (D), *Hyla smaragdina*, KU 75314. Scale bar represents 2 mm.

width 2.4 (2.5), eye–nostril distance 2.9 (2.7), eye diameter 3.2 (2.7), tympanum diameter 1.4 (1.4).

Color in preservative (70 percent ethanol after formalin): Dorsum of head, forearms, fourth and fifth fingers dark brown; dorsum of body, and hind limbs pale brown with few, scattered, dark brown flecks; dorsum of first and second fingers cream with fine brown stippling; axillary area and dorsomedial surface of arms cream; flanks, all ventral surfaces cream, except posterior surface of thighs, periphery of lower jaw and ventral surface of hands and feet cream with fine brown stippling; tarsal fold sharply separating dorsal and ventral colors on foot.

Color in life (from UTA Slide No. 133): Dorsal surfaces pale brown with scattered small dark brown flecks; head and tympanic area darker than other surfaces; tympanum pale brown with cream flecks; posterior surface of thigh and ventral surface of tibia red-orange; first finger pale yellow; flanks cream with brown stippling; iris dull gold with black reticulations.

Variation.—The measurements of the paratypes and the referred specimens are as follows (mm; range followed by mean in parentheses for males and females, respectively): SVL 20.3–23.6 (22.1), 18.4–26.6 (23.7); tibia length 10.9–12.3 (11.5), 10.8–14.2 (12.7); foot length 9.2–10.2 (9.6), 9.2–12.9 (11.2); head length 6.7–7.4 (7.2), 6.6–9.0 (7.8); head width 6.7–8.0 (7.3), 6.4–8.7 (8.0); eye–nostril distance 2.2–2.5 (2.4), 2.1–3.1 (2.6); tympanum diameter 1.0–1.2 (1.1), 1.1–1.6 (1.4). The proportions of the female specimens are given here rather than in Table 1 because we did not examine comparable numbers of females of the other species in the group: tibia/SVL 0.50–0.56 (0.54); foot/SVL 0.45–0.50 (0.47); head length/SVL 0.29–0.36 (0.33); head width/SVL 0.32–0.37 (0.34).

The paratypes and referred specimens are similar to the holotype in proportion and are similar in color in preservative. The ulnar tubercles are more distinct in these specimens than in either the holotype or the paratopotype and the profile of the snout is more rounded; the protuberance illustrated in Fig. 3A is less pronounced in the paratypes.

Distribution and ecology.—*Hyla chimalapa* is known only from the southeastern Oaxacan Highlands, which includes the Sierra Atravesada (sensu Campbell 1984). This area is known locally as the *Chimalapa* region. All specimens have been collected between the town of Rizo de Oro and Cerro Baul—the highest peak in the region, except one (KU 179072) from the Sierra Atravesada. In August 1992, the Cerro Baul area still supported some disturbed cloud forest. This region is characterized by a complex mosaic of mesic cloud forest and relatively xeric pine-oak forests. The type locality is in cloud forest but there are no habitat notes associated with the remaining specimens and they may have been collected in the more xeric areas. The other species in the *H. sumichrasti* group inhabit moderately to extremely xeric habitats and it is possible that *H. chimalapa* occurs in the dry pine-oak forests of the region. The holotype and paratopotype were discovered at night along a wide, shallow stream at the edge of Colonia Rodulfo Figueroa. This stream flows swiftly over a sand and gravel substrate, forming numerous sandbars; in August 1992, these sandbars were covered by dense stands of young willows (*Salix* sp.) that were not present when the types of *H. chimalapa* were collected. Other species of anurans from this area include *Bufo marinus, B. valliceps, Rana maculata, Eleutherodactylus lineatus, E. leprus, Ptychohyla euthysanota,* and *Plectrohyla matudai.*

Life history.—The advertisement call, eggs, and tadpole of *H. chimalapa* are unknown. Adult females (CAS 170128, 170129) collected on 19 Apr 1972 contain partially developed ova, and another adult female (CAS 170123) from this date contains no apparent ova. An adult female (CAS 170114) obtained on 28 Apr 1972 contains

Table 1.—Comparison of selected measurements (mm), proportions, and morphological features of adult males of the *H. sumichrasti* group. Character abbreviations SVL, snout–vent length; TL, tibia length; FT, foot length; HL, head length; HW, head width. Range of values followed by means in parentheses.

Character	*H. sumichrasti*	*H. smaragdina*	*H. chimalapa*	*H. xera*
SVL	22.5–27.1 (24.5)	22.7–25.5 (24.0)	20.1–24.9 (22.1)	25.8–27.9 (26.8)
TL/SVL	0.43–0.53 (0.48)	0.43–0.49 (0.46)	0.50–0.58 (0.54)	0.46–0.50 (0.48)
FT/SVL	0.39–0.48 (0.42)	0.40–0.48 (0.44)	0.43–0.49 (0.45)	0.42–0.45 (0.43)
HL/SVL	0.29–0.33 (0.31)	0.30–0.33 (0.32)	0.31–0.34 (0.33)	0.29–0.32 (0.31)
HW/SVL	0.30–0.34 (0.32)	0.27–0.30 (0.28)	0.32–0.36 (0.34)	0.30–0.32 (0.31)
Snout (dorsal)	Bluntly rounded	Rounded	Acutely pointed	Acutely rounded
Snout (lateral)	Flattened	Rounded	Protruding	Bluntly rounded
Tarsal fold	Variable	Strong	Strong	Weak
Heel fold	Present	Present	Absent	Present
Tibiotarsal articulation	Orbit	Orbit	Snout	Orbit
Hand webbing	I2^{+}—2½ II2^{-}—2½ III2¾—2^{+}IV	I2^{+}—2¾ II2^{-}—3^{+} III3^{-}—2^{+}IV	I2^{+}—2^{+} II2^{+}—2^{+} III2^{+}—2^{-}IV	I2½—2¾ II2^{-}—3^{-} III2½—2^{+}IV
Vomerine teeth	Variable	Present	Absent	Absent
Palmar tubercle	Present	Present	Present	Absent
Ulnar tubercles	Absent	Absent	Present	Absent

a large number of mature ova, as does an adult female (CAS 163309) obtained on 12 Jun 1965. Only one male (KU 179072; 16 Jun 1972) appears to be in breeding condition. This specimen bears nuptial excrescences and a distended vocal sac.

Etymology.—The specific name is treated as indeclinable and refers to the spectacular and still incompletely surveyed *Chimalapa* region of eastern Oaxaca, from which this species is known.

Remarks.—The type locality may be reached by way of a long, tortuous drive along an unpaved road bearing NW from the small town of Rizo de Oro, Chiapas (NE of Tapanatepec on MX Hwy 190). Whether the type locality is in Oaxaca or Chiapas is a matter of local dispute; however, most maps show Cerro Baul to be in Oaxaca. This area is near the continental divide but Colonia Rodulfo Figueroa lies near the headwaters of the Río Mono Blanco, a tributary of the Río Negro (an Atlantic drainage).

The southeastern Oaxacan highlands have complex biogeographic relationships with the proximal highland areas of southern Mexico (Campbell 1984). This area shares approximately the same number of amphibian species with the distant Sierra de los Tuxtlas of Veracruz as it does with the more proximal Sierra Madre de Chiapas (Campbell 1984), but no member of the *H. sumichrasti* group is known from these two regions. The Sierra Madre de Chiapas shares several disjunct, but poorly differentiated, species of cloud forest anurans with the southeastern Oaxacan highlands (Campbell 1984). It is possible that *H. chimalapa* will be discovered in this range, especially if it does inhabit the more widespread pine-oak forests (Breedlove 1973) of the region.

Hyla sumichrasti is known to the east of the southeastern Oaxacan highlands, in the xeric areas of the Sierra Madre del Sur and the Isthmus of Tehuantepec, and to the northwest from the more humid areas in the Central Depression and the cloud forests near Pueblo Nuevo Solistahuacan, Chiapas (Duellman 1970); this species has not been collected in the southeastern Oaxacan highlands. *Hyla sumichrasti* is more variable in its external morphology than the other members of the group. Variation exists both within and among populations in such char-

Fig. 4. *Hyla xera,* holotype (preserved), UTA A-13387.

acters as the presence of vomerine teeth, presence and degree of development of the tarsal fold, overall body proportions (Table 1) and details of color pattern evident in preserved specimens. For this reason we examined populations from both east and west of the southeastern Oaxacan highlands (Appendix 1) in preparing the diagnosis for *H. chimalapa* and the morphometric analysis. Despite the variation evident in *H. sumichrasti, H. chimalapa* is diagnosable on the basis of traditional external characters and proportions (Table 1, Fig. 5).

Duellman (1970) commented that *H. sumichrasti* and *H. smaragdina* may be conspecific, and cited the existence of a large distributional hiatus between the two species along the west coast of Mexico, despite the existence of suitable habitat in Guerrero. We here take the opportunity to report a series of specimens referable to *H. sumichrasti* collected by T. Pappenfuss in 1976 in Guerrero (Appendix 1). The discovery of this population does not support the hypothesis that *H. sumichrasti* and *H. smaragdina* are conspecific.

Hyla xera, new species
Figs. 2B; 3B; 4

Holotype. —UTA A-13387 (original number JAC 6577), an adult male from 5.6 km SSW Zapotitlán Salinas, 1490 m, Puebla, Mexico; obtained on 1 July 1981 by J. A. Campbell.

Paratopotypes. —UTA A-13381–83, 13385, 13386, 13388 adult males, and UTA A-13384, an adult female, all collected with the holotype by J. A. Campbell.

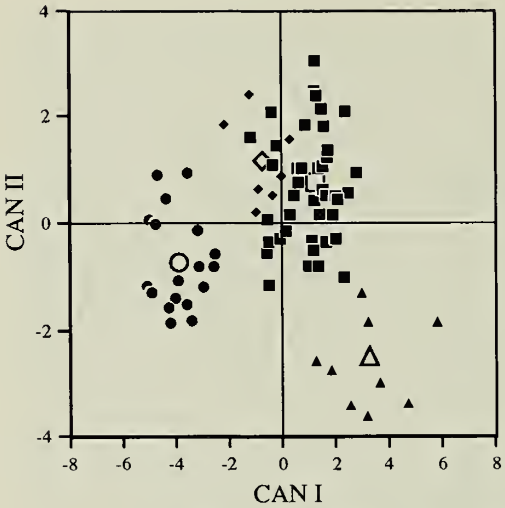

Fig. 5. Plot of canonical discriminant scores for all species in the *Hyla sumichrasti* group: *H. chimalapa* (triangles), *H. smaragdina* (circles), *H. sumichrasti* (squares), and *H. xera* (diamonds). Closed symbols represent individual scores, open symbols indicate group mean scores.

Diagnosis.—Hyla xera is referred to the *H. sumichrasti* group because it has a broad, flat head and large nasals that are in broad contact medially. This species can be distinguished from all other members of the group by the following combination of characters: (1) large SVL in adult males ($\bar{X}$ = 26.8); (2) a uniformly dull gray dorsum, with darker loreal and tympanic areas (in preservative); (3) tympanum distinct; (4) supratympanic fold thick, darkly colored; (5) snout acutely rounded in dorsal view, bluntly rounded in lateral view, sometimes with weak rostral keel; (6) dermal folds on wrist and heel present; (7) tarsal fold weakly developed; (8) fingers long, slender, about one-third webbed; (9) palmar tubercle absent; (10) tibiotarsal articulation extending to anterior margin of orbit; (11) vomerine teeth absent; (12) tongue cordiform; (13) row of ulnar tubercles absent; and (14) transverse dermal fold on heel present.

Hyla xera differs from *H. sumichrasti* by having a distinct tympanum with a thick, darkly colored supratympanic fold; snout more rounded profile (Fig. 3B, C); palmar tubercle absent; fingers relatively longer; vomerine teeth absent; and SVL of adult males probably larger (Table 1; but see Duellman 1970). *Hyla xera* differs from *H. smaragdina* by being larger; snout less rounded in dorsal and lateral view (Fig. 3B, D); supratympanic fold thick, darkly colored; flecking on dorsum less extensive; tarsal fold weakly developed; palmar tubercle absent; fingers longer, more slender; and vomerine teeth absent. *Hyla xera* differs from *H. chimalapa* by being larger and having legs relatively shorter; snout more rounded in dorsal and lateral view (Fig. 3A, B); tarsal fold weakly developed; ulnar tubercles absent; palmar tubercle absent; fingers about one-third webbed; transverse dermal fold on heel present; and supratympanic fold thick, darkly colored.

Description of holotype.—Body robust; head as wide as body, slightly wider than long; head width 31.7 percent SVL; head length 30.0 percent SVL; snout acutely rounded in dorsal view with weak rostral keel, bluntly rounded in profile; distance from eye to nostril equal to diameter of eye; nostril four-fifths distance from eye to tip of snout; top of head flat, smooth; canthus rostralis distinct, rounded; loreal region slightly concave; lips thin; interorbital distance about 70 percent greater than width of eyelid; tympanum distinct without raised annulus, diameter about equal to distance from eye to tympanum; supratympanic fold thick, obscuring dorsal and posterodorsal margins of tympanum, extending posteriorly from orbit, posteroventrally from point above tympanum, becoming indistinct anterior to arm.

Axillary membrane extending about one-third length of upper arm; ulnar tubercles absent; dermal fold on wrist distinct; fingers long, slender, bearing expanded, round, terminal discs; diameter of disc on third finger slightly smaller than diameter of tympanum; relative length of fingers 1 < 2 < 4 < 3; fingers about one-third webbed, without lateral fringe; webbing formula I2½—2¾II2—3^{-}III2½—2^{+}IV; subarticular tubercles indistinct except for round, elevated tubercles on first finger; supernumerary tubercles absent except on prepollex; palmar tubercle absent; prepollex enlarged, bearing horny excrescence barely visible ventrally, covering posterior and dorsal portions of prepollex. Hind limbs long; shank robust; tibia length 48.7 percent SVL; foot length 42.2 percent SVL; heels of adpressed limbs overlapping by one-third length of shank; tibiotarsal articulation extending to anterior margin of orbit; tarsal fold absent; transverse dermal fold on heel distinct; inner metatarsal tubercle small, oval, low; outer metatarsal tubercle absent; subarticular tubercles small, round, slightly elevated on first and second toes, low, round, flat on fourth and fifth toes; supernumerary tubercles absent except on base of first toe; toes long, slender, bearing round discs about the same size as those on fingers; toes about three-fourths webbed, lacking lateral fringe except on fourth toe; webbing formula I1—2^{+}II1—2½III1—2^{+}IV2—1V.

Skin on throat and belly granular, other surfaces smooth; cloacal opening directed posteroventrally at midlevel of thighs; cloacal sheath short. Vomerine teeth absent. Choanae small, slightly ovoid, widely spaced. Tongue cordiform, barely free posteriorly. Vocal slits extending from midlateral base of tongue to nearly to angle of jaw; vocal sac single, median, subgular.

Measurements of the holotype (mm): SVL 26.7; tibia length 13.0; foot length 11.3; head length 8.0; head width 8.5; interorbital distance 3.0; eyelid width 2.0; eye–nostril distance 2.7; tympanum diameter 1.6.

Color in preservative (70 percent ethanol after formalin): All dorsal surfaces dull gray except feet and thighs pale brown; loreal and tympanic areas darker than dorsum of head, dark coloring following and clearly demarcating supratympanic fold; supratympanic areas and dorsal surfaces of shanks with dull silver marbling; posterior surface of thigh dull yellowish brown; flanks and all ventral surfaces dull cream; palmar and plantar surfaces cream with very fine gray stippling.

Variation.—The range of variation (mm; with means in parentheses) of the male paratopotypes are followed by those of the female paratopotype. SVL 25.6–27.9(26.9), 31.2; tibia length 12.5–13.3(12.8), 15.4; foot length 11.0–12.4(11.8), 13.1; head length 8.1–8.9(8.3), 9.1; head width 8.1–8.8(8.4), 10.3; interorbital distance 2.9–3.1(3.0), 3.5; eyelid width 1.9–2.4(2.1), 2.2; eye–nostril distance 2.7–2.8(2.8), 3.1; tympanum diameter 1.3–1.8(1.5), 1.6. Variation in body proportions are summarized in Table 1 and, along canonical axes, in Fig. 5. The coloration (in preservative) of all paratopotypes is very similar to that of the holotype, except UTA A-13382 (male) and UTA A-13384 (female), which have distinctive dull silver and dull brown marbling on the flanks and posterior surfaces of the shanks and tarsi. The transverse dermal fold and tarsal fold are weakly developed in this species and appear to be absent in some individuals in the type series.

Distribution and ecology.—*Hyla xera* is known only from the type locality. This area supports arid tropical scrub (sensu Leopold 1950) and is characterized by scattered mesquite trees (*Prosopis*), other leguminous trees, and many species of cactus. Patches of thorn forest and tropical deciduous forest occur locally, especially in the draws. No permanent water occurs naturally in the Zapotitlán Valley, even the largest stream draining the valley is seasonal. Most specimens (UTA A-13381–87) were taken by day from beneath rocks along a small stream; one male (UTA A-13388) was calling from a rock in this stream at night. Other species of anurans taken from this region are *Bufo occidentalis, Eleutherodactylus nitidus,* and *Scaphiopus multiplicatus.*

Life history.—Little is known about the life history of *H. xera.* The advertisement call, eggs, and tadpole remain undescribed. All male specimens reported herein have well developed nuptial excrescences and may be in breeding condition; however, their vocal sacs are not distended. The oviducts of the female paratopotype contain many well-developed ova.

Etymology.—The specific name is derived from the Greek *xeros* meaning dry, in allusion to the desert habitat of this species.

Morphometric analysis.—We performed a stepwise DFA of 11 morphometric variables (see Materials and Methods) on adult males of *H. sumichrasti* (Chiapas, $n = 16$; Oaxaca: Portillo Nejapa, $n = 13$; Oaxaca: Mitla, $n = 14$—populations combined for analysis), *H. smaragdina* ($n = 18$), *H. xera* ($n = 7$), and *H. chimalapa* ($n = 8$). Morphometric variables 1, 2, 3, 5, and 10 varied significantly among groups ($F < 0.001$) in the stepwise analysis and were included in the canonical discriminant analysis. Group means were different ($F < 0.001$) at each step in the five-step model and 100 percent of the variation was displayed on three canonical axes; the first two axes displayed 95 percent of the variation (CAN I, CAN II; Fig. 5). The standardized (pooled within group variances) coefficients for the canonical variables were: CAN I (CAN II) = 1: −1.62 (1.05), 2: 0.95 (−0.78), 3: −0.77 (−0.02), 5: 1.63 (0.60), 10: −0.17 (−0.36).

All individuals of *H. xera, H. chimalapa,* and *H. smaragdina* were correctly classified in the jackknifed classification matrix of the five-step model. Three individuals of *H. sumichrasti* were misclassified as *H. xera* and one as *H. chimalapa.*

Hyla smaragdina is well separated from the other species along CAN I and *H. chimalapa* is well separated from the other species along both axes. *Hyla sumichrasti* and *H. xera* are significantly different in this analysis, albeit weakly separated from one another along the first two canonical axes; although these two species are similar in overall proportions (Fig. 5), they are clearly distinguishable on the basis of other external characters.

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Appendix 1

Comparative material examined (all from Mexico): *Hyla smaragdina*: *Sinaloa*: 1.6 km E Santa Lucía, 1280 m (KU 68719); Santa Lucía, 1097 m (KU 75295–

333); 2.2 km NE Santa Lucía, Hwy 40, 1157 m (KU 78380–82).

Hyla sumichrasti: *Chiapas*: Linda Vista, ca 2 km NW Pueblo Nuevo Solistahuacán, 1675 m (KU 57857–85). *Guerrero*: Sierra Madre del Sur, 3.1 km SW Rio Santiago on road to Atoyac, 762 m (CAS 143116–143149). *Oaxaca*: 14 km E El Camaron, 1240 m (KU 100934–46); 6.0 km N Mitla (UTA A-2827, 2881–95); 8.8 km N Mitla (UTA A-2916–19); 6.4 km E Mitla (UTA A-2920–29, 2931–33, 3255–56, 3284); 8.8 km E Mitla (UTA A-4673–77); 6.0 km ENE Mitla (UTA A-5889–90).

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A NEW FOSSORIAL SNAKE OF THE GENUS *GEOPHIS* (REPTILIA: SERPENTES: COLUBRIDAE) FROM THE CORDILLERA DE TALAMANCA OF COSTA RICA

Karen R. Lips and Jay M. Savage

Abstract.—*Geophis talamancae,* a new species of colubrid snake from south-central Costa Rica is described. The new form belongs to the *sieboldi* group, which includes five Mexican species, *G. nasalis* (Guatemala), *G. hoffmanni* (Honduras to western Panama), *G. zeledoni* (central Costa Rica), *G. nigroalbus* (eastern Panama to Colombia), and *G. brachycephalus* (northern Costa Rica, Panama and Colombia). We reallocate *Geophis betaniensis* of Colombia, previously referred to the *championi* group, to the *sieboldi* group; present scale counts of *G. godmani* from populations geographically intermediate to those previously known; comment on distinguishing between *Geophis* and *Atractus* on the basis of chin shields and temporal scales; and present a key to the *Geophis* species of Lower Central America and Colombia.

Resumen.—En este trabajo se describe a *Geophis talamancae,* una nueva especie de serpiente colúbrida del centro-sur de Costa Rica. Esta nueva forma pertenece al grupo *sieboldi,* el cual incluye a 5 especies mexicanas y a *G. nasalis* (Guatemala), *G. hoffmanni* (Honduras a Panamá occidental), *G. zeledoni* (Costa Rica central), *G. nigroalbus* (Panamá oriental hasta Colombia) y *G. brachycephalus* (norte de Costa Rica, Panamá, y Colombia). Se reasigna a *Geophis betaniensis* de Colombia, previamente en el grupo *championi,* al grupo *sieboldi*; se proporcionan números de escamas de *G. godmani* de poblaciones intermedias geográficamente a las conocidas anteriormente y se comenta sobre la distinción entre *Geophis* y *Atractus* con base en las escamas geneiales y temporales. Finalmente se presente una clave para las especies de *Geophis* del sur de Centroamérica y Colombia.

A single example of a rather nondescript snake of the genus *Geophis* was collected during a survey of the herpetofauna of the Zona Protectora Las Tablas of the Reserva de la Biosfera la Amistad of Costa Rica, near the Costa Rica–Panama border by the senior author in 1992. A comparison with other *Geophis* confirms that the unique type appears to represent a population that may be called:

Geophis talamancae, new species
Fig. 1

Holotype.—CRE 5343, an adult female from Costa Rica: Puntarenas Province: Cantón Coto Brus: Zona Protectora Las Tablas, Finca Jaguar, 1800 m elevation; taken 1 Sep 1992 by Karen R. Lips.

Etymology.—The species name is derived from the Cordillera de Talamanca, the mountain range from which the specimen was collected.

Definition.—The features listed below characterize the species and follow the format used by Downs (1967) in his revision of the genus: 1) dorsal scale rows in 15-15-15 rows, strongly keeled on posterior half of body; 2) no anterior temporal; 3) one supraocular and one postocular scale; 4) snout blunt and shovel-shaped, rostral barely projecting posteriorly between internasals; 5) dorsal surfaces of body and of head uniform iridescent black; 6) venter white with black bands on posterior edges of scutes.

Diagnosis.—The new form is a member of the *sieboldi* group (Downs 1967), previously represented by 12 species ranging from Mexico to Colombia and including four that occur in Costa Rica and Panama. *Geophis talamancae* may be distinguished from *G. brachycephalus* by having the dorsal scales on the anterior half of the body smooth and a uniform dorsal coloration (in *brachycephalus* the dorsal scales are keeled except on the neck and there is often a distinct dorsal pattern of light, usually red, bars, spots and/or stripes). The new form differs from both *Geophis zeledoni* and *G. hoffmanni* in the keeling of the dorsal scales since these two forms have keels only on dorsal scales above the vent. Unlike *G. nigroalbus,* which has the postocular and supraocular separated by an anterior projection of the parietal, the supraocular is in broad contact with the postocular in *G. talamancae.* The new species is distinguished from *G. betaniensis* of west-central Colombia (features for that form in parentheses) by having keeled posterior dorsal scales (smooth dorsal scales) and one (two) postocular. Finally, it differs most obviously from the several species of the *G. championi* group, all of which are endemic to Costa Rica and/or Panama, in the shape of the head and associated features of scutellation. *Geophis talamancae* has an elongate snout that is rounded in dorsal outline, a rostral that barely extends posteriorly between the internasals, and a short postnasal that is higher than wide (Fig. 1). In the four members of the *championi* group (*G. championi, G. downsi, G. godmani,* and *G. ruthveni*), the elongate snout is pointed, the rostral separates the internasals for much of their length and the postnasal is broad, the width being at least 75% of its height.

General characteristics.—Head not distinct from neck; snout elongate, rounded in dorsal profile; rostral not extending posteriorly between internasals; its length from above about ⅕ its distance from frontal; internasals large, rounded anteriorly, slightly shorter than suture with prefrontal; prefrontals short, their median suture about ⅔ length of frontal; frontal slightly wider than long, quadrangular, in contact with prefrontals, supraoculars, and parietals, distinctly angulate anteriorly; parietals moderately long, broad, their median suture almost equal to length of frontal; parietal does not contact prefrontal above middle of orbit, but meets the supraocular and postocular scales. There is one postocular and one supraocular scale on each side of the head (Fig. 1).

Nasal divided, postnasal about the same size as prenasal, their combined length about 70% length of loreal; loreal relatively long, slightly more than ½ length of snout, slightly more than 2 times eye diameter; eye small, contained about 4⅓ times in snout length (tip of snout to anterior border of eye), its vertical diameter about equal to distance from supralabials; supralabials 6-6, 3 and 4 in contact with orbit on both sides, 5th in contact with parietal; anterior temporal directly above 6th supralabial, not fused with nuchals along parietal margin.

Mental rounded anteriorly, definitely broader than long, separated from chin shields by first pair of infralabials; infralabials 6-6, first 3 in contact with anterior chin shields; anterior chin shields slightly longer than broad, longer than posterior chin shields; posterior chin shields short, in contact anteriorly, diverging posteriorly; 3 gulars separate chin shields from first ventral.

Dorsal scale rows 15-15-15, keeled on posterior half of body and tail; posterior dorsal scales without discernible apical pits. Ventrals 138; anal entire; subcaudals 33. Ventrals + subcaudals 171. Standard length (snout-to-vent) 185 mm, tail length 33 mm; tail length 16 percent of total length.

Coloration.—Dorsal surfaces of head and body uniform dark charcoal grey to black. Head color extends ventrally to supralabials, infralabials, mental, and chin shields.

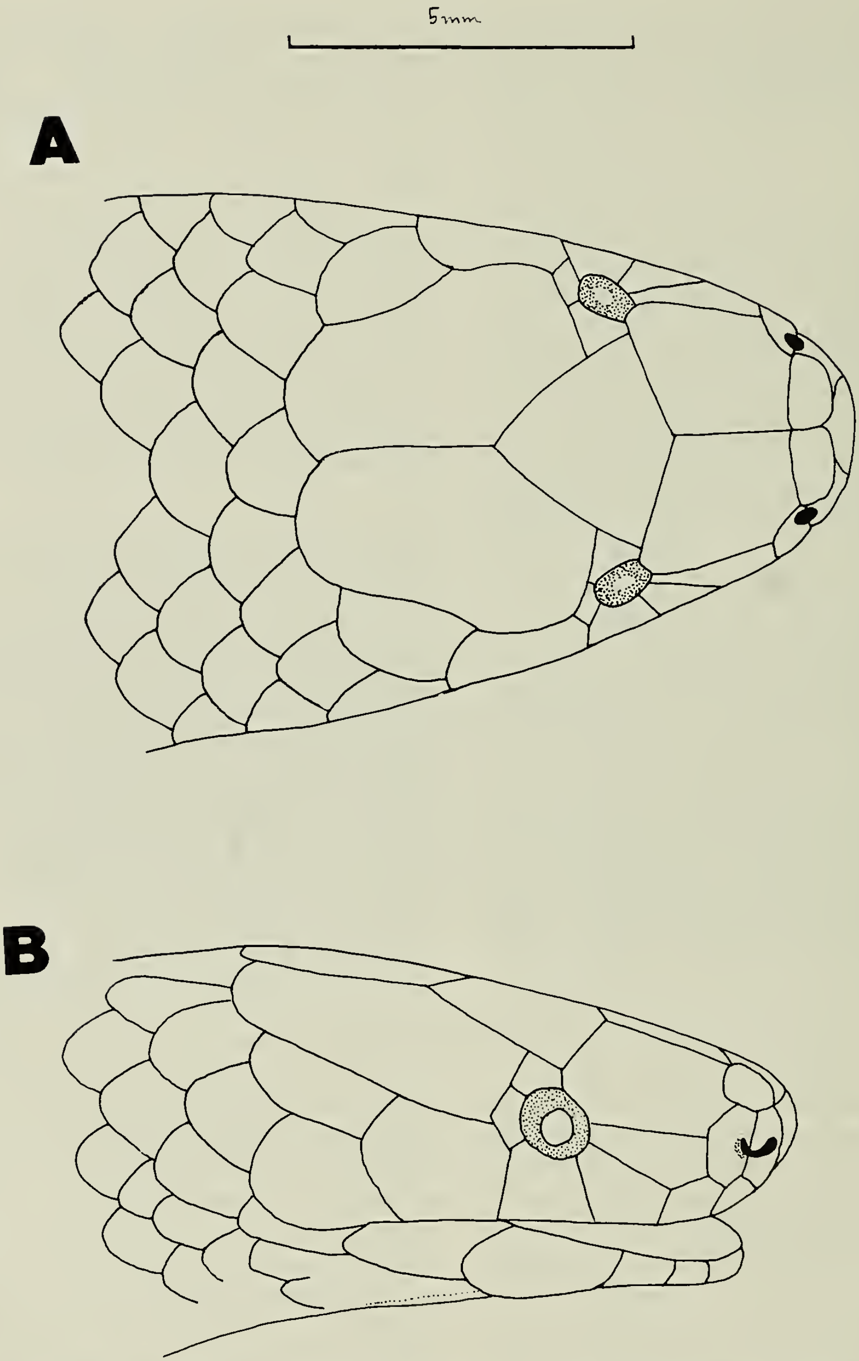

Fig. 1. Semidiagrammatic representation of A) dorsal and B) lateral head scutellation for the holotype (CRE 5343) of *Geophis talamancae*.

Gular area immaculate creamy white, becoming flecked with black on first ventral and becoming progressively more flecked along anterior edge of scutes, until only a very thin white posterior border remains on scutes near vent. Subcaudals completely black, without white markings.

Distribution.—Known only from the type locality in the Lower Montane Rainforest (Holdridge 1967, Tosi 1969) in the Cordillera de Talamanca of Costa Rica near the Panama border at 1800 m elevation.

Remarks.—The type specimen was collected from beneath a series of saplings whose roots were enclosed in plastic bags that had recently (within 4 months) been transported from the region of the central Cordillera de Talamanca along the Carretera Interamericana, about 100 km northwest of the type locality. There is a slight possibility that this snake might have been brought to the Las Tablas area in this shipment. However, a second specimen probably of the same species (white belly with distinct black bands on ventral scutes, uniform black dorsum) was collected from the Las Tablas area earlier in the year but escaped before an accurate identification could be made.

Four specimens of *Geophis godmani* were also collected from the Las Tablas area, representing an intermediate population between the two previously known but disjunct localities: a population from the Cordillera Central and extreme northern edge of the Cordillera de Talamanca in Costa Rica, and a population 250 km ESE of Las Tablas on Volcán Barú in Chiriquí, Panamá. The Panamanian specimens are represented only by heads and necks (Downs 1967) so variation in ventral and subcaudal counts from the southern part of the range was unknown. Because *G. brachycephalus* and *G. hoffmanni* have distinctly lower segmental counts on Volcán Barú than in Costa Rica, Downs (1967) predicted that Panamanian *G. godmani* would vary similarly.

All four specimens have 15-15-15 scale rows; no postocular, no supraocular, and no temporal scales. The number of ventrals for the three males (CRE 5344, 5319, 5072) ranges from 139–141; subcaudals 34–38; ventrals + subcaudals 173–179. The single female specimen (CRE 5337) has 140 ventrals, 27 subcaudals, and 167 ventral + subcaudals. These values do not differ substantially from those of specimens from the north in Costa Rica contra Downs' (1967) prediction. Geographical variation in *G. godmani* exists, however, in the amount of ventral pigmentation between those specimens from the area of the Barva-Poas volcanoes (venter almost uniformly bright yellow in color) and those from Volcán Turrialba south through the Cordillera de Talamanca to Las Tablas (bright yellow color of venter limited to anterior edge of scutes, posterior edge black). It is clear from the differences in ventral color that the escaped snake mentioned above was not *G. godmani.*

Relationships.—The new species is referred to the *Geophis sieboldi* group (Downs 1967) on the following basis: snout long, projecting well beyond lower jaw, rounded in dorsal outline; rostral not produced posteriorly between internasals; internasals short, their greatest length 33–62% of suture between prefrontals; postnasal short, width about 50% of height; prefrontals and loreals elongate; no anterior temporal; rounded mental; maxillary extends forward to suture between second and third supralabials, with 14 subequal teeth, tip of maxillary toothless; posterior end of maxillary tapering to a blunt point.

The *sieboldi* group as understood by Downs (1967) in his generic revision included four Mexican species (*Geophis petersi, G. russatus, G. sallei,* and *G. sieboldi*), one Guatemalan form (*G. nasalis*), one Nicaraguan endemic (*G. dunni*) and *G. brachycephalus* (Costa Rica to Colombia), *G. hoffmanni* (Honduras to western Panamá), *G. nigroalbus* (eastern Panamá to Colombia) and *G. zeledoni* (Costa Rica). Downs provided detailed descriptions of most of these forms but gave belated recognition to *G. nigroalbus* and *G. russatus* only in footnotes (p. 146 and p. 138, respectively). Campbell and Murphy (1977) added another Mexican species (*G. pyburni*) to the group. Within the genus, *G. talamancae* most closely resembles *G. nigroalbus* but differs most obviously in the relation of the parietal to the supraocular and postocular (bordering them posteriorly in *talamancae,* separating them in *nigroalbus*).

Restrepo & Wright (1987) on the occasion of describing *Geophis betaniensis* from Colombia expressed difficulty in accepting Downs' (1967) definitions of species groups and referred their new form to the *championi* group. This decision was reached in part because *G. betaniensis* keyed out to *G. championi* in Downs' key (couplet 29) to the genus. When they used Savage's (1981) key to Costa Rican and Panamanian *Geophis,* they reached a couplet (number 4) that distinguished between *G. hoffmanni* and *G. zeledoni* (*sieboldi* group species) and this seems to be the basis for their puzzlement over species group definitions.

Both keys (Downs 1967, Savage 1981) are artificial ones based upon the most obvious characters of the included species and are designed for field identifications. No attempt was made by either author to design a key in which presumably related form (i.e., members of the same species group) were placed together.

Downs (1967), contrary to Restrepo & Wright (1987), provided unambiguous definitions of the seven species groups that he recognized within *Geophis.* Members of the *championi* group differ from *G. betaniensis* (features for that species in parentheses) in the following characteristics: snout elongate, pointed (rounded); rostral produced posteriorly between internasals (barely projecting between internasals); internasals elongate, greatest length 67–100% of prefrontal suture (50%); postnasal long, width at least 75% of height (postnasal short, width about 50% of height); mental acuminose (rounded). These differences clearly preclude inclusion of *G. betaniensis* in the *championi* group.

Comparison of the features of head shape and scutellation of *Geophis betaniensis* with those of the other species groups of *Geophis* (Downs 1967) show a complete concordance between the Colombian species and members of the *sieboldi* group (see list of characteristics at the beginning of this section). In terms of skeletal and dentitional features the *championi* and *sieboldi* groups are very similar except that in the latter there is no tooth on the tip of the maxillary (present in the former) and the hemipenes of the *championi* group differ in lacking capitation. Unfortunately, features of the hemipenes were not included by Restrepo & Wright (1987) in their original description because the only specimens referred to *G. betaniensis* are both females. Nevertheless we believe that evidence from physiognomy (general shape of the head) and scutellation support the inclusion of *G. betaniensis* in the *sieboldi* group.

Because Colombian species of *Geophis* are sympatric with members of the superficially similar genus *Atractus,* another fossorial group, Restrepo & Wright (1987) discussed features of external morphology that may be utilized to distinguish between them. After some discussion with Frances J. Irish, who is undertaking a systematic revision of *Atractus,* they concluded that the presence (in *Atractus*) and absence (in *Geophis*) of an anterior temporal scale and the number of chin shields (two pairs in *Geophis* and one pair in *Atractus*) are diagnostic for those species found in Central and South America.

Unfortunately, the situation is more complicated than these authors suggest. As pointed out by Savage (1960) and Downs (1967), presence or absence of the anterior temporal exhibits both interspecific and some intraspecific variability in both genera; those *Geophis* characteristically having an anterior temporal are confined to Mex-

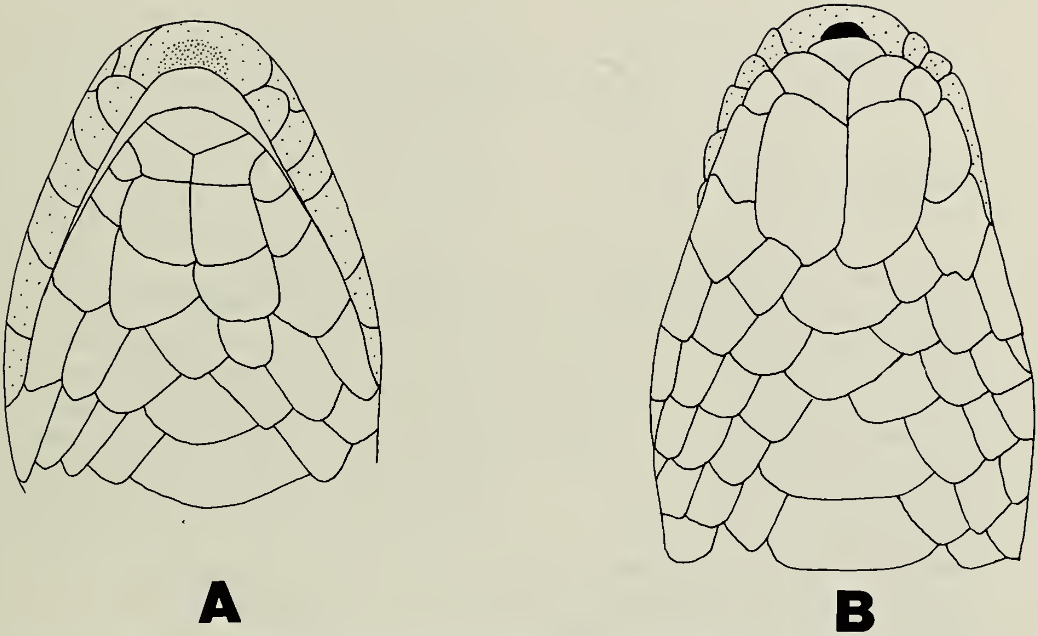

Fig. 2. Diagrammatic differences in chin shields between A) *Geophis* and B) *Atractus.*

ico, and most examples of *Atractus* consistently have one.

Savage (1960) had previously noted that *Geophis* and *Atractus* from the area of geographic overlap in Panamá and Colombia could be distinguished on the basis of the chin shield feature. Downs (1967) however, questioned the utility of this character since it is difficult in some cases to distinguish the posterior chin shield from the adjacent gular scales in *Geophis,* which approaches the condition found in *Atractus.* Nevertheless, although the posterior pair of chin shields are often small and usually separated by a median gular scale, there is no ambiguity in using this feature to separate lower Central and South American *Geophis* from *Atractus* (Fig. 2).

Key to Species of *Geophis* from Lower Central America and Colombia

1a. Supraocular shields present 2
1b. No supraocular scales 10
2a. Two postoculars .... *G. betaniensis* (Colombia)
2b. One postocular 3
3a. Uppermost dorsal scales keeled at least on posterior half of body and tail 4
3b. Dorsal and caudal scales smooth or smooth except for some faintly keeled scales above vent 8
4a. Dorsal scales on body (exclusive of neck) and tail distinctly keeled 5
4b. Dorsal scales on anterior half of body smooth 6
5a. Dorsal scales in 15 rows; dorsum dark, often with light lateral blotches, crossbands, or stripes . ... *G. brachycephalus* (Costa Rica to Panamá)
5b. Dorsal scales in 17 rows; dorsum light with dark blotches or saddles .... *G. dunni* (Nicaragua)
6a. Postocular and supraocular in contact, excluding parietal from margin or orbit 7

6b. Postocular and supraocular separated by extension of parietal that meets orbit .... *G. nigroalbus* (Colombia)

7a. Snout pointed; rostral markedly produced posteriorly between internasals; mental pointed .... *G. ruthveni* (Costa Rica)

7b. Snout rounded; rostral barely produced posteriorly between internasals; mental rounded .... *G. talamancae* (Costa Rica)

8a. Five or fewer supralabials ..... . *G. hoffmani* (Honduras to Panamá)

8b. Six or more supralabials 9

9a. Snout pointed; rostral markedly produced posteriorly between internasals; mental pointed anteriorly; ventrals plus subcaudals 156–158 .. *G. championi* (Panamá)

9b. Snout rounded; rostral barely produced posteriorly between internasals; mental rounded; ventrals plus subcaudals 180–191 . ... *G. zeledoni* (Costa Rica)

10a. Uppermost dorsal scales keeled at least on posterior third of body and on tail; ventrals 122–133; subcaudals 41–46 .... *G. downsi* (Costa Rica)

10b. Dorsal scales smooth; ventrals 132–145; subcaudals 26–36 *G. godmani* (Costa Rica to Panama)

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Applications published in the *Bulletin of Zoological Nomenclature*

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Case No.

2886 *Doris grandiflora* Rapp, 1827 (currently *Dendrodoris grandiflora*; Mollusca, Gastropoda): proposed conservation of the specific name.

2859 *Johnstonia* Quatrefages, 1866 (Annelida, Polychaeta): proposed conservation.

2889 *Mastotermes darwiniensis* Froggatt, 1897 and *Termes meridionalis* Froggatt, 1898 (currently *Amitermes meridionalis*) (Insecta, Isoptera): proposed retention of neotypes following rediscovery of syntypes.

2713 COLYDIIDAE Erichson, 1842 (Insecta, Coleoptera): proposed precedence over CERYLONIDAE Billberg, 1820 and ORTHOCERINI Blanchard, 1845 (1820); and *Cerylon* Latreille, 1802: proposed conservation of *Lyctus histeroides* Fabricius, 1792 as the type species.

2783 *Cryptophagus* Herbst, 1792, *Dorcatoma* Herbst, 1792, *Rhizophagus* Herbst, 1793 and *Colon* Herbst, 1797 (Insecta: Coleoptera): proposed conservation as the correct spellings, and proposed conservation of *Lyctus bipustulatus* Fabricius, 1792 as the type species of *Rhizophagus.*

2861 ELMIDAE Curtis, 1830 and *Elmis* Latreille, 1802 (Insecta, Coleoptera): proposed conservation as correct spelling and of feminine gender respectively.

2858 *Hydrophoria* Robineau-Desvoidy, 1830 (Insecta, Diptera): proposed designation of *Musca lancifer* Harris, [1780] as the type species.

2881 *Sicus* Scopoli, 1763 and *Myopa* Fabricius, 1775 (Insecta, Diptera): proposed conservation by the designation of *Conops buccata* Linnaeus, 1758 as the type species of *Myopa.*

2835 *Allestes* Müller & Troschel, 1844 (Osteichthyes, Characiformes): conservation proposed.

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 30 March 1994 in Vol. 51, 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.

1752 *Zanclea costata* Gegenbaur, 1856 (Cnidaria, Hydrozoa): generic and specific names conserved.

1753 *Gebia major capensis* Krauss, 1843 (currently *Upogebia capensis*; Crustacea, Decapoda): neotype replaced, so conserving the usage of *G. capensis* and also that of *G. africana* Ortmann, 1894 (currently *Upogebia africana*).

1754 *Histoire abrégée des insectes qui se trouvent aux environs de Paris* (Geoffroy, 1762): some generic names conserved (Crustacea, Insecta).

1755 *Podisus* Herrich-Schaeffer, 1851 (Insecta, Heteroptera): *P. vittipennis* Herrich-Schaeffer, 1851 designated as the type species.

1756 ANTHRIBIDAE Billberg, 1820 (Insecta, Coleoptera): given precedence over CHORAGIDAE Kirby, 1819.

1757 *Cryptus* Fabricius, 1804 and CRYPTINAE Kirby, 1837 (Insecta, Hymenoptera): conserved.

1758 *Vipio* Latreille, 1804 (Insecta, Hymenoptera): *Agathis longicauda* Boheman, 1853 designated as the type species.

1759 *Acamptopoeum* Cockerell, 1905 (Insecta, Hymenoptera): *Camptopoeum submetallicum* Spinola, 1851 designated as the type species.

1760 *Rhipidocystis* Jaekel, 1901 (Echinodermata, Eocrinoidea): *R. baltica* Jaekel, 1901 designated as the type species.

1761 *Filimanus* Myers, 1936 (Osteichthyes, Perciformes): *Filimanus perplexa* Feltes, 1991 designated as the type species.

1762 *Cynolebias opalescens* Myers, 1942 and *C. splendens* Myers, 1942 (Osteichthyes, Cyprinodontiformes): specific names conserved.

1763 *Megophrys montana* Kuhl & van Hasselt, 1822 (Amphibia, Anura): generic and specific names placed on Official Lists, and *Leptobrachium parvum* Boulenger, 1893 (currently *Megophrys parva*): specific name conserved.

1764 *Anas arcuata* Horsfield, 1824 (currently *Dendrocygna arcuata*; Aves, Anseriformes): specific name conserved.

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The following people reviewed manuscripts for the *Proceedings* in 1993. C. C. Baldwin, R. C. Banks, F. M. Bayer, A. Berta, J. A. Blake, R. W. Bouchard, T. E. Bowman, G. A. Boxshall, J. M. Bradford, R. O. Brinkhurst, M. R. Browning, N. L. Bruce, R. C. Brusca, E. Campos, M. R. Campos, A. Carvacho, F. A. Chace, Jr., T.-Y. Chan, A. Cheetham, B. Chernoff, K. Coates, J. Corliss, M. M. Criales, G. B. Corbet, N. Cumberlidge, E. B. Cutler, N. J. Cutler, M. Dardeau, M. O. Dillon, R. Drewes, D. Dudgeon, R. J. Emry, K. Fauchald, D. L. Felder, F. D. Ferrari, C. Ferraris, F. Fiers, R. D. Fisher, K. Fitzhugh, O. S. Flint, Jr., A. Fosshagen, C. Fransen, R. Franz, R. J. Gagné, J. Garcia-Raso, A. L. Gardner, J. S. Garth, C. J. Glasby, W. Goldberg, M. Gomon, G. R. Graves, M. J. Grygier, J. Haig, G. Hall, C. W. Hart, Jr., W. Hartman, G. Hartmann, K. Hayashi, L. R. Heaney, R. H. Heard, P. Heideman, M. E. Hendrickx, R. Hershler, R. P. Higgins, B. Hilbig, D. Hillis, H. H. Hobbs, Jr., H. H. Hobbs III, E. Hoberg, D. Holdich, L. B. Holthuis, R. W. Holzenthal, K. Hulsemann, W. Hummon, P. Hutchings, H. F. James, R. F. Jezerinac, D. A. Jones, D. Kathman, B. Kensley, P. Kier, Y. Kikuchi, H. Kishimoto, N. Klein, K. F. Koopman, F. Krapp, R. K. Kropp, J. D. Kudenov, D. Laubitz, M. Ledoyer, D. B. Lellinger, R. Lemaitre, D. Lipscomb, M. Litvaitis, J. Lundberg, A. Mackie, E. Macpherson, C. Magalhaes, R. B. Manning, J. C. Markham, J. W. Martin, W. N. Mathis, R. W. McDiarmid, P. A. McLaughlin, E. Moll, J. C. Morse, H.-G. Muller, T. A. Munroe, G. G. Musser, D. Nelson, T. Newberry, P. K. L. Ng, N. Ngoc-Ho, J. N. Norenburg, S. L. Olson, L, R. Parenti, B. D. Patterson, C. Patterson, D. L. Pawson, R. Paynter, Jr., T. Peterson, M. H. Pettibone, T. Pietsch, F. Pleijel, G. Pretzmann, J. Pruski, J. W. Reid, J. V. Remsen, Jr., R. P. Reynolds, N. Riser, G. Rodríguez, G. Rouse, K. Ruetzler, L. Sandberg, J. M. Savage, S. Schaefer, A. E. Smalley, L. Soto, W. C. Starnes, D. W. Steadman, G. S. Steyskal, G. W. Stocker, J.-O. Stromberg, J. D. Thomas, F. G. Thompson, P. Tongiorgi, M. Türkay, J.-W. Wagele, D. Wake, T. C. Walter, K. Warheit, S. Werman, M. J. Wetzel, D. Wiedenfeld, A. B. Williams, D. E. Wilson, G. D. Wilson, L. D. Wilson, J. Winston, R. Winterbottom, N. E. Woodley, K. Wouters, H. Yeatman, G. R. Zug.

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DESCRIPTION OF A NEW SPECIES OF SUBFOSSIL EAGLE FROM MADAGASCAR: *STEPHANOAETUS* (AVES: FALCONIFORMES) FROM THE DEPOSITS OF AMPASAMBAZIMBA

Steven M. Goodman

Abstract.—Several bones recovered from subfossil deposits at Ampasambazimba, Madagascar, are described as a new species of eagle, *Stephanoaetus mahery.* These bones presumably date from the Holocene. *S. coronatus,* occurring on the African mainland, is the only extant member of this genus, and throughout much of its range feeds extensively on primates weighing up to about 12 kg. Bones of a remarkable assortment of lemurs have been recovered from Ampasambazimba and it is suggested that *S. mahery* may have preyed upon primates. Further, the legendary *Rokh,* a giant bird reputed to have occurred on Madagascar, from the tales of Sinbad and Marco Polo, may have been derived from *S. mahery.*

Résumé.—Une nouvelle espèce d'aigle, *Stephanoaetus mahery,* fait l'objet d'une description réalisée à partir de divers ossements provenant des dépôts subfossiles d'Ampasambazimba, Madagascar. L'âge estimé de ces ossements est de l'holocène. *Stephanoaetus coronatus,* qui se rencontre sur le continent africain, est actuellement l'unique espèce connue dans ce genre. Cette espèce se nourrit communément de primates pesant environ 12 kg. De remarquables ossements de lémuriens ont été retrouvés á Ampasambazimba et il a est suggéré que *S. mahery* pourrait être un prédateur de primates. Par ailleurs, la légende de l'oiseau rock, célèbre oiseau-géant ayant été vécu à Madagascar dont on trouve des détails dans l'Histoire de Sinbad le marin et de Marco Polo pourait être celle de *S. mahery.*

Famintinana.—Taolambiby maro hita avy tao amin'ny farita misy taratsiefan-taolambiby ao Ampasambazimba, Madagasikara, no noheverina fa karazamboromahery vaovao, *Stephanoaetus mahery.* Araka ny tombatombana mikasika ireo taolana ireo, dia efa hatramin'ny vanimpotoana jeolozika "Holocène" no nisian'izy ireo tao ambanin'ny tany. *S. coronatus,* hita any amin'ny kaotinanta afrikana, no hany karazana mitovy amin'io mbola velona ankehitriny izay mivelona ara-dalana amin'ny fihinanana karazana varika milanja sahabo ho 12 kg eo ho eo izay hitany ao amin'ny faritra iainany. Mbola nahitana karazan-taolambiby voafaritra ho varika ihany koa tao Ampasambazimba, noho izany azo heverina fa io *S. mahery* io dia nihaza sy nihinana karazambarika. Ankoatr'izany, ilay angano mikasika an'ilay hoe "Rokh" na ilay vorombe malaza niana tany Madagasikara, nalaina avy tao amin'ny Tantaran'i Sinbad sy Marco Polo dia mety tsy ho hafa fa'ity atao hoe *S. mahery* ity ihany.

The modern bird fauna of Madagascar is well-known for its high level of endemism, of the 201 extant resident species 105 (52%) are endemic (Langrand 1990). During the course of the last few millennia the island has undergone drastic ecological change, a portion of which clearly is human induced (Perrier de la Bâthie 1921, Battistini & Vér-

Fig. 1. Tarsometatarsus of *Stephanoaetus mahery,* new species, holotype, MAD 5491, Muséum National d'Histoire Naturelle, Service de Paléontologie, Paris, left dorsal and right ventral views.

in 1972, Burney 1987). In general, little is known about what effects these changes have had on the avifauna. The best known group of extinct birds on the island is the elephant birds (Family Aepyornithiformes) which consisted of at least seven species in two different genera (Brodkorb 1963). The exact sequence of events that led to their extinction is unknown, but at least one species may have been extant until the turn of the 17th-century, about the same time Europeans arrived on Madagascar (Flacourt 1658, p. 165). Other smaller bird species are known to have gone extinct in the past few millennia (Milne Edwards & Grandidier 1895, Andrews 1897, Goodman & Ravoavy 1993).

One of the best known subfossil localities on Madagascar is Ampasambazimba, located about 85 km west of the capital city of Antananarivo. The site is at the edge of a former lake created by the damming of a river by a lava flow. Subsequently, the lava barrier was downcut, and the lake drained and successionally infilled to form a marsh (MacPhee et al. 1985). During excavations at Ampasambazimba a large number of bird bones were recovered, which until now remained largely unstudied. The majority of this material consists of waterbirds, but bones of raptorial birds were also recovered. Within this material are elements of a large eagle previously unknown to science and here it is proposed to call it:

Stephanoaetus mahery, new species
Figs. 1, 2

Holotype.—Left tarsometatarsus, collections of the Laboratoire de Paléontologie, Museum National d'Histoire Naturelle, Paris, MAD 5491 (Figs. 1, 2). The element is complete except a portion of the hypotarsus is broken.

Locality.—Ampasambazimba, Madagascar, and accessioned in 1925 as part of a collection of over 750 specimens donated by "Gouvernment general de Madagascar

Fig. 2. Comparison of *Stephanoaetus coronatus* (MNHN 1901.209) tarsometatarsus (top) and *S. mahery* (MNHN MAD 5491) tarsometatarsus (bottom).

par l'intermediaire de M. Samat" and consisting of "ossements d'oiseaux sub-fossiles provenant d'Ampasambazimba, Antsirabe, et Morarano près de Betafo (W. d'Antsirabe)." The locality listed in the general catalog for the holotype is Ampasambazimba. Before 1925 several different excavations were conducted at this site and it is impossible to determine during which season the holotype was collected.

Chronology.—No radiometric date is available for the *Stephanoaetus mahery* remains. They are presumed to be Quaternary, probably Holocene. This is supported by material of *Megaladapis grandidieri,* an extinct lemur excavated from Ampasambazimba, that has yielded a radiocarbon date of 1035 ± 50 years B.P. (Tattersall 1973). However, since no stratigraphic information is available for the Ampasambazimba material reported on herein, it is unknown if the *Megaladapis* and *Stephanoaetus* remains were associated.

Measurements of holotype.—Greatest length 108.0 mm; proximal breadth 26.1 mm; and distal breadth 27.9 mm. (See von den Driesch 1976, fig. 62a–c for illustrations and descriptions of the measurements.)

Etymology.—The name *mahery* is from the Malagasy adjective meaning powerful. This is in reference to the presumed strength this eagle would have possessed.

Diagnosis.—The falconiform tarsometatarsus is one of the most distinctive osteological elements of raptors and has important systematic characters for diagnosing genera (Jolly 1977). The type specimen of *S. mahery* is exceptionally robust in both overall size and proportions. Articular surfaces and muscle attachments are exceptionally prominent. The specimen was compared to all genera of African eagles, and with the exception of *Stephanoaetus,* these are morphologically different. The Ampasambazimba tarsometatarsus is referred to the genus *Stephanoaetus* by the following characters (terminology follows Baumel [1979]): position of foramina vascularia proximalia, particularly in reference to the crista plantaris mediana; configuration of the sulcus extensorius and associated muscle attachments; and proportion and morphology of the trochlea metatarsi I, fossa metatarsi, foramen vasculare distale, sulcus hypotarsi, and crista hypotarsi (medialis and lateralis). The holotype tarsometatarsus of *S. mahery* differs from comparative material of *S. coronatus* by being longer ($t_{10} = 2.15$, $P = 0.028$, Table 1). Further, the cristae plantares are more prominent and sulcus flexorius deeper in *coronatus* than *mahery.*

Paratypes.—All in collections of the Laboratoire de Paléontologie, Museum National d'Histoire Naturelle, Paris, and consisting of distal pedal phalanges (claws)—first digit of right side (MAD 5428) and left side (MAD 5423), distal one-quarter of left ulna (MAD 5587), and pelvic fragment (MAD 4944). Except for MAD 5428, which is from Ampasambazimba and is part of the same accession as the holotype, exact collection localities of the other bones are unknown, but are presumably from Quaternary deposits on Madagascar.

Discussion.—The genus *Stephanoaetus* was previously unrecorded on Madagascar, and *S. mahery* represents the largest known bird of prey to inhabit the island during the Quaternary. The extant raptor community contains distinctly smaller birds, except for the Madagascar Fish Eagle (*Haliaeetus vociferoides*), which in modern times is limited to the northern and northwestern portion of Madagascar, is one of the rarest eagles in the world (Langrand 1990).

The majority of raptors show sexual size-dimorphism with females being larger than males, as is the case with *S. coronatus* (Brown et al. 1982). Since comparative material of *S. coronatus* used in this study is comprised of both sexes, and the holotype subfossil tarsometatarsus is larger than all of these modern specimens, it is concluded that *S. mahery* does not fall within size variation of *S. coronatus* (Table 1). Six of the eleven specimens of *S. coronatus* used in

Table 1.—Tarsometatarsus measurements (mm) of the holotype of *Stephanoaetus mahery* and a series of extant *S. coronatus*.

Taxa	Greatest length	Proximal breadth	Distal breadth
mahery, sp. nov.			
MAD 5491	108.0	26.1	27.9
coronatus			
Male (n = 2)	99.7, 102.4	22.2, 25.8	23.5, 27.2
Female (n = 2)	100.5, 102.9	25.2, 25.3	26.2, 27.2
Combined (n = 11)[1]	102.0 ± 2.7	25.1 ± 1.6	27.0 ± 1.4
	98.2–105.9	22.0–26.7	23.5–28.9

[1] Combined descriptive statistics presented as mean ± standard deviation and followed by range.

this study were captive birds; no significant difference in size or osteological characters was found between wild and captive individuals. The paratype material of *S. mahery* is difficult to distinguish from modern *S. coronatus*, at least in part due to the fragmentary nature of some of the bones.

One intriguing question associated with the discovery of *S. mahery* is what did it eat? Food habits of *S. coronatus*, the only extant member of this genus and which occurs throughout much of sub-Saharan Africa (Brown et al. 1982), have been studied in the Kibale Forest of Uganda (Skorupa 1989, Struhsaker & Leakey 1990), where this immensely powerful eagle feeds on an assortment of relatively large prey. This includes blue duiker (*Cephalophus monticola*) and Peter's duiker (*C. callipygus*), adults of the latter species weigh up to 20.5 kg (Kingdon 1982); red colobus (*Colobus badius*), adult males weigh between 9 and 12.5 kg (Kingdon 1974); black and white colobus (*C. guereza*), adult males weigh up to 10.5 kg (Struhsaker 1975); and a variety of smaller primates, carnivores, and birds. By number, over 80% of this eagle's diet at Kibale is composed of primates (Struhsaker & Leakey 1990).

On the basis of tarsometatarsus length, the general size of *S. mahery* is estimated to be comparable to that of *S. coronatus*, and it is assumed that the former species would have been capable of taking equivalent size prey. Further, the long hind talons of *S. coronatus* are important to subdue large prey. The hind talons of *S. mahery* resemble those of *S. coronatus* in absolute size and massiveness (Fig. 3). Thus, it is assumed that *S. mahery* would have been as formidable a predator as modern *S. coronatus*.

Fourteen species of lemurs, seven of which are extinct, have been identified from the Ampasambazimba material (Tattersall 1973, Dewar 1984). If indeed these species were temporally sympatric, and there is evidence that they were, this assemblage would represent the highest primate species diversity known for any site, fossil or modern, on the island (Nicoll & Langrand 1989), and perhaps anywhere else in the world. Body weights of lemurs known from the deposits of Ampasambazimba and that might have been preyed upon by *S. mahery* include (from L. Godfrey, pers. comm. for extinct taxa [*] and Richard & Dewar [1991] for extant taxa): **Archaeolemur edwardsi* (24.5 kg), **Hadropithecus stenognathus* (16.7 kg), **Mesopropithecus pithecoides* (9.7 kg), **Pachylemur insignis* (10.0 kg), *Indri indri* (6 kg), and *Propithecus* spp. (3.6–5.8 kg).

Primatologists studying behavior of modern lemurs have observed that several large diurnal and social species have a strong stereotypic response to birds of prey flying overhead (Sauther 1989, Macedonia 1990). Evolution of this behavior is difficult to explain in light of little evidence of the extant raptors predating on this group of lemurs, young or old (Goodman et al. 1993). Recent

Fig. 3. Comparison of *Stephanoaetus coronatus* (MNHN 1901.209) first digit from left and right side (top) and *S. mahery* first digit left side (MNHN MAD 5423) and first digit right side (MNHN MAD 5428) (bottom).

discovery of another extinct eagle on Madagascar in the genus *Aquila,* and the possibility that it ate diurnal lemurs, has been interpreted as a potential evolutionary force in the development of this anti-predator behavior (Goodman 1994). Now that Quaternary deposits in Madagascar have yielded remains of *Stephanoaetus,* an eagle larger than *Aquila* and a presumed primate specialist, this explanation can be further supported. Hunting techniques used by *S. coronatus* such as puncturing the prey's heart with its massive and powerful hind talons or by flight blows (Brown et al. 1982, Leland & Struhsaker 1993) may leave no or subtle tell-tale marks in the victim's bone remains. However, a detailed study of food remains recovered from *S. coronatus* nests and feeding sites might reveal some characters that would help to diagnose how this eagle dispatches and dismantles prey. These characters could then be compared to lemur material excavated at Ampasambazimba to determine if some of the bones recovered from the site are prey remains of *S. mahery.*

The legendary *Rokh* of numerous Middle Age travelers, including Marco Polo, and from the tales of Sinbad and *A Thousand and One Nights,* may have been a bird found on Madagascar. Several authors have equated the *Rokh* with elephant birds (e.g., Lavauden 1931), while others have rejected this idea and identified it as a bird of prey (Decary 1937, Allibert 1992). If indeed the *Rokh* is not totally imaginary, inhabited Madagascar, and was a large raptor, it may have been derived from *S. mahery.*

Comparative material examined.—Few skeletons of large eagles exist in the world's museum collections, and a substantial portion of these are those of birds that died in captivity (*). The holotype of *S. mahery* was compared to modern skeletal material of the following eagles (See Acknowledgments for definitions of acronyms.): *Haliaeetus vociferoides* (MNHN not cataloged; UA 77), *H. vo-*

cifer (BMNH 1954.38.51; MNHN 1908.60), *Ichthyophaga ichthyaetus* (BMNH not cataloged), *Terathopius ecaudatus* (UMMZ 158569), *Spilornis cheela* (MNHN A4025), *Morphnus guianensis* (FMNH 106705), *Harpia harpyja* (BMNH 1862.3.19.14, 1862.3.14.19; MNHN *1878.577), *Pithecophaga jefferyi* (BMNH 1910.2.11.1a, *1961.23.1; FMNH *106496), all extant *Aquila* spp. (excluding *A. gurneyi*), *Hieraaetus fasciatus* (MNHN *1870.326, *1910.424), *Lophaetus occipitalis* (FMNH 313295; MNHN 1880.32; USNM 431671), *Spizaetus cirrhatus* (BMNH 1850.8.15.13; FMNH *289556), *S. ornatus* (BMNH 1952.1.177; FMNH *288164; MNHN *1889.150), *Stephanoaetus coronatus* (AMNH *4256; BMNH 1952.1.178, 1954.30.42; MNHN *1901.209; NMK OB125, OB849; USNM *345669, *346652, *346654, *346655, 432180), and *Polemaetus bellicosus* (BMNH 1853.10.21.1, 1952.1.179, 1954.30.43, 1957.9.1, 1984.101.1; USNM 430533).

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A GIANT *PRESBYORNIS* (AVES: ANSERIFORMES) AND OTHER BIRDS FROM THE PALEOCENE AQUIA FORMATION OF MARYLAND AND VIRGINIA

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Abstract.—*Presbyornis isoni,* new species, is described from a humerus and an alar phalanx from marine sediments of the late Paleocene Aquia Formation in Maryland. About the size of the smallest living species of crane (Gruidae), it was much larger than any previously known member of the Presbyornithidae. Other fragmentary bird remains from the Aquia Formation are noted, several of which may be referable to the suborder Phaethontes of the Pelecaniformes. Additional Paleocene birds from eastern North America occur in the Hornerstown Formation of New Jersey, which is now considered to be Danian (early Paleocene) in age, rather than late Cretaceous.

The marine sediments of the Aquia Formation crop out in the Chesapeake Bay area of Maryland and Virginia. They are of late Paleocene (Landenian) age and overlie the Brightseat Formation (Danian), between which there is a disconformity representing about 3.6 million years, a period of time approximately equivalent to that of the exposed Aquia Formation (Hazel 1969). The Aquia is divided into an upper Paspotansa Member and a lower Piscataway Member, the latter having sometimes been designated in earlier literature as the Piscataway Formation or Piscataway Indurated Marl Member of the "early Eocene." These sediments accumulated in a pelagic environment, well off shore, and are reasonably productive of vertebrate fossils, e.g., turtles (Weems 1988), but so far have yielded very few bird remains. A recently collected humerus is the largest and most diagnostic avian fossil yet discovered in the Aquia Formation, As it merits description, I have taken the opportunity to review the few other avian fossils found so far in the same strata.

Class Aves
Order Anseriformes
Family Presbyornithidae Wetmore, 1926

Genus *Presbyornis* Wetmore, 1926
Presbyornis isoni, new species
Figs. 1, 2

Holotype.—Left humerus lacking proximal third, collections of the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, USNM 294116. Collected in March 1993 by Ronald M. A. Ison.

Type locality.—Maryland, Charles County, east bank of the Potomac River, from the area designated as Bluebanks, south of Liverpool Point and north of Douglas Point (Widewater Quadrangle, USGS 7.5 minute series).

Horizon and age.—Near the base of the Upper Paleocene (Landenian), Aquia Formation, Piscataway Member. The specimen came from near the base of the bluff exposed at the type locality, which is probably upper nannoplankton zone NP5, but possibly lower NP6 (Laurel M. Bybell, USGS, pers. comm.). On the scale of Berggren et al. (1985), the age would be somewhere between 61 and 62 million years.

Measurements of holotype (mm).—Distal width, 23.3; depth through radial condyle, 12.9; greatest diameter of brachial depression, 8.8; width and depth of shaft at approximate midpoint, 10.8 × 8.2.

Fig. 1. Humeri in palmar view (A–C) and phalanx 1 of major alar digit (D–E) of Presbyornithidae: A, *Presbyornis isoni* new species, holotype (USNM 294116); B, *Telmabates antiquus* (AMNH 3170); C, *Presbyornis pervetus* (cast, USNM 483163); D, *Presbyornis isoni* new species, paratype (USNM 294117); E, *Presbyornis pervetus* (cast, USNM 483164). All figures natural size.

Paratype.—Left phalanx 1 of major alar digit, abraded along the posterior edge, USNM 294117. Collected in June 1984 by Eugene Hartstein at the same locality as the holotype.

Measurements of paratype (mm).—Length, 40.6; greatest diameter of proximal articulation, 9.5.

Etymology.—Named in honor of the collector, Ronald M. A. Ison, an enthusiastic amateur paleontologist.

Diagnosis.—Much larger than *Presbyornis pervetus* Wetmore, 1926, or any other known members of the family. Apart from size, there are no discernable differences between *P. isoni* and *P. pervetus,* save that the olecranal fossa appears less distinct in the former, which may be a size-related factor.

Discussion.—*Presbyornis* is a remarkable bird that exemplifies an early stage in the evolution of the Anseriformes, combining a long-legged, shorebird-like body with the head of a duck (Olson & Feduccia 1980). *Presbyornis pervetus* occurs abundantly in lacustrine deposits of the early Eocene Green River Formation of Wyoming, Colorado, and Utah, and a slightly smaller form is found in the Paleocene of Utah and Mon-

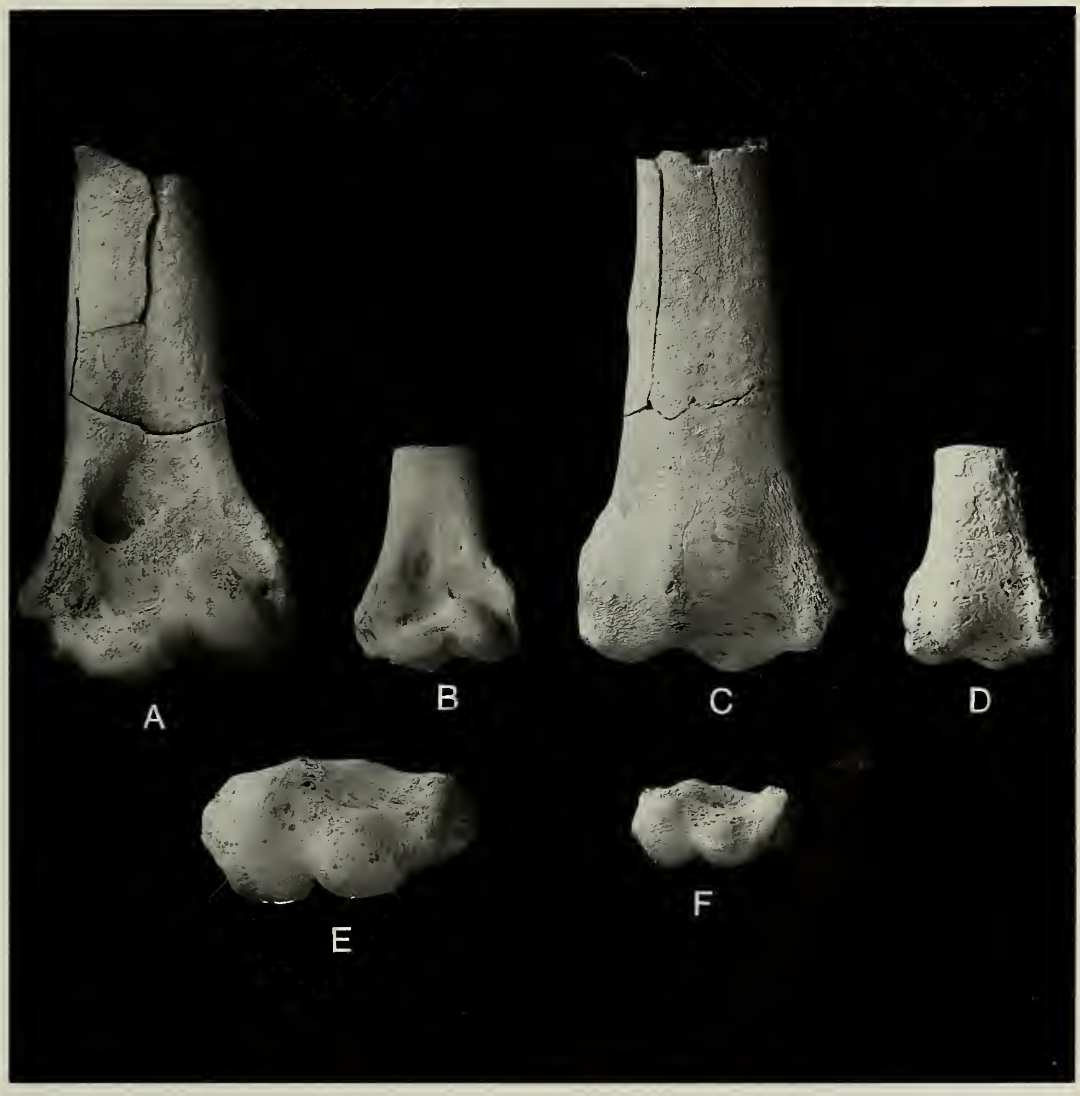

Fig. 2. Left humeri of *Presbyornis*: (A, C, E) *P. isoni* new species, holotype (USNM 294116); (B, D, F) *P. pervetus* (part of UCMP 136541). A–B, palmar view; C–D, anconal view; E–F, distal view. Specimens coated with ammonium chloride. 1.5×.

golia (Olson 1985a:171). The contemporaneous genus *Telmabates,* from Patagonia, is very similar to *Presbyornis* and was synonymized with that genus by Feduccia & McGrew (1974). Further study, however, has shown that the limb proportions of *Telmabates* differ sufficiently from *Presbyornis* to merit retention of the genus (Per Ericson, Swedish Museum of Natural History, Stockholm, pers. comm.). The type species, *T. antiquus,* was considerably larger than *Presbyornis pervetus.*

Presbyornis isoni was much larger than either. To put the relative differences in terms of modern analogs for size, *Presbyornis pervetus* would have been about the size of the largest species of *Burhinus,* the Bush Stone-curlew, *B. magnirostris,* of Australia.

Telmabates antiquus was about the size of a Limpkin, *Aramus guarauna,* whereas *Presbyornis isoni* would have been the size of a Demoiselle Crane, *Anthropoides virgo.*

It is possible, given its much larger size, that the feeding adaptations of *P. isoni* may have been different from those of *P. pervetus,* and that were the entire skeleton available it might be assigned to a different genus. As it is, however, there is no distinction whatever to be made between these taxa except on size.

The considerable assemblage of birds known from the Hornerstown Formation of New Jersey (Olson & Parris 1987) are now believed to be Danian (early Paleocene) rather than latest Cretaceous in age (see below), and are older than *P. isoni.* Most of these birds were referred to the "form family" Graculavidae, which shares similarities with the Presbyornithidae. *Presbyornis isoni* was larger than any of these species except *Laornis edvardsianus,* which was much larger than *P. isoni.* The species in the Hornerstown most similar to *P. isoni* is *Anatalavis rex,* which was a much smaller bird in which the brachial depression is longer, narrower, and not as deep, and in which the shaft appears to have been relatively shorter and more curved.

Although the alar phalanx referred to *P. isoni* is not a particularly diagnostic element, its size and overall similarity to the same element in *Presbyornis* makes it highly unlikely that it would belong to some other family altogether. That two elements of this presumed land bird were discovered at the same site, the sediments of which were deposited well off shore and where bird bones are scarce, suggests that they may have come from the same individual, despite having been collected years apart.

Order Pelecaniformes Sharpe
Suborder Phaethontes

The modern tropicbirds (Phaethontidae, *Phaethon*), are the most primitive and divergent of the Pelecaniformes, relegated to a separate suborder Phaethontes. The first fossil assigned to the family was *Prophaethon shrubsolei* Andrews (1899), known from a skull, mandible, and partial postcranial skeleton from the early Eocene (Ypresian) London Clay of England. Harrison & Walker (1976) restudied the specimen and created a new order and family for it, only the latter being justified, however (Olson 1985a). The only other fossil member of the Phaethontes is *Heliadornis ashbyi* Olson (1985b), known from three associated bones from the Middle Miocene (Langhian) Calvert Formation of Maryland, which was referred to the Phaethontidae.

Family Prophaethontidae
Harrison & Walker, 1976
Genus *Prophaethon* Andrews, 1899
Prophaethon? sp.

Material examined.—Distal end of right humerus, USNM 483158. Collected 1 m from top of chalky shell band of Aquia Formation at Capital Beltway and Central Avenue, Prince Georges, County, Maryland (Lanham Quadrangle, USGS 7.5 minute series), by Calvin F. Allison, Jr. in 1973. Distal width, 7.6 mm.

Right coracoid lacking part of the acrocoracoid and the lateral process of the sternal end, USNM 483159. Collected by T. B. Ruhoff at a road cut on Indian Head Highway, about 200 m north of Piscataway Creek, Prince Georges County, Maryland (Piscataway Quadrangle, USGS 7.5 minute series). "About 10–12 feet above road." This is evidently the same as the type locality of the fossil turtle *Catapleura ruhoffi* (Weems 1988). Length to internal distal angle 28.5 mm.

Remarks.—The humerus is extremely similar to that in modern tropicbirds of the genus *Phaethon,* practically the only noticeable difference being the indistinctness of the external tricipital groove, but this may be an artifact as the specimen is considerably worn in this area. It comes from a bird much smaller than any living tropicbird, about the size of a Common Tern, *Sterna hirundo,* and thus much smaller than *Prophaethon shrubsolei* or *Heliadornis ashbyi,* although the distal end of the humerus is unknown in either of those species.

The coracoid from the Aquia was compared directly to that from the holotype of *P. shrubsolei* and is very similar in overall shape and proportions, but much smaller. At the sternal end, the specimens are lacking complementary portions and hence can scarcely be compared. Both have a shallow scapular facet. It is apparent that in the smaller species the procoracoid process would not have projected as much anteriorly, and the procoracoid foramen is more sternally situated (i.e., farther from the scapular facet). Also the triossial groove in the procoracoid is deeper in *Prophaethon.*

The Aquia coracoid is small and if not from a bird the same size as represented by the humerus, would be from a slightly larger individual or species. These two bones seem to be sufficiently diagnostic to be referred to the Phaethontes, but they are assigned only provisionally to the Prophaethontidae on the basis of their age.

Aves Incertae Sedis

Size 1

Distal third of right ulna, USNM 483160. Same collection data as the coracoid of *Prophaethon*? sp. mentioned above. Depth of distal end through external condyle, 4.4 mm. This specimen is from a small bird, possibly smaller than *Prophaethon*? sp. Its morphology is quite unlike the distinctive condition in modern *Phaethon,* in which the carpal tubercle is developed as a strong hook, and is more similar to that in Procellariiformes, but as we do not know what the ulna looked like in ancient Phaethontes, it cannot be ruled out that this fossil belongs in that group.

Abraded distal end of left tibiotarsus lacking internal condyle, USNM 294118. Collected from "Top Gully" of Aquia Formation at the Hampton Mall Site, Central Avenue near Capital Beltway, Prince Georges County, Maryland (Lanham Quadrangle, USGS 7.5 minute series), in 1984 by Eugene Hartstein. Depth through external condyle, 3.7 mm. This is from a species small enough to be of comparable size to *Prophaethon*? sp., but it bears no resemblance to the tibiotarsus in *Phaethon.* It is similar, however, to that element in the genus *Palaeotringa,* from the Hornerstown Formation (Olson & Parris 1987), though much smaller than any of its known species.

Size 2

Proximal half of phalanx 1 of major alar digit, USNM 483161. Same collection data as USNM 483159. Greatest diameter of proximal articulation, 5.0 mm.

Proximal shaft of left humerus including pectoral crest, USNM 483162. The label with this specimen, in Alexander Wetmore's hand, says only "Piscataway Formation, Virginia, from Ted Ruhoff." Width and depth of shaft just distal to pectoral crest, 4.0 × 5.0 mm.

These two specimens come from a bird the size of modern *Phaethon lepturus,* and such little morphology as remains on them is actually quite similar to that of *Phaethon,* so that they might well be from the same species and perhaps belong among the Phaethontes.

Size 3

Proximal end of right carpometacarpus New Jersey State Museum 13532. Collected as float at Belvedere Beach, Potomac River, King George County, Virginia (Passapatanzy Quadrangle, USGS 7.5 minute series), 27 Dec 1985 by Eugene Hartstein. Proximal depth through alular metacarpal, 13.3 mm. Although not found in situ, the specimen is most probably Paleocene as the exposures at this locality are entirely a green glauconitic sandy marl of the Paspotansa Member of the Aquia Formation. The bone comes from a bird slightly larger than *Phaethon rubricauda,* the largest modern tropicbird, but differs considerably from that genus. It has some resemblance to the carpometacarpus in the Sulidae but again is quite different, though it could still belong to some member of the Pelecaniformes.

The age of the "Cretaceous" birds of New Jersey.—The record of Paleocene birds from marine deposits is quite scanty and the specimens discussed above would probably be the only ones known from North America were it not for the fact that the fairly diverse avifauna derived from the marine sediments of the basal Hornerstown Formation in New Jersey, long considered to be late Cretaceous (Maastrichtian) in age, are probably Paleocene as well. These fossil birds have received attention since the early 1870's, when many of the taxa were originally described by O. C. Marsh. The fauna has been recently revised by Olson & Parris (1987).

The age of the basal Hornerstown has been, and still is, a highly contentious issue. The birds from here were originally regarded as Cretaceous (Marsh 1870, 1872), then Paleocene (Wetmore 1930), then Cretaceous (Baird 1967). Weems (1988) cites some of the more recent literature giving evidence for the basal Hornerstown being Paleocene, but still notes some dissention.

There seems to be consensus that the upper Hornerstown is definitely Paleocene, so that if the basal part were Cretaceous, then the K/T boundary would have to lie *within* the Hornerstown, which, if true, should have attracted international attention. I get the impression that local pride may be involved, with the New Jersey contingent holding out for a Cretaceous attribution, Mesozoic fossils presumably being more glamorous than Cenozoic ones. Nevertheless, personnel of the U.S. Geological Survey will have none of this and place the outcropping portions of the basal Hornerstown in nannoplankton zone NP 3 (Laurel M. Bybell, USGS, pers. comm.), which is Danian, Lower Paleocene, between about 64 and 65 million years in age (Berggren et al. 1985). A Cretaceous assignment may have arisen either through reworking of Mesozoic macrofossils into the younger sediments, or through the persistence of otherwise Mesozoic taxa into the earliest Tertiary.

Although it makes no great difference one way or another as far as avian evolutionary history is concerned, as birds with some of the same general morphological attributes existed before and after the Hornerstown Formation, the refinements brought about by modern microfossil analysis would appear to necessitate the New Jersey birds being relinquished as part of Mesozoic history.

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A NEW SPECIES OF OWL OF THE GENUS *BUBO* FROM THE PLEISTOCENE OF CUBA (AVES: STRIGIFORMES)

Oscar Arredondo and Storrs L. Olson

Abstract.—*Bubo osvaldoi,* new species, is described from three bones from a Pleistocene cave deposit in the Sierra de Galeras, Pinar del Río, western Cuba, with two additional paratypes referred from Baire in the province of Santiago de Cuba, in the eastern part of the island. The species is the only representative of the genus *Bubo* and the tribe Bubonini in the Antilles and in size was larger than any living owl.

Resumen.—Se describe una especie nueva de búho, *Bubo osvaldoi,* de tres huesos del Pleistoceno hallados en una cueva de la Sierra de Galeras, en Pinar del Río, Cuba occidental, y de otros dos huesos paratipos procedentes de Baire, provincia de Santiago de Cuba, en el oriente de la isla. La espécie es el único miembro del género *Bubo* y de la tribu Bubonini conocido hasta ahora en las Antillas y era mayor que cualquiera de las formas conocidas de búhos vivientes.

The Quaternary avifauna of Cuba is remarkable for the number and size of the extinct owls that have been discovered there (summarized by Arredondo 1976, 1982). These include the truly enormous strigids of the endemic genus *Ornimegalonyx,* of which four species have been named (Arredondo 1982), and two species of barn owls (*Tyto*) that far exceed in size any living species of Tytonidae. *Pulsatrix arredondoi* (Brodkorb 1969) is slightly smaller than its Neotropical relative *P. perspicillata,* but belongs to a genus otherwise unknown in the Antilles. It was previously known only from the type locality, Cueva Paredones in Habana Province, but Arredondo has recently identified a tarsometatarsus of *P. arredondoi* from Cueva Calero in Matanzas Province.

Here we present evidence of yet another very large extinct Cuban owl, amidst what could already have been regarded as a plethora. Our collaboration on this began when Arredondo forwarded for evaluation three fossil specimens from Pinar del Río, at the western end of Cuba, along with a manuscript describing them as a new species of *Bubo.* This called to mind two enigmatic bones that Olson had studied some years previously that came from the former province of Oriente, at the opposite end of the island. These had originally been sent in January 1947 by Abelardo Moreno, then of the Museo Poey, to Alexander Wetmore, at the Smithsonian Institution. Wetmore had had a drawing made of these bones and left a folder of correspondence concerning them, but they remained unpublished. We have concluded that these probably belong to the same species as represented by the bones from Pinar del Río, which cannot be referred to any known species of owl, living or fossil.

Class Aves Linnaeus, 1758
Order Strigiformes Wagler, 1830
Family Strigidae Vigors, 1825

The fossil material treated below may be distinguished from *Tyto* (Tytonidae) by the

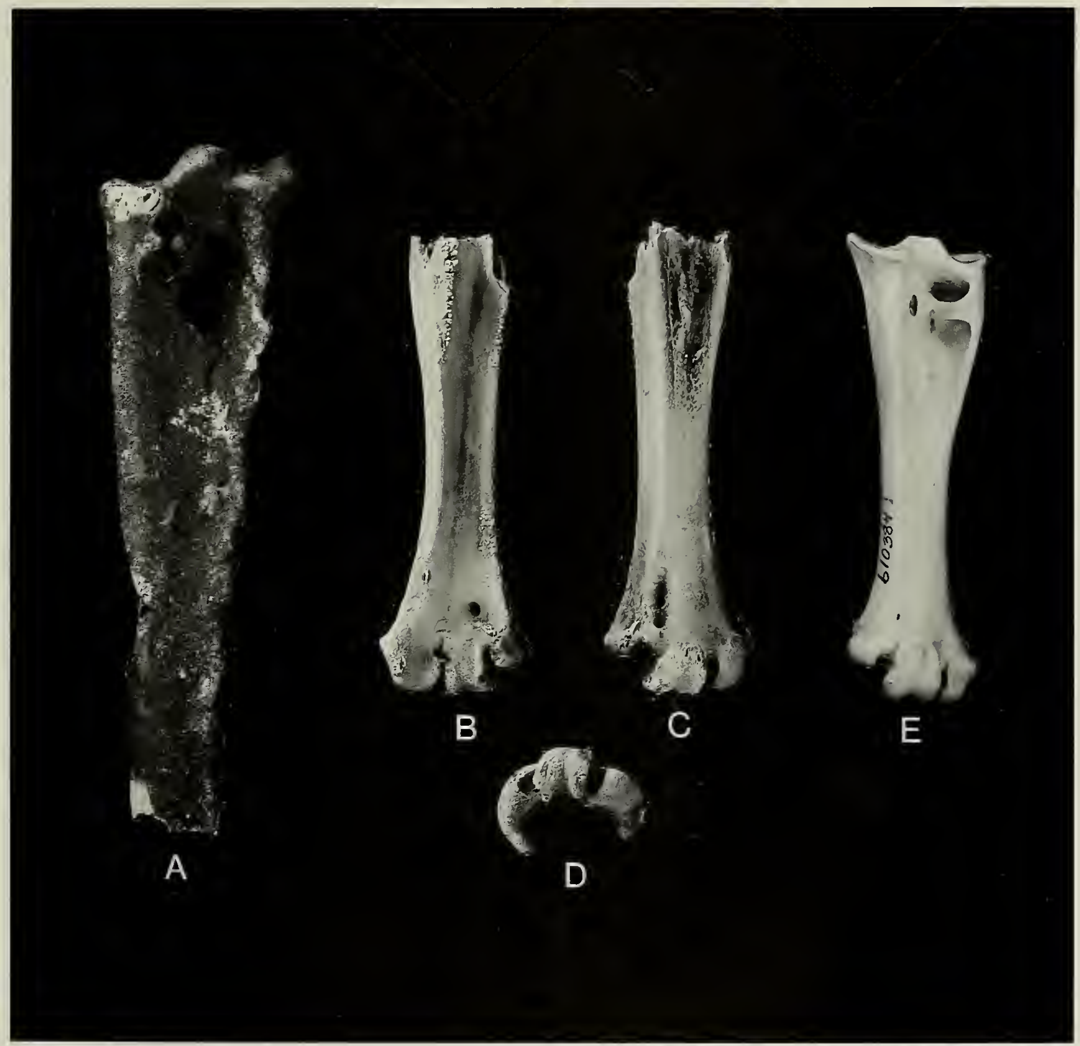

Fig. 1. Tarsometatarsi of strigid owls. A, anterior view of *Ornimegalonyx oteroi* (MNHN unnumbered, lacking distal end), showing the immense size compared to otherwise very large owls; B, C, D, posterior, anterior, and distal views of *Bubo osvaldoi,* new species, holotype (MNHNCu-27, coated with ammonium chloride to enhance detail); E, anterior view of *B. bubo* (USNM 610384) female, largest available specimen of the species. Figures three-fourths natural size.

proportionately short, robust tarsometatarsus, the more anteroposteriorly expanded external condyle of the femur, and the shallower brachial depression of the humerus.

Genus *Bubo* Duméril, 1806

The Cuban fossils, although from a very large owl, are nonetheless dwarfed by the gigantic Cuban owls of the genus *Ornimegalonyx,* in which the proportions of the tarsometatarsus are very different (Fig. 1). They are clearly referable to the group of largest strigid owls (Tribe Bubonini) that includes the genera *Bubo, Nyctea, Ketupa,* and *Scotopelia,* concerning which Ford (1967:82) wrote: "Each of these genera has some osteological characteristics by which it can be separated, but the differences are not great and it is questionable as to whether or not they actually warrant separation." We would echo these sentiments, as we likewise find little in the osteology of at least *Nyctea* or *Ketupa* that would merit separating them from *Bubo* (we did not examine skeletons of *Scotopelia*). *Ketupa* and *Scotopelia* are Asian and African genera, respectively, whose traditional generic characters involve external aspects of the feet that are adaptations for fishing. *Nyctea* is hardly more than a *Bubo* adapted to life in Arctic tundra. On geographical grounds alone, *Bubo* is the only genus of Bubonini likely to have colonized Cuba, and we find nothing in the Cuban fossils to suggest a closer relationship to any of the other owls of that tribe than to *Bubo.* In *Strix nebulosa,* the largest New World member of the Strigini, the femur and humerus are proportionately much more elongate and gracile, the wing of the inner trochlea is less pronounced, and the attachment of M. tibialis anticus is more distinct and raised than in the Cuban fossils, which conform with *Bubo* in all these respects.

Bubo osvaldoi, new species
Figs. 1–4

Holotype.—Right tarsometatarsus of an adult lacking the proximal end above the attachment for M. tibialis anticus (Fig. 1B, C). Deposited in the Museo Nacional de Historia Natural de Habana (MNHNCu-27.1).

Type locality.—Cueva del Mono Fósil, southern side of the Sierra de Galeras, Cordillera de Guaniguanico, Municipality of Viñales, Province of Pinar del Río, Cuba. This is also the type locality of the fossil platyrrhine monkey *Paralouatta varonai* (Rivero and Arrédondo, 1991).

Age.—Quaternary, probably Pleistocene, at least as judged by the mineralization and associated fauna of the holotype and topotypes.

Measurements of holotype (mm).—Length from distal end of attachment of M. tibialis anticus to trochleae, 63.3; least width of shaft, 11.9; depth of shaft at midpoint, 7.8; distal width across trochleae, 24.8; depths of inner, middle, and outer trochleae, 12.1, 9.8, 14.9.

Topotypical paratypes.—Complete right femur, lacking the internal condyle and abraded about the trochanter, MNHNCu 27.3 (Fig. 2B). Shaft of left tarsometatarsus, lacking the proximal portion and the digital trochleae, MNHNCu-27.2. These specimens and the holotype appear to be very heavily mineralized and are blackish in color, mottled with orangish brown. The paratypical tarsometatarsus is from an individual slightly larger than represented by the holotype and the specimen is highly polished and evidently water worn.

Additional paratypes.—Right femur lacking internal condyle, anterior surface of head, and a piece out of the posterior face of the shaft, USNM 447022 (Figs. 2A, 3A–C). Left humerus lacking proximal end and the external part of the distal articulation, USNM 447023 (Figs. 3D, 4B). The only information we have concerning these specimens is that they came from a "mine" (perhaps a cavern exposed in roadwork or similar activity) in the vicinity of Baire, Oriente Province (now in the Provincia de Santiago de Cuba). They are creamy white in color and are very light to the touch, as though lacking organic constituents, perhaps through leaching. The same site is the type locality of the sloth *Neocnus baireiensis* Mayo (1980), described from material presumably collected at the same time as the owl bones and for which there is likewise no more precise information.

Measurements of paratypes (mm).—Tarsometatarsus MNHNCu-27.2: least width of shaft, 11.5; depth of shaft at midpoint, 7.2 (worn). Femur MNHNCu-27.3: length, 101.5; proximal width 22.7; depth of head 9.4; width and depth of shaft at midpoint, 9.8 × 9.4; depth through external condyle,

Fig. 2. Femora of *Bubo* in anterior view. A, *B. osvaldoi,* new species (USNM 447022); B, *B. osvaldoi,* new species (MNHN 27.3, coated with ammonium chloride to enhance detail); C, *B. bubo* (USNM 610384) female, largest available specimen of the species; D, *B. bubo* (USNM 343007) male; E, *B. virginianus* (USNM 501314) female; F, *B. virginianus* (USNM 555903), male. Size differences between the two femora of *B. osvaldoi* are closely comparable to those between sexes in other species of the genus. Note the different position of the intermuscular line in *B. osvaldoi.* Figures three-fourths natural size.

19.0. Femur USNM 447022: length, 112.4; proximal width 27.7; depth of head 10.3; width and depth of shaft at midpoint, 11.5 × 9.9; depth through external condyle, 21.9. Humerus USNM 447023: length from distal end of pectoral crest to entepicondyle, 99.1; length (diagonal) of brachial depression, 17.6.

Etymology.—The species is dedicated to the discoverer of the specimens from Pinar del Río, Osvaldo Jiménez, speleologist and amateur paleontologist.

Diagnosis.—Larger than any modern species of Bubonini (Table 1), which includes the largest modern owls. Distal foramen of tarsometatarsus much larger. The intermuscular line on the anterior face of the shaft of the femur is unique in originating at the distal end of the trochanteric crest and running diagonally across the shaft, whereas in *Bubo* and other owls examined the line originates at the neck of the femur or near the trochanter and runs parallel, or nearly so, to the sides of the shaft (Fig. 2). Humerus small relative to the hindlimb.

Comparative material examined.—Skeletons from the collections of the National Museum of Natural History, Smithsonian Institution (USNM) as follows: *Bubo bubo* (4 males, 1 female, 1 unsexed, 1 female

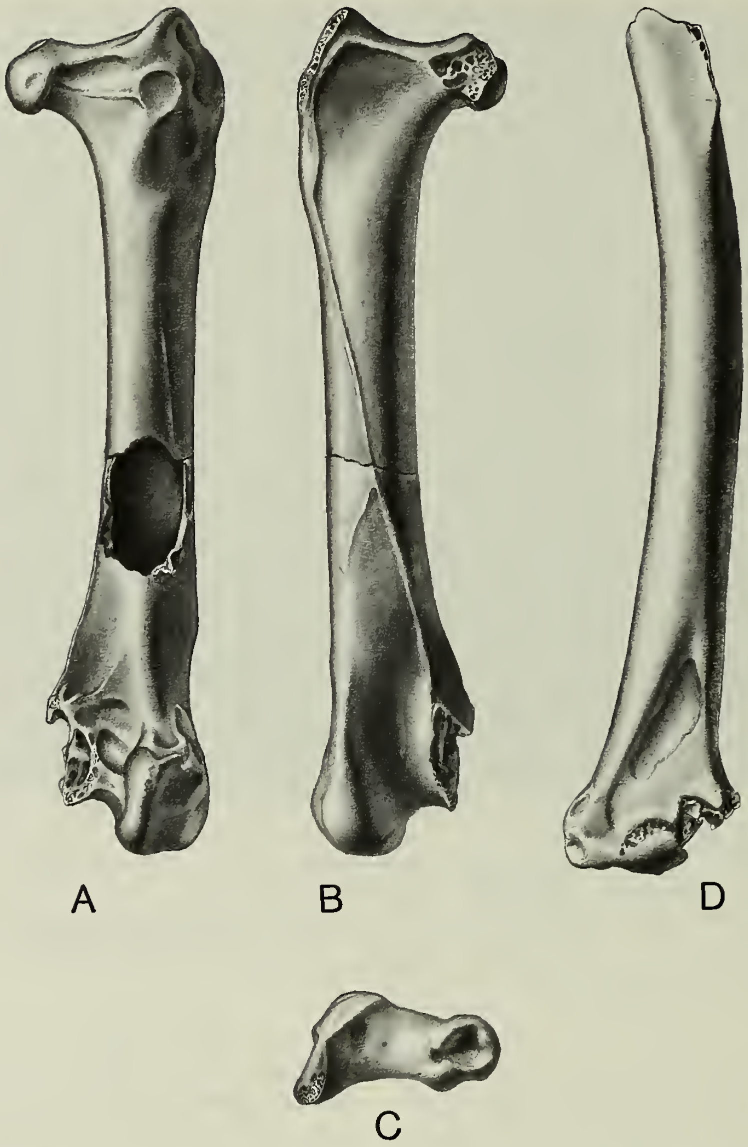

Fig. 3. Drawings of the two paratypes of *Bubo osvaldoi,* new species, from Baire, Santiago de Cuba: A, femur in posterior view (USNM 447022); B, same, anterior view; C, same, proximal view; D, humerus in palmar view (USNM 447023). Natural size.

trunk; Sweden, Greece, and Korea), *Bubo virginianus* (6 males and 6 females; Pennsylvania, District of Columbia, Florida, Minnesota, New Mexico, Arizona, and California), *Bubo africanus* (2 males, 4 females, and 1 male trunk; Sudan, Tanzania, Zimbabwe, and Transvaal), *Bubo lacteus* (1 male and humeri of a female; Kenya and Zimbabwe), *Bubo philippensis* (1 female; Luzon), *Bubo sumatrana* (1 unsexed; Borneo), *Ketupa ketupu* (1 female and 1 female trunk; Borneo and Java), *Ketupa blakistoni* (1 unsexed; Japan), *Ketupa zeylonensis* (2 females and 1 unsexed; Thailand and un-

Fig. 4. Humeri of *Bubo* in palmar view. A, *B. bubo* (USNM 610384) female, largest available specimen of the species; B, *B. osvaldoi*, new species (USNM 447023); C, *B. virginianus* (USNM 501314), female. Figures three-fourths natural size.

known localities), *Nyctea scandiaca* (2 males and 2 females; Alaska, Maryland, and District of Columbia). The following specimens of *Scotopelia* in the American Museum of Natural History were measured and examined for us: *S. peli* (2 unsexed; Zaire), *S. bouvieri* (1 unsexed; Zaire), *S. ussheri* (1 female; Sierra Leone).

Comparison with other fossil species.—The only other extinct insular species of *Bubo* is *B. insularis* from Corsica and Sardinia, which was described as being smaller than *B. bubo* (Mourer-Chauviré & Weesie 1986), and hence is even smaller than *B. osvaldoi*. As ascertained from the review in Mourer-Chauviré & Weesie (1986), most of the other fossil species attributed to the genus *Bubo* are smaller than *B. insularis*. According to Brodkorb & Mourer-Chauviré (1984), *Bubo sinclairi* L. Miller, based on scanty and poorly preserved material from Quaternary cave sites in California, falls within the range of size variation of *B. virginianus* and is probably a synonym of that species.

Bubo florianae Kretzoi, 1958, is based on a pedal phalanx from the early Pliocene of Hungary that probably falls within the range of size variation of *Bubo bubo* (Jánossy 1977). *Bubo bubo davidi* (Mourer-Chauviré 1975) was described from the Pleistocene

Table 1.—Selected measurements of large owls (Strigidae) compared with *Bubo osvaldoi*, new species. For numbers of specimens see Comparative Material Examined. FEM = length of femur. HUM = length of humerus from distal end of pectoral crest to entepicondyle. TMT 1 = length of tarsometatarsus from distal end of attachment of M. tibialis anticus to trochleae. TMT 2 = width of tarsometatarsus across trochleae.

Species	FEM	HUM	TMT 1	TMT 2
Bubo osvaldoi	101.5–112.4	99.1	63.3	24.8
Bubo bubo	93.5–104.5	97.7–110.7	46.6–50.4	18.9–23.0
Bubo virginianus	75.1–86.1	76.9–89.7	36.5–41.0	16.1–19.2
Bubo africanus	64.5–72.2	69.6–74.6	42.0–52.4	13.1–13.9
Bubo lacteus	91.1	104.9–106.4	46.4	23.1
Bubo philippensis	77.2	85.0	43.0	20.8
Bubo sumatrana	60.6	75.3	28.2	17.5
Ketupa ketupu	75.9–78.9	81.8	51.1	15.9
Ketupa blakistoni	102.7	116.7	48.7	21.2
Ketupa zeylonensis	82.0–97.1	87.3–104.1	52.4–56.1	16.3–19.9
Nyctea scandiaca	83.8–92.6	92.8–102.4	28.3–32.0	17.6–20.2
Scotopelia peli	92.1–96.2	—	—	22.2
Scotopelia bouvieri	65.3	—	—	13.2
Scotopelia ussheri	73.8	—	—	14.2

of France as a larger temporal form of the modern species, although there is overlap, particularly with the largest specimen of *Bubo bubo* that we examined, which exceeds any of those reported by Mourer-Chauviré (1975). There were otherwise no qualitative differences shown by the fossil form and it cannot, therefore, be identified with the Cuban bird.

Bubo binagadensis Burchak-Abramovich, 1965, from the Pleistocene of Azerbaijan, was described from a femur that was said to be not less than the size of that in the eastern forms of fishing owls (genus *Ketupa* assumed, although we may wonder if Burchak had access to any comparative material) and much larger than in *Bubo bubo.* Neither illustrations nor measurements accompanied the description, only some indecipherable "indices of massiveness," so we cannot determine anything further about this taxon at present.

Discussion.—Although bubonine owls are diverse in the Old World, only two taxa occur today in the New World—the Snowy Owl (*Nyctea scandiaca*), which is circumpolar in the high Arctic, and the Great Horned Owl (*Bubo virginianus*), which has probably the greatest latitudinal breeding range of any bird in the world, nesting from northern Canada and Alaska to Tierra del Fuego. It does not occur in the West Indies, however, and *Bubo osvaldoi* is thus the first and only member of the Bubonini recognized in the Antilles.

In size, *Bubo osvaldoi* exceeds any living owl (Table 1), there being no overlap in tarsal measurements. The smaller of the two fossil femora is exceeded only by the one unsexed specimen of *Ketupa blakistoni* and by the largest female specimen available of *Bubo bubo.* As females are the larger sex in owls, if we assume that the small fossil femur is from a male, then on a sex per sex basis there would probably be no overlap in any hindlimb measurements between *Bubo osvaldoi* and living owls. The humerus in *B. osvaldoi,* however, falls within the size range of several of the larger species of owls (Table 1), suggesting that the wing in this insular form may have been reduced relative to the overall size of the bird.

There is considerable variation in proportions of the hindlimb, especially the tar-

Fig. 5. Tarsometatari of *Bubo* in anterior view to show the great differences in proportions between various species. A, *B. virginianus* (USNM 613846); B, *B. africanus* (USNM 490288); C, *B. sumatranus* (USNM 559827). Figures three-fourths natural size.

sometatarsus, in *Bubo.* Compared to *B. bubo,* the tarsometatarsus in *B. africanus,* for example, is quite long and slender, whereas that in *B. sumatranus* is extraordinarily short and stout (Fig. 5). That of *B. osvaldoi* is of more typical proportions and is similar to that of *B. bubo.*

It is not necessary to assume that *B. osvaldoi* is most closely related to *B. virginianus* simply because the latter is the only geographically proximate bubonine in the New World. Olson (1984) reported a mandibular symphysis of a very large owl from the Pleistocene at Ladds, Georgia, that surely represents a species otherwise as yet unknown in North America. Although this specimen seemed to be more similar in morphology to *Strix* than to *Bubo,* it is not very diagnostic. Regardless, it indicates that extinct lineages of large owls remain to be discovered in the fossil record of North America, so that a progenitor of *B. osvaldoi* from a lineage other than that giving rise to *B. virginianus* may yet be found.

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XENISTHMUS BALIUS, A NEW SPECIES OF FISH FROM THE PERSIAN GULF (GOBIOIDEI: XENISTHMIDAE)

Anthony C. Gill and John E. Randall

Abstract.—Xenisthmus balius is described from nine specimens from Jana Island, Saudi Arabia. It is distinguished from other xenisthmids in having the following characters in combination: dorsal-fin rays VI + I,13; anterior rim of posterior nostril raised, without well-developed membranous flap; scales of body mainly cycloid; head and body pale, with reticulate, brown mottling dorsally.

The Xenisthmidae are a family of small (mostly less than 25 mm SL, and all less than 40 mm SL), sand-diving fishes that live in sand patches adjacent to coral reefs or reef rubble throughout the Indo-Pacific. Several synapomorphies distinguish xenisthmids from other gobioid fishes and support monophyly of the family: lower lip with uninterrupted, free ventral margin; basibranchial 2 absent; premaxillary ascending processes greatly reduced; rostral cartilage ossified; and hypobranchial 3 reduced to small cartilage nubbin, or absent (Springer 1983, 1988; Gill & Hoese 1993). The family includes five genera: *Allomicrodesmus* Schultz, *Paraxenisthmus* Gill & Hoese, *Rotuma* Springer, *Tyson* Springer, and *Xenisthmus* Snyder (of which *Gignimentum* Whitley, *Luzoneleotris* Herre, *Platycephalops* Smith, and *Kraemericus* Schultz are synonyms). *Xenisthmus* species are distinguished from other xenisthmids by a single synapomorphy, third branchiostegal ray with an expanded proximal head, and by the following combination of symplesiomorphies: first dorsal-fin spines 6; scales present on body; and palatine teeth absent (Gill & Hoese 1993). Recent fieldwork by the second author and associates in the Persian Gulf has resulted in the discovery of a distinctive new *Xenisthmus* species, described herein.

Materials and Methods

Measurements were made with dial calipers, recorded to the nearest 0.1 mm. All measurements to the snout tip were made to the mid-anterior tip of the snout. Standard length (SL) was measured from the snout tip to the middle of the caudal-fin base. Predorsal, preanal and prepelvic lengths were measured from the snout tip to the base of the anteriormost spine of the relevant fin. Head length was measured from the snout tip to the dorsal edge of the gill opening. Head width is the broadest measurement between the posterior edges of the preopercles. Body width was measured at the pectoral-fin base. Snout length was measured over the shortest distance from the snout tip to the orbital rim, without compressing the fleshy edge of the latter. Orbit diameter was measured as the horizontal width of the eyeball. Bony interorbital width was the least measurement. Caudal peduncle length was measured from the base of the posteriormost anal-fin ray to the ventral edge of the caudal peduncle at the vertical through the posterior edge of the lower hypural plate. Caudal peduncle depth was measured obliquely between the bases of the posteriormost anal- and dorsal-fin rays. Pectoral-fin base depth was the vertical depth of the fleshy lobe. Measurements of fin spines and rays excluded any filamentous membranes. Pectoral-fin length was measured as the length of the longest ray. Caudal-fin length was measured as the length of the ventralmost ray on the upper hypural plate.

The last ray in the anal- and second-dorsal fins is divided at its base and was counted as a single ray. "Scales in lateral series" was counted from the upper edge of the pectoral-fin base along the midside of the body to the posterior edge of the hypural plate. The pattern of interdigitation of first-dorsal-fin proximal pterygiophores between neural spines is given as a dorsal-fin pterygiophore formula following Birdsong et al. (1988:175). Gill-raker counts include all elements on the outer face of the first arch; the angle raker is included in the lower-limb (second) count. Osteological details were determined from radiographs and a cleared and stained paratype (USNM 326758). Institutional codes follow Leviton et al. (1985). Counts and morphometric values are given first for the holotype, followed, where different, by ranges or frequency distributions for the paratypes. Frequency distributions are presented in the form "x fy," where "x" is the count and "f" indicates that the following value, "y," is its frequency. Where counts were recorded bilaterally from the holotype, both counts are given and separated from each other by a slash; the first count presented is the left count.

Xenisthmus balius, new species

Figs. 1–3

Holotype.—BPBM 30458, 25.5 mm SL female, Persian Gulf, Saudi Arabia, northeast side of Jana Island, base of dropoff in 15 m, J. E. Randall, A. B. Tarr and J. E. Burfhard, 15 Jun 1984.

Paratypes.—BPBM 33308, 26.4 mm SL male, 29.0 mm SL female, Persian Gulf, Saudi Arabia, west side of Jana Island, reef flat, sand and rubble with small patches of mostly dead coral, 1.5 m, J. E. Randall, L. J. McCarthy, B. E. Stanaland and A. B. Tarr, 13 Sep 1985; AMNH 97301, 29.4 mm SL female, Persian Gulf, Saudi Arabia, southeast side of Jana Island, base of dropoff in 17 m, J. E. Randall, L. J. McCarthy, B. E. Stanaland and A. B. Tarr, 13 Sep 1985; AMS I.34236-001, 23.2 mm SL male, collected with AMNH 97301; BMNH 1993.9.25:1, 19.1 mm SL male, collected with AMNH 97301; BPBM 33353, 3, 18.0–31.0 mm SL females, collected with AMNH 97301; USNM 326758, 26.1 mm SL male (subsequently cleared and stained), collected with AMNH 97301.

Diagnosis.—A species of *Xenisthmus* with the following combination of characters: dorsal-fin rays VI + I,13; anterior rim of posterior nostril raised, without well-developed flap; scales of body mainly cycloid; head and body pale, with reticulate, brown mottling dorsally.

Description.—Dorsal-fin rays VI + I,13, all segmented rays branched; first dorsal-fin pterygiophore formula 3-22110; anal-fin rays I,12 (I,12 f7; I,13 f1), all segmented rays branched; pectoral-fin rays 17/16 (16 f2; 17 f14), upper 1/1 (1 f15; 2 f1) and lower 1/1 (0 f1; 1 f14; 2 f1) rays unbranched; pelvic-fin rays I,5, inner ray unbranched; segmented caudal-fin rays 9 + 8; branched caudal-fin rays 7 + 7 (6–8 + 6–7 = 12–15); upper unsegmented caudal-fin rays 8 (7 f1; 8 f5; 9 f2); lower unsegmented caudal-fin rays 8 (7 f3; 8 f4; 9 f1); scales in lateral series 70/67 (60 f1; 61 f2; 62 f2; 63 f3; 64 f2; 65 f4; 66 f1; 68 f1); scales in transverse series counted anterodorsally from anal-fin origin 21/22 (20 f3; 21 f6; 22 f7); scales in transverse series counted posterodorsally from anal-fin origin 22/21 (20 f5; 21 f7; 22 f4); circumpeduncular scales 36 (35 f1; 36 f6; 37 f1); predorsal scales 20 (16 f3; 17 f2; 18 f2; 19 f1); gill rakers 3 + 11 (3–4 + 9–12 = 13–16); pseudobranch lobes 5 (4 f3; 5 f5); vertebrae 10 + 16; epurals 2.

As thousandths of SL: head length 235 (213–246); predorsal length 333 (310–344); prepelvic length 227 (211–241); preanal

Fig. 1. Right lateral view (reversed) of *Xenisthmus balius,* holotype, BPBM 30458, 25.5 mm SL female, Jana I., Saudi Arabia, Persian Gulf; scales omitted.

length 569 (534–571); first dorsal-fin origin to second dorsal-fin origin 188 (183–207); second dorsal-fin base length 361 (328–375); anal-fin base length 271 (284–309); pectoral-fin base depth 71 (68–79); first dorsal-fin origin to pelvic-fin origin 165 (159–178); second dorsal-fin origin to anal-fin origin 133 (129–156); snout length 35 (38–44); orbit diameter 47 (44–61); head width 133 (129–148); body width 118 (117–148); bony interorbital width 20 (19–24); snout tip to retroarticular tip 98 (91–99); caudal peduncle length 149 (147–171); caudal peduncle depth 98 (108–119); length of first spine of first dorsal fin 78 (58–89); length of third spine of first dorsal fin 98 (72–94); length of sixth spine of first dorsal fin 67 (52–89); length of spine of second dorsal fin 78 (74–91); length of first segmented ray of second dorsal fin 94 (84–106); length of last segmented ray of second dorsal fin 110 (82–123); anal-fin spine length 55 (48–73); length of first segmented anal-fin ray 90 (71–100); length of last segmented anal-fin ray 106 (94–121); pectoral fin length 192 (158–211); pelvic-fin spine length 39 (33–53); fourth segmented pelvic-fin ray length 173 (161–192); caudal-fin length 184 (170–207).

Body covered with small, cycloid scales (a few, irregularly distributed ctenoid scales present on caudal peduncle of some specimens); ventral contour of body full scaled, except for narrow area beneath branchiostegal membranes; predorsal scales extending anteriorly to or slightly posterior to vertical through posterior edge of preopercle (Fig. 2); no scales on operculum or cheek; cycloid scales present on pectoral-fin base; narrow band of scales on fleshy portion of caudal-fin base, these usually cycloid, but sometimes with several, irregularly distributed ctenoid scales; no scales on dorsal- or anal-fin bases.

Distribution of sensory pores and superficial neuromasts on head as shown in Fig. 2; lower lip fleshy and protruding, with uninterrupted, free ventral margin; anterior nostril in short tube; posterior nostril with raised rim, without prominent membranous flap anteriorly (Fig. 3A) (small flap present in only one 29.0 mm SL paratype); tongue weakly indented anteriorly; gill opening extending anteriorly to about midway between verticals through posterior edge of preopercle and posterior edge of eye (Fig. 2); female urogenital papilla flattened and trapezoid, broader anteriorly, with multiple fleshy lobes posteriorly surrounding wide gonopore (Fig. 3C); male urogenital papilla

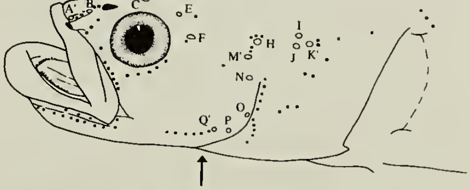

Fig. 2. Right lateral view (reversed) of head of *Xenisthmus balius,* holotype, BPBM 30458, 25.5 mm SL, showing distributions of superficial neuromasts and lateralis pores. Letter codes for lateralis pores follow Akihito (1984); left components of paired pores and neuromasts not shown. Upper arrow indicates anterior extent of median predorsal scales; lower arrow indicates anterior extent of gill opening.

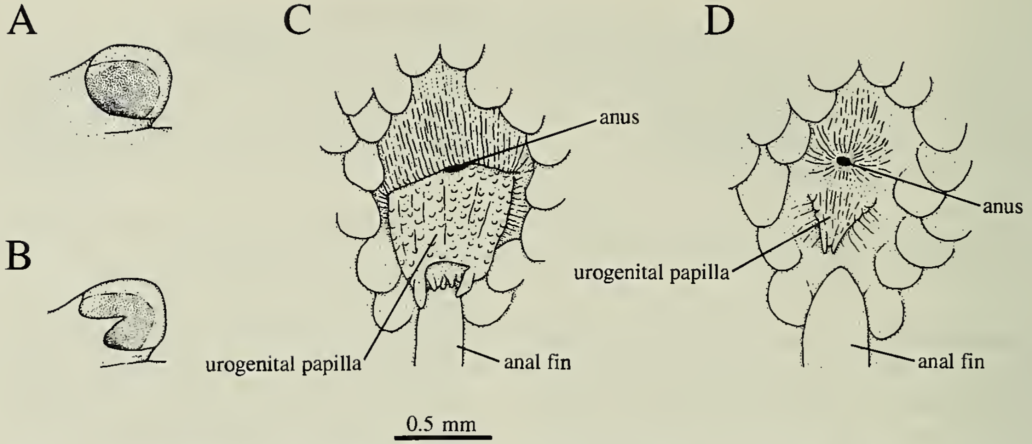

Fig. 3. A–B, diagrammatic representation of right posterior nostrils in dorsomedial view of *Xenisthmus* species without (A) and with (B) well-developed membranous flaps; anterior is to left. C–D, ventral view of urogenital papillae of (C) female, BPBM 30458, 25.5 mm SL holotype, and (D) male, BPBM 33308, 26.4 mm SL paratype of *Xenisthmus balius,* both drawn to same scale; anterior is to top.

moderately flattened and triangular, pointed posteriorly, with small lobe posteriorly on either side of gonopore (Fig. 3D).

Upper jaw with two or three (anteriorly) or two (posteriorly) rows of small, conical teeth, the outer-row teeth largest and slightly curved; lower jaw with three (anteriorly) or two (posteriorly) rows of small, conical teeth, the outer-row teeth largest and slightly curved; vomer, palatines and tongue edentate.

Preserved coloration.—Head and body pale yellow to pale brown with reticulate mottling of irregular, brown to dark grey-brown melanophores, these darkest on mid-side; three short, brown to dark grey-grown bars extending from eye, one from mid-anterior part of orbital rim to mid-side of upper lip, one from below mid-ventral part of orbital rim to behind posterior edge of maxilla, and one from posteroventral part of orbital rim to middle of cheek; mid-side of lower lip and adjacent inner part of lower jaw brown to dark grey-brown; upper part of pectoral-fin base with irregular cluster of large, brown to dark grey-brown melanophores beneath and immediately behind operculum, sometimes with additional cluster on ventral part of fin, and more-posterior, smaller cluster near bases of upper few rays; short dark grey-brown bar of melanophores on caudal-fin base; first dorsal fin hyaline with cluster of brown to dark grey-brown melanophores on middle of all or most spines, sometimes with cluster more distally; second dorsal fin hyaline with cluster of brown melanophores between bases of each ray, a cluster of brown melanophores on middle of each ray, and an additional one or two rows of melanophores on each ray; anal fin hyaline, sometimes with clusters of brown melanophores between ray bases and on middle of each ray; caudal fin hyaline with one or two large, irregular, dark grey-brown to dark grey melanophores on bases of lowermost two rays on upper hypural plate, often with a few small clusters of brown melanophores arranged in slightly concave or reticulate columns on remainder of fin; pectoral fins hyaline, with irregular patch of brown to dark grey-brown melanophores basally on upper half of fin, sometimes with additional cluster on ventral half of fin; pelvic fins hyaline.

Live coloration (based on a color photograph by L. J. McCarthy of BPBM 33308, 29.0 mm SL female, when freshly dead).—Similar to preserved coloration, except ground coloration of head and body pale pinkish brown, becoming white ventrally, with dark grey-brown and dark grey markings on head, body and fins dark grey to black.

Etymology.—The specific epithet is from the Greek 'balios', meaning spotted or dappled, and alludes to the distinctive coloration of the species.

Remarks.—*Xenisthmus balius* closely resembles *X. chapmani* (Schultz 1966) from Espiritu Santos, Vanuatu (New Hebrides), in having mostly cycloid scales, and relatively high numbers of segmented dorsal- and anal-fin rays. It differs from the holotype and only known specimen of *X. chapmani* in having fewer segmented dorsal- and anal-fin rays (13 and 12–13 [usually 12], respectively, versus 14 and 13 for *X. chapmani*), fewer vertebrae (10 + 16 versus 10 + 17) and a different first dorsal-fin pterygiophore formula (3-22110 versus 3-12210), and in lacking well-developed membranous flaps on the posterior nostrils (see Fig. 3A, B). *Xenisthmus balius* also closely resembles an undescribed *Xenisthmus* species from the Red Sea (to be described by the first author and D. F. Hoese) in lacking well-developed membranous flaps on the posterior nostrils, and in having relatively high numbers of segmented dorsal- and anal-fin rays, relatively few ctenoid scales, and a more-or-less mottled body coloration. The Red Sea species differs from *X. balius* in having more segmented rays in the second dorsal and anal fins (15 and 14, respectively), and in having fewer head pores (e.g., 3 versus 5 preopercular pores (Fig. 2, pores M′, N, O, P, Q′); 1 versus 2 nasal pores (Fig. 2, pores A′, B)).

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CRABS OF THE FAMILY HOMOLODROMIIDAE (CRUSTACEA: DECAPODA: BRACHYURA), V. *DICRANODROMIA SPINOSA,* A NEW SPECIES FROM THE WESTERN ATLANTIC

Joel W. Martin

Abstract.—A new species of the primitive homolodromiid crab genus *Dicranodromia, D. spinosa,* is described from among the specimens examined by M. J. Rathbun (1937) and previously considered to belong to the species *D. ovata* A. Milne Edwards. The new species is represented by 10 known specimens, one of which was formerly a paratype of *D. ovata* A. Milne Edwards, all collected in the western Atlantic. The species is easily distinguished from the other two American species, *D. ovata* and *D. felderi,* by the overall size, by the spination and setation of the carapace and pereiopods, and by the relative lengths of the terminal segments of pereiopod 5.

At the time of publication of M. J. Rathbun's fourth and final volume on the crabs of America (Rathbun 1937), the genus *Dicranodromia* A. Milne Edwards, 1880, contained four species: *D. ovata* A. Milne Edwards, *D. mahieuxii* A. Milne Edwards, *D. doederleini* Ortmann, and *D. baffini* (Alcock & Anderson). Only one of these species was known from the Americas: *Dicranodromia ovata* A. Milne Edwards, 1880, the type species of the genus. The total number of specimens of *D. ovata* known to Rathbun, including the four specimens that comprised the type series (see Martin 1990), apparently was 14. In my description of a second American species of *Dicranodromia* from the western Atlantic, *D. felderi,* I noted that several lots among those labeled *D. ovata* in the collections of the National Museum of Natural History appear to contain unrecognized species (Martin 1990). One of those species, curiously one that is represented by most of the specimens examined and discussed by Rathbun, is described herein.

Specimens upon which this report is based are in the holdings of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and were previously labeled *Dicranodromia ovata.* Type material of *D. ovata* was borrowed from the Museum of Comparative Zoology, Harvard University (MCZ) (the holotype female, MCZ 6510, and two female paratypes, MCZ 6511 [herein reassigned to the new species] and MCZ 2745), and the Muséum national d'Histoire naturelle, Paris (the third female paratype, MNHN MP-B24324). Illustrations were made with the aid of a Wild M5APO dissecting stereoscope and drawing arm. The abbreviation CL indicates carapace length.

Dicranodromia spinosa, new species
Figs. 1, 2

Dicranodromia ovata.—Milne Edwards and Bouvier, 1902 (in part) [see discussion].
Dicranodromia ovata.—Rathbun 1937:60, fig. 15, table 16 (in part only), and plate 13, figs. 3, 4. Not *Dicranodromia ovata* A. Milne Edwards, 1880.

Male holotype.—USNM 68887, male, CL (carapace length) = 6.1 mm. State University of Iowa Biological Expedition to Florida Keys and the West Indies, Station 63.

Handwritten labels state "26767" and "abd. drawn" [abdomen drawn; the telson of this specimen was figured on p. 61 of Rathbun 1937].

Type locality.—There are no additional data in the vial containing USNM 68887. However, in Rathbun's (1937) table of material of *D. ovata* (p. 64), there is only one male listed as being from the State University of Iowa collections, and the station number given in the table is 63, which corresponds to the label in USNM 68887. Therefore, the type locality, from Rathbun's table 16, is "Off American Shoal Light [Florida, U.S.A.], N. by E. ½ E. about 8 mi.," from a depth of 85–95 fm (156–174 m), 29 Jun 1893, from "under simple ascidian" (Rathbun 1937:64).

Designated paratypes.—USNM 57068, female, CL = 6.9 mm, clearly mature (but not ovigerous), State University of Iowa Biological Expedition to Florida Keys and the West Indies, Station 35, 21 Jun 1893, 5 mi N.N.W. Sand Key Light, 90 fm (165 m), off Key West, Florida. USNM 68914, female (not ovigerous, as indicated on label and in table 16 of Rathbun 1937, so possibly eggs lost at some time in past), CL = 7.1 mm, State University of Iowa Expedition, Station 64, off American Shoal Light, N. by W. about 8 mi, "about 110 fathoms" (201 m), 29 Jun 1893. USNM 57069, female (ovigerous), CL = 9.2 mm [9.8 mm according to Rathbun 1937:61], State University of Iowa, Station 52, American Shoal Light, 10 mi. N by W ½ W., 105 to 110 fm (192–201 m), 27 Jun 1893. This specimen photographed as *D. ovata* in Rathbun (1937, pl. 13, figs. 3, 4).

Additional material (not paratypic).—USNM 68917, female (damaged), ovigerous, CL = 7.8 mm [label states "2 females (1 ovig)" but only 1 crab, an ovigerous female, found]. USNM 68862, 2 females, CL = 5.4 mm (juvenile); CL = 10.1 mm (mature female). USNM 68917, female (damaged), CL = 7.8 mm. USNM 68877, female (ovigerous), CL = 9.8 mm. MCZ 6511, small mature female, CL = 6.5 mm. Florida, off Key West, 24°15′00″N, 82°13′00″W, 152–229 fm (278–419 m), 1877–1878, "Blake" Station 5. According to Rathbun (1937, 64: table 16) this is a figured paratype of *D. ovata,* although not figured by her. This specimen is herein reassigned to *Dicranodromia spinosa.*

Diagnosis.—Small species, known specimens not exceeding 10.1 mm total carapace length (including rostral horns). Carapace covered with small spinules interspersed with simple, short setae; spinules often longer and sharper along anterolateral borders. Rostral horns broad, blunt, with spinules dorsally and occasionally extending ventrally (not visible in dorsal view). Postorbital tooth small, usually compound. Chelipeds and pereiopods 2 and 3 covered with minute spinules and long, plumose setae. Propodus of pereiopod 5 extremely short, less than twice length of dactylus.

Description.—Carapace (Fig. 1A–C) inflated, strongly convex in cross section and less so from front to back; covered with small blunt-tip spines, among which are short, simple, amber-colored setae. Rostral teeth broad and spinose dorsally; some specimens with spines extending ventrally from midpoint between rostral teeth. Carapace spines becoming slightly smaller posteriorly, and more or less absent in broad region just posterior to cervical groove, presumably because fourth and fifth pereiopods contact carapace here. Postorbital tooth small, extending laterally to just beyond cornea, and usually bifid or compound (Fig. 1C). Region between rostral horns slightly depressed. Eyes large relative to carapace; eyestalk with several blunt spines on frontodorsal surface. Third maxillipeds with numerous spines, especially on external surface of merus. Chelipeds (Fig. 2A) covered with spines and with long, lightly plumose setae; each seta extending outward for some distance before bending rather abruptly to create protective layer of horizontally-oriented setae around chela. Dactylus with

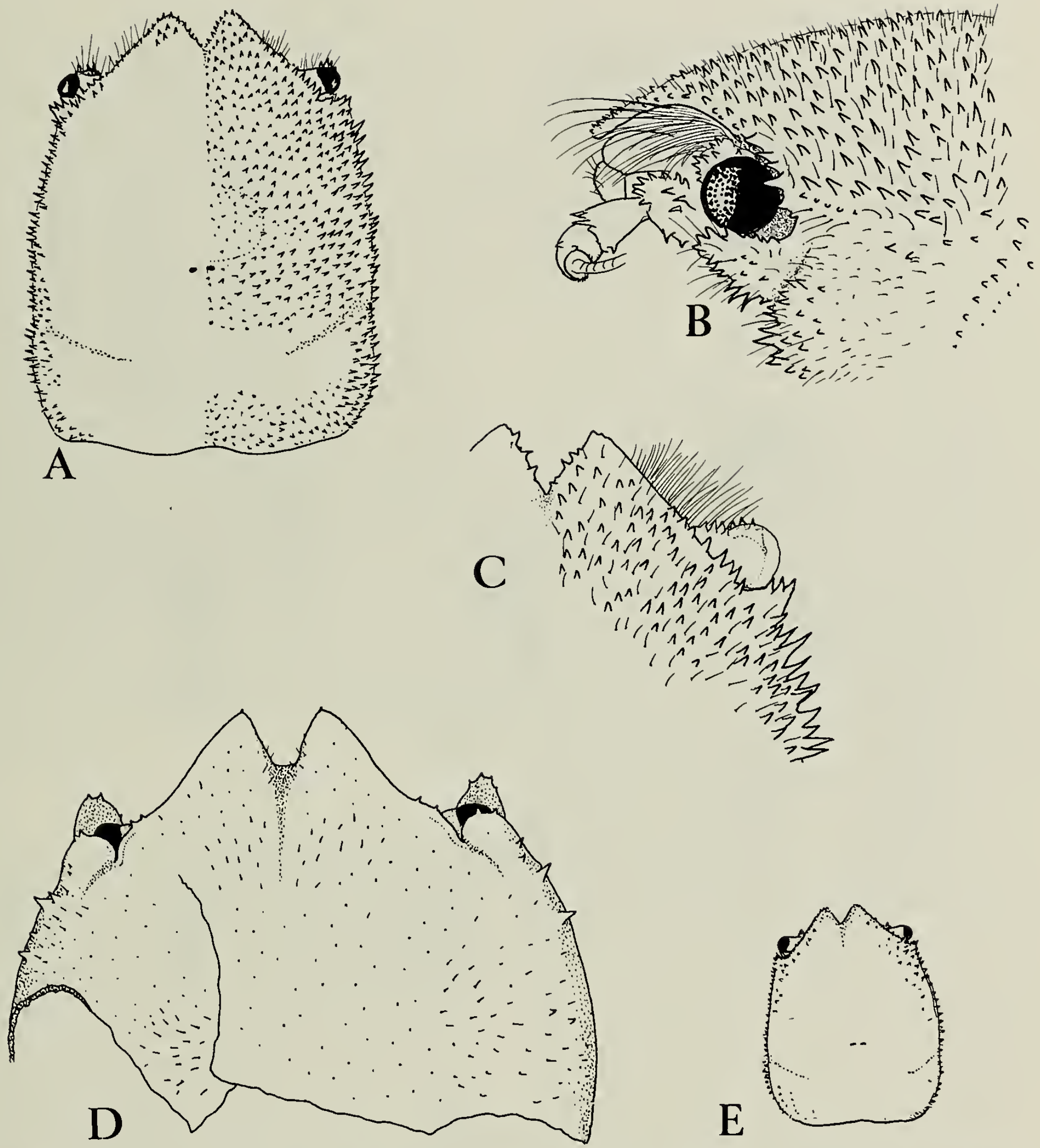

Fig. 1. *Dicranodromia spinosa,* new species, holotype male, USNM 68887. A, dorsal view of carapace, spination illustrated for right side only; B, lateral view of frontal region of carapace and orbit; C, higher magnification of anterior right side of carapace showing details of spination of postorbital tooth and carapace along lateral surface; D, anterior part of carapace of *Dicranodromia ovata* A. Milne Edwards, 1880, female holotype (MCZ 6510); E, dorsal view of holotype male of *Dicranodromia spinosa,* illustrated at same magnification as D for size comparison.

small basal tooth. Fixed finger with 4 rounded teeth, distalmost of which is bifid to allow insertion of opposing tip of dactylus (Fig. 2A). Tips of fingers bone white, glossy; hand light brown or tan, with color extending to midpoint of dactylus and to approximately basal ¼ of fixed finger. Pereiopods 2 and 3 (e.g., Fig. 2B) similarly spinose, covered with same lightly plumose setae seen on chelipeds. Dactylus (Fig. 2C) stout, recurved,

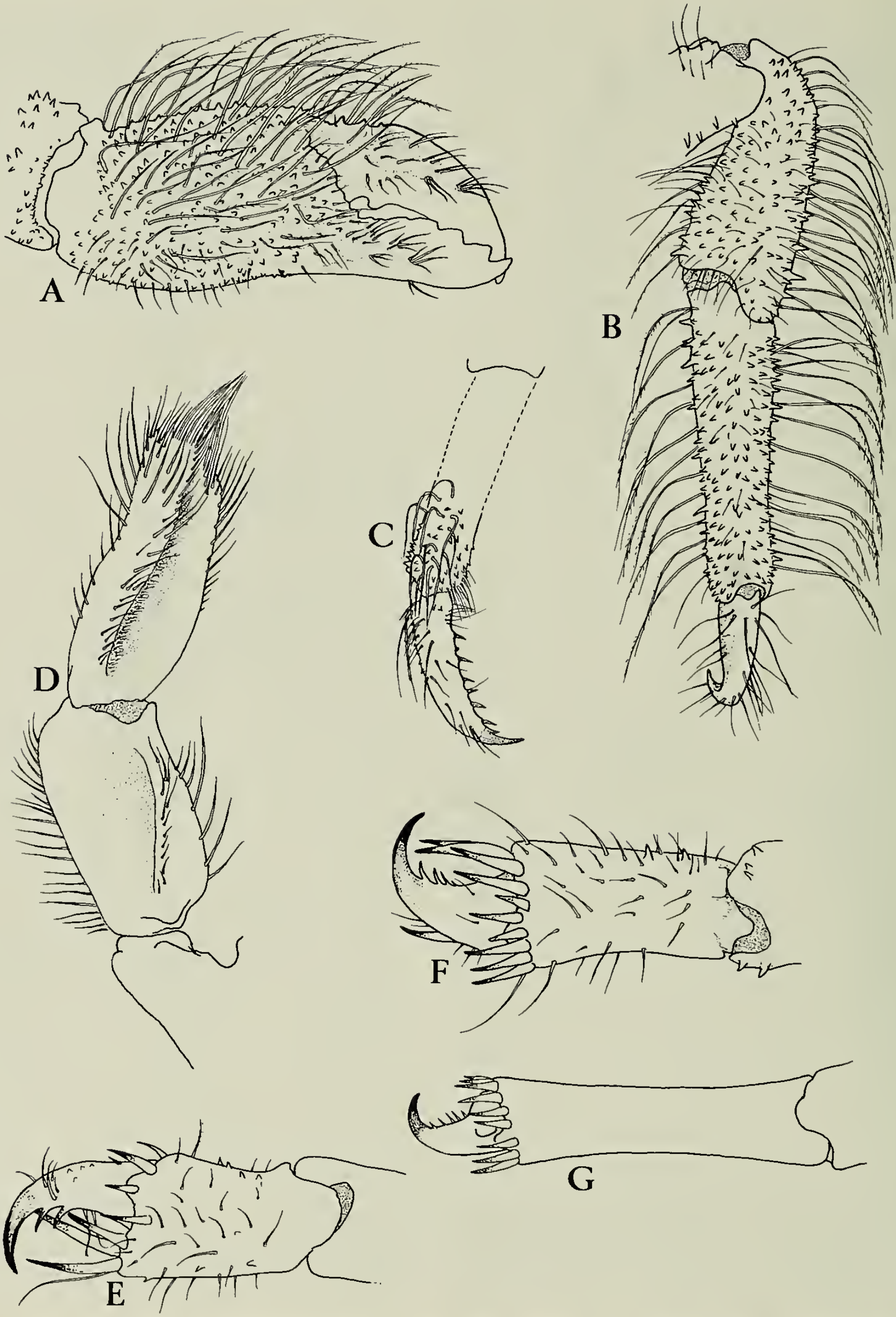

Fig. 2. *Dicranodromia spinosa,* new species: A, right chela, outer view; B, third pereiopod (second walking leg) [note orientation of dactylus to propodus and covering of spines and plumose setae]; C, same pereiopod as B, turned approximately 90° to show ventral margin of dactylus; D, first pleopod, right side, posteromesial view; E, dactylus and propodus of left fourth pereiopod; F, dactylus and propodus of left fifth pereiopod. *Dicranodromia ovata* A. Milne Edwards, 1880, female holotype (MCZ 6510): G, dactylus and propodus of fifth pereiopod (setation omitted) [note relative lengths of propodus and dactylus as compared to those in F].

with 6–7 sclerotized spines along ventral border. Pereiopods 4 (Fig. 2E) and 5 (Fig. 2F) short, stout. Dactylus of pereiopods 4 and 5 strong, recurved, distally sclerotized, with 3–4 teeth along former ventral border. Propodus of pereiopods 4 and 5 relatively short, clearly less than twice length of dactylus, and with distal circlet of strong, distally sclerotized spines; these spines more numerous, and more similarly sized, on pereiopod 5 (Fig. 2F). Male abdomen and telson spinose [not smooth as indicated in Rathbun's (1937) fig. 15], and without terminal setae shown in that illustration. Male first pleopod (Fig. 2D) two-jointed, heavy, with deep groove along most of length of distalmost article, which bears dense tuft of setae distally; entire pleopod more or less typical for the family (e.g., see Martin 1990, Báez & Martin 1989).

Etymology.—From the Latin "spina" (thorn) in reference to the rather dense covering of small spines on the carapace and pereiopods.

Discussion

All four species of the genus *Dicranodromia* known to Rathbun (1937) were described prior to 1890; a fifth species of *Dicranodromia* was described 100 years later (Martin 1990). Only two of these species, *D. ovata* A. Milne Edwards and *D. felderi* Martin, were previously known from the western Atlantic. Recently, Guinot (1993) described two more species of *Dicranodromia*: *D. karubar,* from Indonesia, and *D. foersteri,* from the Chesterfield Islands.

Dicranodromia spinosa is rather easily separated from the other two western Atlantic species, *D. ovata* and *D. felderi,* by its relatively small size and by the spination and setation of the carapace and pereiopods. The largest specimen attributable to *D. spinosa* is but 10.1 mm total carapace length (the larger of two individuals in USNM 68862). In contrast, the holotype of *D. ovata* was originally measured as being 26 mm (the holotype is in poor condition, making further measurements difficult; see Martin 1990), and *D. felderi* reaches a carapace length of 32 mm (Martin 1990).

The possibility that the new species consists merely of young or juvenile forms of either of the previously recognized species, with a loss of spination and setation as the crabs grow larger, was considered. It is true that the larger of the specimens listed here as *D. spinosa* have relatively smaller and fewer carapacial spines. However, the small (6.1 mm CL) holotype of *D. spinosa* is a mature male, as evidenced by the form of the first male pleopod (Fig. 2D). Additionally, several of the *D. spinosa* females are clearly mature, despite their size, with well developed pleopods bearing eggs in some cases, lending support to recognition of a small species as opposed to a series of juveniles. In contrast, one of the MCZ paratypes of *D. ovata* (MCZ 2745) (and the only MCZ paratype that is, in my estimation, truly *D. ovata*) is an immature female, the abdomen and pleopods not yet having their adult shape or setation, although the carapace length of that crab is 10.4 mm, larger than any specimen of *D. spinosa.* Finally, the relative lengths of the dactylus and propodus of the fifth pereiopod differ rather markedly between *D. spinosa* and either *D. ovata* (compare Fig. 2F to fifth pereiopod of *D. ovata* holotype, Fig. 2G) or *D. felderi* (see Martin 1990). An error exists in my 1990 paper, where the *fourth* pereiopod of the holotype female of *D. ovata* (Martin 1990: fig. 5f) was incorrectly referred to in the figure legend as the fifth pereiopod.

Although a decrease in overall spination of the carapace and pereiopods might be explained as an ontogenetic phenomenon, it is less likely that allometric changes in the relative lengths of pereiopod segments could be explained as normal ontogenetic changes.

Milne Edwards & Bouvier (1902) included text figures (their figs. 5 and 6) and plates (pl. 2 figs. 1–16; pl. 3 figs. 1–4), but it is difficult to determine which figures were taken from which specimens, and their illustrations are too stylized to determine whether a given drawing is of *D. ovata* or *D. spinosa.*

In light of the morphological differences and nearly threefold size difference between specimens of *D. spinosa* and the holotype of *D. ovata* (MCZ 6510), it is somewhat surprising that Rathbun (1937) made no reference to morphological variation or to differences in life history parameters (i.e., maturation at a very small size). Indeed, in the type series alone, the difference in CL between mature specimens is more than fourfold (26 mm for the holotype, MCZ 6510, vs. 6.1 mm for MCZ 6511). Because Rathbun referred to several specimens of *D. spinosa* in her written description of *D. ovata* (e.g., Rathbun 1937:61, where she treated USNM 57069 [now a paratype of *D. spinosa*] as a mature female of *D. ovata*), it is clear that her description of *D. ovata* includes a conglomerate of characters of these two species, and is thus of very limited value in identification of species of *Dicranodromia.* The same is true for the excellent figures of Milne Edwards & Bouvier (1902: plate II, figs. 1–16), which included figures of the holotype as well as the paratypes, at least one of which is now attributable to *D. spinosa.*

In addition to the specimens described herein as *D. spinosa,* all of which were part of the series available to Rathbun, there are at least two more lots housed at the USNM currently labeled *D. ovata* but belonging to undescribed species (see Martin 1990).

It is interesting to note that all of the specimens I have herein referred to *D. spinosa* are from off Florida. Thus, not only are they morphologically different from true *D. ovata,* but they are rather far removed geographically as well, the holotype of *D. ovata* being from Barbados, and the MCZ 2745 paratype being from Guadeloupe, Lesser Antilles. Thus, as far as is presently known, *D. spinosa* is restricted to the Florida Keys, while *D. ovata,* much rarer than was previously believed, is known from only two specimens (possibly three; the paratype housed at the Muséum national d'Histoire naturelle, Paris, France [MNHN MP-B24324], from off Havana, Cuba, is damaged and can not with certainty be assigned to either species), and is known only from deeper waters (greater than 274 m) in the Lesser Antilles.

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GLYPHOCRANGON FIMBRIATA, A NEW SPECIES OF CARIDEAN SHRIMP (CRUSTACEA: DECAPODA: GLYPHOCRANGONIDAE) FROM SIO GUYOT, MID-PACIFIC MOUNTAINS

Tomoyuki Komai and Ichiro Takeuchi

Abstract.—A new species of caridean shrimp, *Glyphocrangon fimbriata,* is described and figured on the basis of one female and one male specimen collected from Sio Guyot, Mid-Pacific Mountains, at depths of 1300–1312 m. The species resembles *G. sicaria* Faxon, 1893, and *G. vicaria* Faxon, 1896, but differs from them in the anterior second (lateral) carina being anteriorly produced as a large tooth, and the dactyls of the posterior three pairs of pereopods bearing a setal fringe on the distal part. The discovery of the new species confirms the existence of glyphocrangonid shrimp in the northern hemisphere of the Mid-Pacific.

The Mid-Pacific Mountains between the Mariana Islands and the Hawaiian Islands rise 2000 to 4000 m from the abyssal ocean floor at depths of 5000 to 6000 m. The tops of several guyots of the Mountains are covered with ocean sediments (e.g., Karig et al. 1970, Nemoto & Kroenke 1985). In spite of the possibility that there are particular benthic communities endemic to the guyots, only a few studies on the fauna have been done (e.g., Wilson et al. 1985). During January to March 1993, the Ocean Research Institute, University of Tokyo, conducted the KH-93-1 cruise of the R/V *Hakuho-Maru* to investigate the benthic fauna associated with these guyots. The material obtained from Sio Guyot (18°18′N, 171°06′E) using ORE type beam trawl, contained two specimens of a new species of glyphocrangonid shrimp, described and illustrated below. The type specimens are deposited in the Natural History Museum and Institute, Chiba (CBM). The abbreviation CL indicates the postorbital carapace length. The terminology for the carinae and spines on the carapace follows Holthuis (1971) and Chace (1984).

Glyphocrangon fimbriata, new species
Figs. 1–3

Material examined.—Holotype: CBM-ZC 214, ovig. female (CL 22.5 mm), Sio Guyot, Mid-Pacific Mountains, 18°16.05′N-18°15.87′N, 171°20.99′E-171°22.01′E, 1300–1312 m, KH-93-1 (R/V *Hakuho-Maru*), sta 7, 31 Jan 1993, ORE type beam trawl of 4 m span. Paratype: CBM-ZC 215, 1 male (CL 15.5 mm), collected with holotype.

Description.—Body (Fig. 1) moderately robust. Integument firm, without pubescence.

Rostrum (Fig. 1) strongly upturned anteriorly, overreaching anterior margin of scaphocerite (0.56 times as long as carapace in holotype and 0.72 times as long in paratype); dorsolateral margins with 2 pairs of subequal teeth, anterior pair situated at about level of proximal ⅓ of rostrum and posterior pair at level of posterior margin of orbit; dorsal surface concave, not septate, with median carina extending from apex of rostrum to level of anterior pair of lateral teeth; dorsolateral and ventrolateral mar-

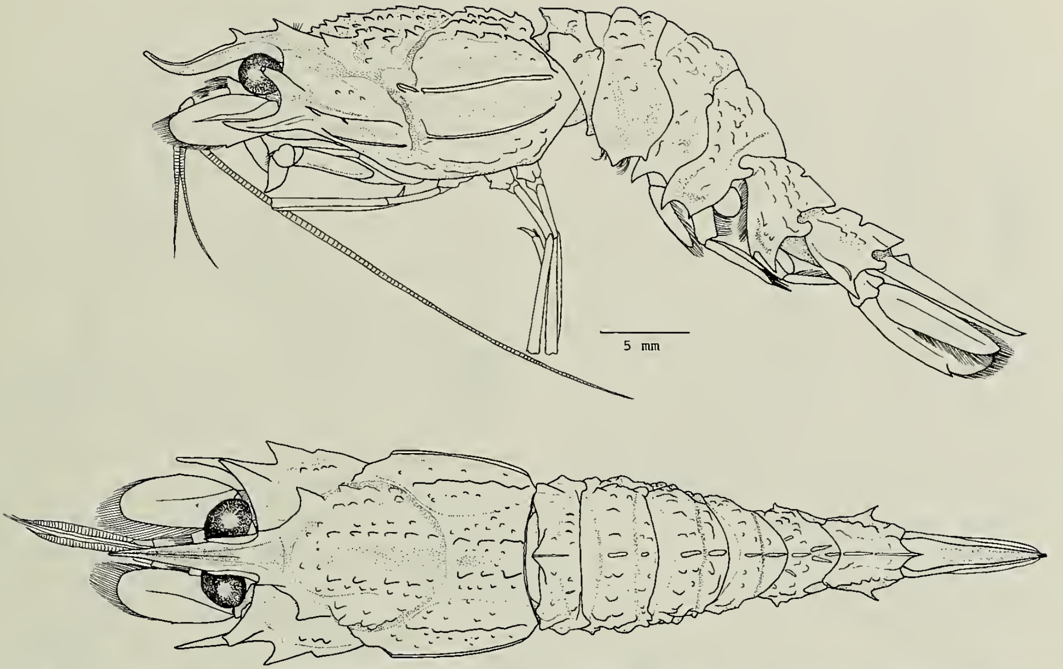

Fig. 1. *Glyphocrangon fimbriata,* new species. Holotype, ovig. female (CL 22.5 mm), entire animal in lateral view (top) and dorsal view (bottom).

gins sharply ridged; ventral surface flattened, with median carina in distal part.

Carapace (Fig. 1) with first (submedian) carina composed of forwardly directed, small, rather acute tubercles, 5–8 anterior to cervical groove, 3 posterior to that; median area between submedian carinae smooth except for few tubercles in anterior area, anteriormost situated medially or submedially. Anterior second (intermediate) carina composed of 3 tubercles and strong triangular tooth continuous with dorsolateral carina of rostrum; posterior second (intermediate) carina not entire, margin faintly eroded. Anterior third (antennal) carina not continuous with antennal spine, reduced to row of 3–5 small tubercles; posterior third (antennal) carina entire except for extremely anterior portion interrupted, not forming lobe or tooth anteriorly. Anterior fourth (lateral) carina not continuous with antennal spine, separated in 2 sections by distinct notch at about midlength of carina, anterior section forming moderately large tooth not reaching level of posterior margin of orbit, posterior section terminating anteriorly in blunt tooth; posterior fourth (lateral) carina entire. Anterior fifth (sublateral) carina prominent; posterior fifth (sublateral) carina less distinct, interrupted posteriorly in few parts. Sixth (submarginal) carina less distinct, separated into some sections. Space between anterior first and second carinae with 2 rows of tubercles; space between posterior first and second carinae with row of tubercles close to first carina, and scattered tubercles; spaces between posterior parts of second, third and fourth carinae smooth except for few small tubercles. Antennal spines unarmed marginally, more than ¾ as long as, and diverging more than branchiostegal spines. Branchiostegal spines overreaching level of proximal segment of antennular peduncle, very slightly divergent.

Abdomen (Fig. 1) with teeth and tubercles low, blunt, or rounded. First somite with some longitudinally elongate tubercles along posterior margin and 1 strong tubercle slightly produced beyond anterolateral margin of tergum; median carina thick, with sharply ridged dorsal margin, overhanging anterior section of first somite. Median carina on each somite posterior to first divided into anterior and posterior sections by blunt notch in second to fourth somites and V-shaped incision in fifth and sixth somites. Fifth somite with posteriorly divergent submedian carina on posterior half. Posterior margins of fourth to sixth somites convexly produced. Pleuron of first somite tapering anteroventrally to blunt point, and those of second to fifth somites with 2 ventral teeth; teeth on second somite directed ventrally, anterior tooth slightly larger than posterior tooth; teeth on third to fifth somites directed posteroventrally, anterior tooth distinctly stronger than posterior tooth in third and fourth somites, and weaker than posterior one in fifth somite. Sixth somite with posteriorly divergent dorsal margin; pleuron with strong posteroventral tooth directed posteriorly. Telson (Fig. 1) elongate triangular, gradually tapering to sharp point, 0.65 times as long as carapace, posterior part upturned; dorsolateral margin sharply ridged; dorsal surface concave, with strong, acute median tubercle proximally.

Thoracic sternite deeply depressed, unarmed. Abdominal sternites unarmed.

Eye (Fig. 1) moderately large, with pigmented cornea.

Antennule (Fig. 2A) with peduncle falling slightly short of anterior margin of scaphocerite; proximal segment with stylocerite showing as rounded lobe; distal 2 segments, combined, subequal in length to proximal segment, intermediate segment obscured by long setae dorsally. Antennular flagella (Fig. 1) distinctly longer than peduncle.

Scaphocerite (Fig. 2B) ovate, 0.5 times as long as carapace and 1.65 times as long as broad, with small lateral tooth slightly posterior to level of midlength, lateral margin proximal to lateral tooth bearing short setae. Carpocerite falling somewhat short of distal margin of blade.

Mouthparts as usual in genus (Fig. 2C–G). Third maxilliped (Fig. 3A–C) quite stout, not reaching beyond anterior margin of scaphocerite; distal 2 segments (Fig. 3B, C) with strong spines on ventromesial margin and mesial face, mesial face concealed by long setae; ultimate segment terminating in curved, sharply pointed apex; exopod with articulated distal lash.

First pereopod (Fig. 3D) incompletely subchelate; palm (Fig. 3E) narrowed distally in dorsal view, with tufts of stout setae mesially; carpus short, bearing setae dorsomesially; ischium with broad laminar expansion ventrally, distal margin bluntly pointed. Second pereopods with right member of pair (Fig. 3F) slightly longer and with more carpal articles than left (right with 26 in holotype, 27 in paratype; left with 21 in holotype, 23 in paratype); chela of each (Fig. 3G) barely as long as distalmost article of carpus, with palm somewhat flattened; fixed finger short, terminating in strong corneous spine; dactyl broad, terminating in 2 unequal corneous spines; ischium distinctly longer than merus, ventral margin somewhat expanded. Third pereopod (Fig. 3H) with dactyl slightly flattened, simple, 0.3 times as long as propodus, dorsolateral and dorsomesial margins of distal ⅖ with row of setae curved backward (Fig. 3I); carpus 0.7 times as long as propodus. Fourth pereopod (Fig. 3J) with dactyl similar to that of third pereopod, distal ⅓ with marginal setae (Fig. 3K); propodus with setae on dorsodistal margin and with row of scattered setae on dorsal and lateral surface; carpus 0.7 times as long as propodus, with short setae on extensor surface. Fifth pereopod (Fig. 3L) with dactyl almost similar to that of fourth pereopod, with dorsolateral marginal setae on distal ⅓ (Fig. 3M); propodus with setae on dorsodistal margin, lateral and dorsal surfaces nearly naked; carpus 0.7 times as long as propodus, without setae.

Branchial formula shown in Table 1.

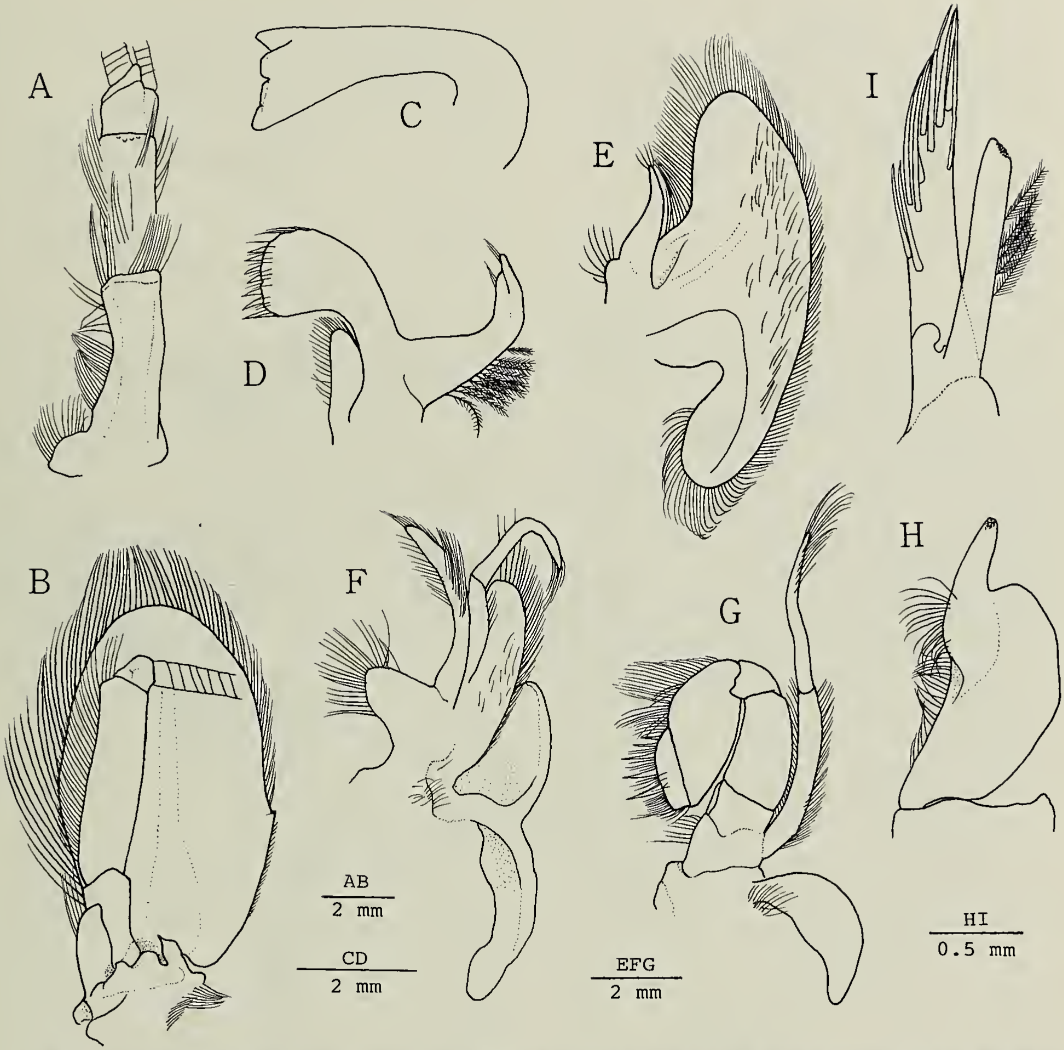

Fig. 2. *Glyphocrangon fimbriata,* new species. Cephalic, abdominal appendages, and mouthparts (left side). A–G, holotype, ovig. female (CL 22.5 mm); H, I, paratype, male (CL 15.5 mm). A, antennule, dorsal; B, antenna, ventral; C, mandible; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, endopod of male first pleopod; I, appendix masculina and appendix interna of male second pleopod.

Male first pleopod with endopod (Fig. 2H) slightly less than half length of exopod, mesial margin deeply concave; appendix interna well developed, defined mesially by wide U-shaped sinus. Male second pleopod with appendix masculina somewhat longer than appendix interna, bearing more than 20 long spines (Fig. 3I). Uropod (Fig. 1) not reaching posterior end of telson; exopod equal in length to endopod, with faint transverse suture, lateral margin convex, terminating posteriorly in acute tooth.

Eggs large, ovate, 3.3 × 2.4 mm, 26 in number.

Coloration (preserved in 10% buffered formalin).—Body entirely pale orange, distal part of rostrum and telson, and margins of carinae darker. Cornea of eye light brown. Eggs reddish yellow.

Habitat.—Sio Guyot is an exceptionally

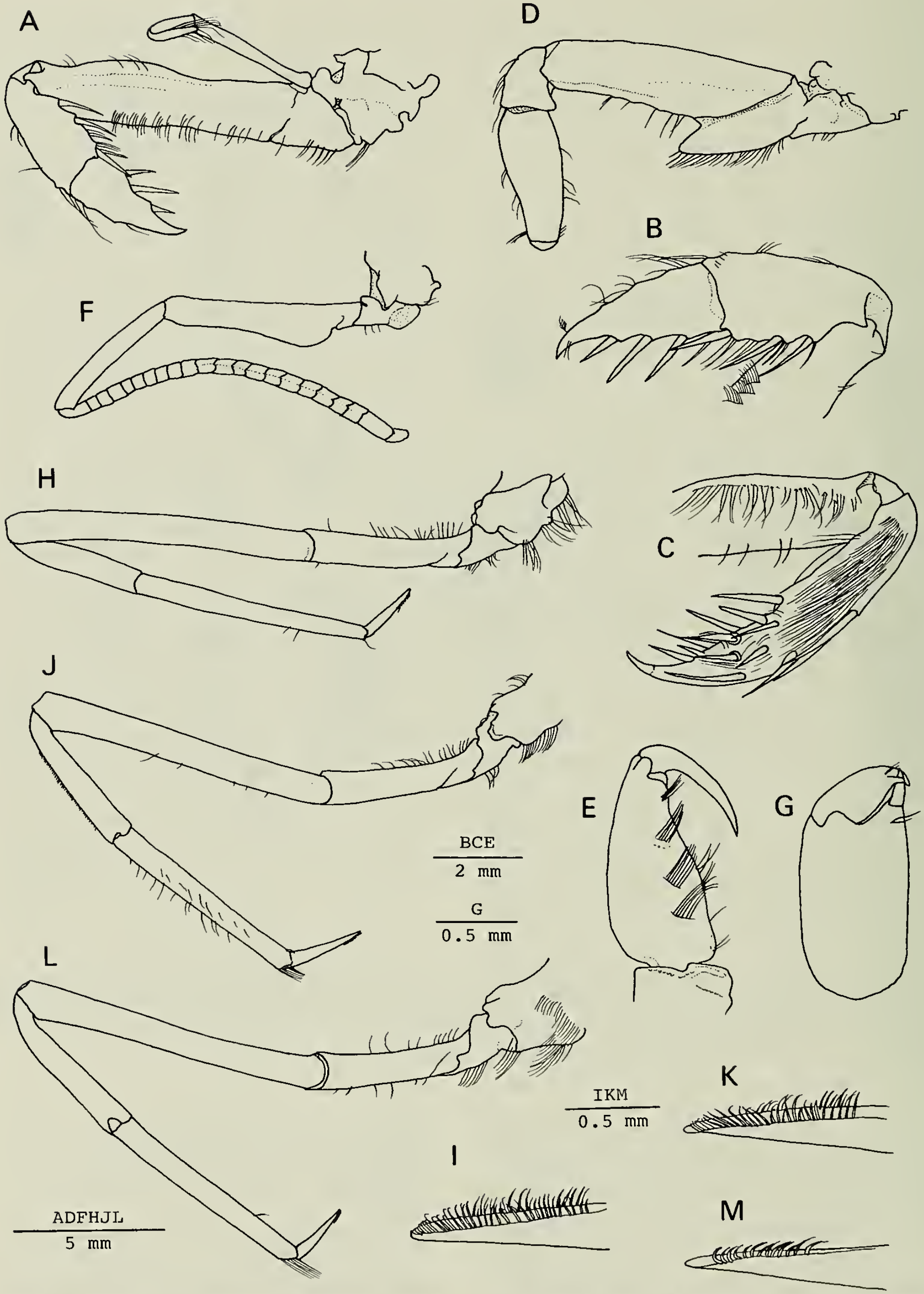

Fig. 3. *Glyphocrangon fimbriata*, new species. Holotype, ovig. female (CL 22.5 mm), left thoracic appendages. A, third maxilliped, lateral; B, same, distal two segments and distal part of antepenultimate segment, lateral; C, same, mesial; D, first pereopod, lateral; E, same, chela, dorsal; F, second pereopod, lateral; G, same, chela, dorsal; H, third pereopod, lateral; I, same, distal part of dactyl, lateral; J, fourth pereopod, lateral; K, same, distal part of dactyl, lateral; L, fifth pereopod, lateral; M, same, distal part of dactyl.

Table 1.—*Glyphocrangon fimbriata,* new species. Branchial formula.

	Maxillipeds			Pereopods				
	1	2	3	1	2	3	4	5
Pleurobranchs	–	–	–	1	1	1	1	1
Arthrobranchs	–	–	2	1	1	1	1	–
Podobranchs	–	–	–	–	–	–	–	–
Epipods	1	1	–	–	–	–	–	–
Exopods	1	1	1	–	–	–	–	–

large guyot situated at the western edge of the Mid-Pacific Mountains. The summit is divided into two flat-topped areas covered with pelagic sediment (Nemoto & Kroenke 1985); the northern summit, 2820 km^2, is greater than the area of the Island of Oahu, Hawaiian Islands, at sea level, and the southern summit is 230 km^2. The sampling station where the types of the new species were collected is situated in the middle of the northern summit.

The silt attached to the end of the trawl was preserved with 10% buffered formalin for sediment analysis. The ignition loss of the silt, which was ashed for two hours in a muffle furnace at 500°C (Kuwabara 1987), was 2.1%. The median particle diameter of the grain-size distribution is 5ϕ. The seawater four meters above the bottom had a temperature of 3.33°C, a salinity of 34.56‰ and oxygen concentration of 1.80 ml/l; measurements were made by CTD (Sea-Bird Electronics, Inc.: Model SBE 911 plus) with rosette samplers (Niskin-type 121).

Etymology.—The Latin *fimbriata* (fringed) refers to the characteristic fringe of setae on dactyl of the third to fifth pereopods.

Distribution.—Known only from Sio Guyot; at depths of 1300–1312 m.

Remarks.—Chace (1984) reviewed the genus *Glyphocrangon* and provided a key to the 38 species then recognized. Following Chace's key, the present new species appears close to *Glyphocrangon sicaria* Faxon, 1893, and *G. vicaria* Faxon, 1896, both known from the eastern Pacific. The anterior second lateral carina on the carapace produced anteriorly as a strong tooth and the dactyls of the posterior three pairs of pereopods bearing marginal setae in the distal part distinguish immediately the new species from both *G. sicaria* and *G. vicaria.* Other than these characters, *G. fimbriata* differs from *G. sicaria* in the absence of rows of granules on each intercarinal space on the carapace between the posterior second and third lateral carinae and between the posterior third and fourth lateral carinae, and in having the antennal spine less divergent than the branchiostegal spine. Faxon (1895) (under the name of *Glyphocrangon nobilis*) and Wicksten (1979) mentioned that *G. vicaria* possesses transverse corrugations on the dorsal surface of the rostrum, which are lacking in the new species.

Subsequent to Chace's (1984) work, Kensley et al. (1987) described three species from eastern Australia, *G. holthuisi, G. lowryi,* and *G. navacastellum,* and Burukovsky (1990) further added one species, *G. waginii,* from the Sala-Y-Gomez Ridge, eastern Pacific. These four species do not show close affinity with the new species.

The biogeographical distribution of the previously known species of *Glyphocrangon* has been also reviewed by Chace (1984). The genus is well represented in the Indian Ocean and the Philippine region in the western Pacific. Regarding the Mid-Pacific in the northern hemisphere, however, only one unidentified species of the genus has been recorded from Agassiz Guyot (17°51′N, 178°25′E) by Wilson et al. (1985). It remains uncertain, however, whether the new species is conspecific with the species recorded by Wilson et al. (1985). Further studies on each guyot of this poorly studied area are needed to prove the affinities and biogeographic distribution of the present new species.

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OCCURRENCE OF TWO LITHODID CRABS (CRUSTACEA: DECAPODA: LITHODIDAE) IN THE COLD SEEP ZONE OF THE SOUTH BARBADOS ACCRETIONARY PRISM

Enrique Macpherson

Abstract.—Two species of lithodid crabs from a cold seep area south of the island of Barbados, Caribbean Sea, are reported. One of the species, *Paralomis arethusa,* is new, and is described. The other species is *Lithodes manningi* Macpherson. This is the first report of representatives of this family in areas of emissions of chemically reduced fluids.

The discovery of new communities associated with emissions of chemically reduced fluids has received great attention in the last years (e.g., Jones 1985). These benthic assemblages were first discovered at hydrothermal vents in the Galapagos Ridge (Londsale 1977), and more recently "cold-seep communities" have been found in the Caribbean area (Jolliver et al. 1990), Oregon (Kulm et al. 1986) and Japan (Laubier et al. 1986), revealing the existence of organisms closely related to those inhabiting hydrothermal vents. The study of the fauna of these zones has revealed the existence of many new forms exhibiting adaptations of great scientific interest (e.g., Hecker 1985).

The decapod crustacean fauna of these ecosystems has been studied by several authors (e.g., Williams 1980, Williams & Chace 1982, Williams & van Dover 1983, Williams & Rona 1986, Guinot 1988, Saint-Laurent 1988, Guinot 1989). The discovery of two species of lithodid crabs, one of them new, in the cold seep community south of Barbados is the first report of this family in these zones.

The specimens are deposited in the Muséum national d'Histoire naturelle, Paris. Measurements given refer to the length of the carapace, excluding rostrum (CL), and the maximum width of the carapace, excluding the lateral spines (CW).

Paralomis arethusa, new species
Figs. 1, 2

Material examined.—Holotype, DIAPISUB Expedition, sta DS01/2, 10°19′64″N, 58°53′42″W, 1691 m, 24 Dec 1992, Female (CL 15 mm, CW 14.5 mm).

Description.—Carapace as long as wide, somewhat hexagonal in contour. Dorsal surface of carapace covered with minute granules of various sizes, but without spines. Regions well-defined. Gastric region more prominent than others, with thick granule on apex and 2 thick granules posteriorly, near the gastro-cardiac groove. Cardiac region more prominent than branchial regions. Each branchial region with 1 thick median granule.

Rostrum with straight lower median spine slightly directed downwards, smooth ventrally; with 2 slightly divergent dorsolateral spines.

Carapace margins armed with few spines. Postocular spine not overreaching cornea. First anterolateral spine larger than postocular. Three or 4 spines of various sizes and several large granules on each branchial edge. Posterior margin smooth.

Abdominal segments covered with minute granules.

Ocular peduncles with distodorsal spine. First segment of antennal peduncle with 1

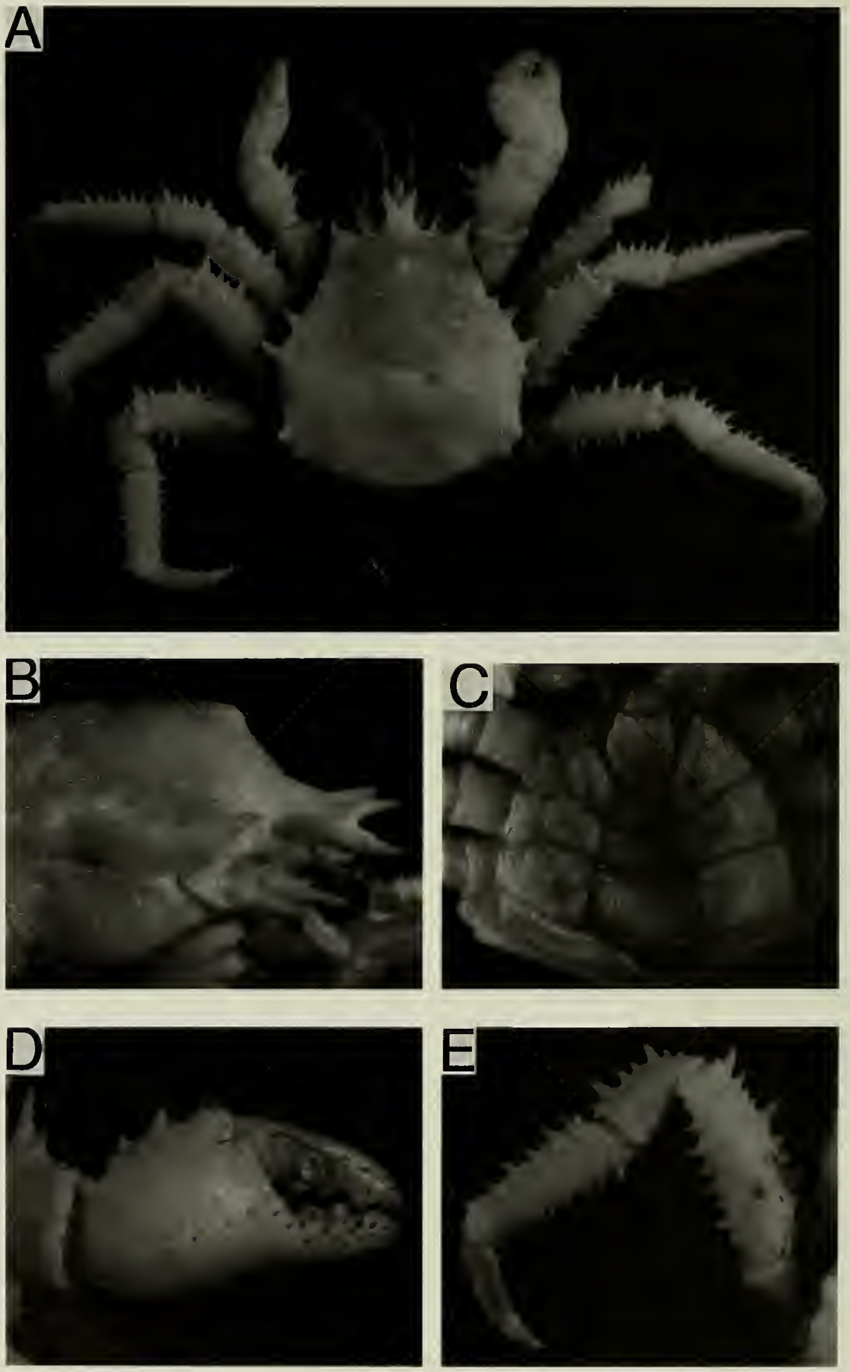

Fig. 1. *Paralomis arethusa,* new species, holotype, female, CL 15 mm. A, dorsal view; B, anterior part of the carapace, lateral view; C, abdomen; D, right cheliped; E, third left ambulatory leg.

spine on outer margin. Second segment with 2 spines on outer border. Acicle with large central spine not overreaching antennal peduncle, and 2 spines on outer border; inner border smooth.

Chelipeds subequal in length, right stouter than left. Merus bearing 2–3 spines and few granules at end of dorsal border, 2 small spines on outer surface. Carpus with 3 strong spines on dorsal border, rest of article smooth, except for some granules. Dorsal border of hand with 5–6 small spines, few granules on outer and ventral surfaces. Fingers without granules, bearing numerous tufts of setae.

Walking legs moderately long and depressed. First and second walking legs slightly longer than third.

Third leg 1.5 times carapace length. Coxa with several granules. Merus 3 times longer than high, about twice carpus length, and slightly longer than propodus. Row of 8–9 spines on dorsal border, another row of 9–10 spines on ventral margin and 4 spines on proximal half of posterior surface. Carpus with row of 7–9 spines on dorsal margin. Propodus 2.5 times longer than high, somewhat longer than dactylus, with row of 10–11 spines on dorsal margin and another row of 10 spines on ventral margin. Dactylus slightly curved, with row of 13 corneous spines on ventral margin; tuft of setae along dorsal border.

Etymology.—The name refers to the Nymph of the Fountains, *Arethusa,* of the Greek mythology, in reference to the emissions of fluids that characterize these areas.

Remarks.—There are about 47 species in the genus *Paralomis* White, 1856 (Macpherson 1988, 1992), four of which occur in the Caribbean area: *P. cubensis* Chace, 1939, *P. grossmani* Macpherson, 1988, *P. pectinata* Macpherson, 1988 and *P. serrata* Macpherson, 1988. The new species resembles *P. serrata* from the coast of Colombia, in having the dorsal surface of the carapace smooth, covered with minute granules, without spines or large granules, and without crest on the terminal borders of the merus and carpus of each cheliped. However, they can be distinguished by several features. The carapace is more or less pyriform in *P. serrata,* clearly hexagonal in the new species. The anterolateral and lateral spines of the carapace are clearly larger in *P. arethusa* than in *P. serrata.* The inner border of the scaphocerite is smooth in the new species, but with two spines in *P. serrata.*

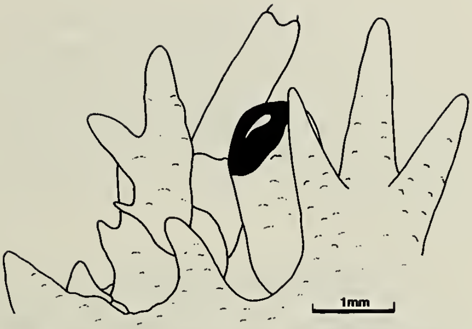

Fig. 2. *Paralomis arethusa,* new species, holotype, female, CL 15 mm. Rostrum and anterior left part of carapace, dorsal view, showing antennal peduncle.

Among the remaining species in the genus, *P. formosa* Henderson, 1888 from the southeastern Atlantic (Macpherson 1988) is morphologically the closest species to *P. arethusa.* The new species resembles *P. formosa* in the shape of the carapace and the armature of the chelipeds and legs. However, the two species can be readily separated by several characters. *P. formosa* has several well-developed spines on the dorsal surface of the carapace, whereas these spines are absent in the new species. The antennal acicle bears two or three spines on each side in *P. formosa,* whereas only two on the outer border in *P. arethusa.*

Lithodes manningi Macpherson, 1988

Lithodes manningi Macpherson, 1988:62, figs. 27, 28, pl. 14.

Material examined.—DIAPISUB Expedition, sta DS16/7, 11°13′82″N, 59°21′82″W, 1236 m, 8 Jan 1993, Male (CL 15.6 mm, CW 14.0 mm).

Remarks.—This species was described from two large specimens (CL 103 and 120 mm) collected in Dominica and French Guiana, at depths between 640 and 777 m. Except for the size difference, the specimen examined agrees quite well with the type specimens.

Acknowledgments

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A NEW GENUS AND TWO NEW SPECIES OF DEEP-WATER HERMIT CRABS (DECAPODA: ANOMURA: PAGURIDAE) FROM THE SOUTHERN OCEAN

Patsy A. McLaughlin

Abstract.—A diagnosis of the new genus, *Bathypaguropsis,* is provided, together with descriptions and illustrations of the new species *B. yaldwyni* from New Zealand and *B. marionensis* from Australia. Both new species are inhabitants of depths in excess of 250 m.

During ongoing studies of the hermit crab fauna in the collections of the National Museum of New Zealand, Wellington, numerous lots of a very distinctive species were observed. In having 13 pairs of trichobranchiate gills and a massive operculate right cheliped with obliquely articulating dactyl, they appeared at first assignable to the genus *Pylopaguropsis* Alcock, 1905. However, upon closer examination, it was found that females lacked the paired first pleopods modified as gonopods, that are characteristic of *Pylopaguropsis* species. Additionally, males are provided with four, albeit rather reduced, unpaired pleopods on the left side. Males of *Pylopaguropsis* have only three unpaired left pleopods (Alcock 1905, McLaughlin & Haig 1989). It became apparent that these specimens represented not only a new species, but a new genus. More recently, one lot of specimens from the Northern Territories Museum of Arts and Sciences, Darwin, Australia, was found to represent a second new species assignable to this new genus.

The specimens have been collected during the Northern Prawn Cruise (NPC), and cruises of the F.V. *Chiyo Maru* (CM), R/V *James Cook* (JC), R/V *Tangaroa* (New Zealand Oceanographic Institute; NZOI), F.R.V. *Soela,* (Commonwealth Scientific, Industrial and Research Organization, CSIRO). With the exception of two specimens of *Bathypaguropsis yaldwyni,* new species, and one specimen of *B. marionensis,* new species, that have been deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), all other materials remain deposited in their respective institutions, *B. yaldwyni* in the National Museum of New Zealand (NMNZ), and *B. marionensis* in the Northern Territories Museum (NTM). Shield length (SL), measured from the tip of the rostrum to the midpoint of the posterior margin of the shield provides an indication of specimen size; ♀♀ indicates ovigerous females.

Bathypaguropsis, new genus

Fig. 1

Type species.—*Bathypaguropsis yaldwyni,* new species.

Diagnosis.—Cephalothoracic shield (Fig. 1A, B) with central dorsal surface sometimes only weakly calcified; rostrum well developed. Cardiac sulci (cf. Morgan & Forest 1991) extending more than half length of posterior carapace; area between cardiac sulci and sulci cardiobranchialis at least partially chitinous or weakly calcified anteriorly. Thirteen pairs of trichobranchiae. Ocular acicles triangular, dorsal surface flattened or slightly convex. Antennal peduncle with supernumerary segmentation;

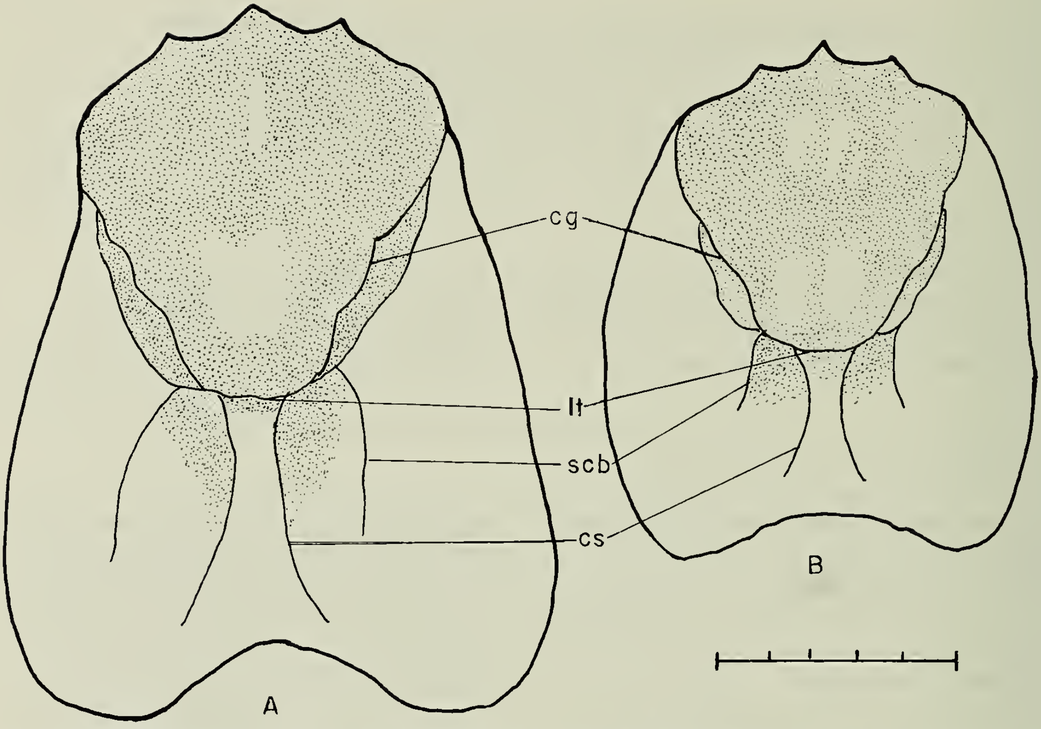

Fig. 1. Diagrammatic cephalothorax with stippling depicting areas of chitinization and/or calcification: cg—cervical groove; lt—linea transversalis; scb—sulcus cardiobranchialis; cs—cardiac sulcus. A, *Bathypaguropsis yaldwyni,* new species; B, *Bathypaguropsis marionensis,* new species. Scale equals 5 mm.

acicle tapering; flagellum with scattered setae.

Maxillule with 1 strong bristle on internal lobe of endopod; external lobe articulated, not recurved. Maxilla with distal lobe of scaphognathite subtriangular. Ischium of third maxilliped with well developed crista dentata and 1 accessory tooth. Sternite of third maxilliped unarmed.

Right cheliped massive; chela operculate or nearly so; propodal-carpal articulation approximately 30° from perpendicular; dactyl articulating obliquely with palm. Left cheliped moderately elongate, slender; propodal-carpal articulation approximately 30–60° counter-clockwise from perpendicular; dactyl and fixed finger opening obliquely.

Ambulatory legs with dactyls and propodi similar. Fourth pereopods not subchelate, with propodal rasp consisting of 1 or more, sometimes incomplete, rows of scales.

Males with paired gonopores, each partially masked by tuft of stiff setae; no paired pleopods or sexual tubes. Four unpaired pleopods on left, with exopods only moderately well developed, endopods markedly reduced. Females with paired gonopores. No paired pleopods; left 2nd to 5th unpaired, 2nd to 4th with both rami well developed and egg-carrying, 5th reduced as in males.

Tergite of first abdominal somite with chitinous or weakly calcified short rectangular plate; tergites of somites 2–5 indicated by transverse bands of fibrils; tergite of sixth somite divided by deep transverse furrow in posterior third. Uropods asymmetrical. Telson with transverse suture; posterior lobes subtriangular; terminal margins oblique, unarmed or spinulose.

Gender.—Feminine.

Etymology.—From the Greek *bathys* meaning deep, and *pagouros* meaning crab, reflecting the deep-water habitat of this genus.

Remarks.—As alluded to previously, *Bathypaguropsis,* shares certain characters with *Pylopaguropsis.* These include 13 pairs of trichobranchiate gills; simple triangular ocular acicles; a moderately well developed, non-recurved external endopodal lobe on the maxillule; massive, operculate right cheliped; and small left cheliped with obliquely opening dactyl and fixed finger. *Bathypaguropsis* is immediately distinguished from *Pylopaguropsis* by the absence, in females, of paired first pleopods modified as gonopods, the presence in males of four unpaired pleopods, and the configuration of the dactyl and fixed finger of the right chela, the ventral surfaces of which are convex rather than concave. Although the external endopodal lobe of the maxillule in both genera is usually moderately well developed and not recurved, it is articulated in *Bathypaguropsis,* but not in *Pylopaguropsis.*

The cephalothoracic shields of both species of *Bathypaguropsis* usually exhibit some amount of reduced calcification; however, it is neither uniform in degree nor consistent in pattern. Analogously, the areas of the posterior carapace between the cardiac sulci and the sulci cardiobranchialis are typically chitinized or calcified, the extent appearing to increase with increased body size. Correspondingly, the tergite of the first abdominal somite is clearly delineated in specimens of all sizes, but noticeably better calcified in larger individuals.

In the two known species of *Bathypaguropsis,* the fifth pereopods appear somewhat longer than seen in most pagurids, and in the vast majority of the specimens examined, these appendages were preserved in a dorsally directed position above or along side the carapace such as depicted in species of *Dromia* or *Hypochoncha* (e.g., Rathbun 1937, pls. 8–11). Both species appear to be inhabitants of gastropod shells; however, it is not known at the present time whether this positioning is a special shell-use adaptation, or whether the modification is related to gill grooming.

Bathypaguropsis yaldwyni, new species
Figs. 1A, 2, 3

Holotype.—♀ (SL 10.4 mm), Solander Trough, 46°30′S, 165°14.4′E, CM 149, 545–573 m, in shell of *Fusitriton* sp., 10 Sep 1987, coll. R. Stewart, NMNZ CR8067.

Paratypes.—1 ♂ (SL 4.4 mm), N North Cape, 34°13.8′S, 173°02.9′E, JC JO6/048/81, 375–388 m, 22 Apr 1981, coll. D. S. Horning, NMNZ CR8087.—2 ♂ (SL 5.4, 7.6), NE Bay of Islands, 35°05′S, 174°44′E, NPC T36, 457–481 m, 10 Jan 1969, NMNZ CR8027.—1 ♂ (SL 6.2 mm), off Cape Brett Light, 35°07′S, 174°43′E, NPC, 402–439 m, 11 Jan 1969, NMNZ CR8214.—1 ♂ (SL 5.8 mm), N of Gt. Barrier Island, 35°27′S, 175°06′E, NPC, 351–384 m, 10 Jan 1969, NMNZ CR8080.—1 ♀ (SL 3.4 mm), Rangatira Knoll, 37°17.4′S, 176°53.6′E, NZOI O.588, 292–337 m, 23 Jan 1981, NMNZ CR8129.—1 ♂ (SL 8.3 mm), E of Mayor Island, 37°20′S, 176°28.0′E, NZOI R.99, 22 Jan 1979, NMNZ CR8151.—1 ♂, 2 ♀ (5.2–5.9 mm), 22 km east Alderman Island, 15 km north Mayor Island, 410–415 m, Jul, 1987, coll. R. Macgrath, NMNZ CR7523.—1 ♂ (SL 8.5 mm), NW Westport, 41°24.8′S, 170°45′E, JC D4, 371 m, 24 Nov 1970, NMNZ CR8105.—1 ♂ (SL 11.2 mm), off Puysegur Bank, 46°12.3′S, 165°55.4′E, CM, 388–454 m, in shell of *Fusitriton* sp., 11 Sep 1987, coll. R. Stewart, NMNZ CR7519.—1 ♀♀ (SL 10.5 mm), Solander Trough, 46°30′S, 165°14.4′E, CM 149, 545–573 m, in shell of *Fusitriton* sp., 10 Sep 1987, coll. R. Stewart, NMNZ CR7516.—1 ♀, 1 ?♀ (SL 9.5, 9.6 mm), Solander Trough, 46°31.9′S, 165°44.4′E, CM, 320–346 m, in shells of *Fusitriton* sp., 10 Sep 1987, coll. R. Stewart,

NMNZ CR7517, 7518.—2 ♂, 1 ♀, 1 ♀♀ (SL 8.2–10.0 mm), off Puysegur Bank, 46°35.6′S, 165°40.9′E, CM 145, 532–544 m, 10 Sep 1987, coll. R. Stewart, NMNZ CR8118, USNM 267573.—1 ♀♀ (SL 9.8 mm), Northern Campbell Plateau, 47°30.5′S, 169°14.7′E, CM, 506–529 m, in shell of *Fusitriton* sp., 13 Sep 1987, coll. R. Stewart, NMNZ CR7514.—2 ♂ (SL 9.4, 10.6 mm), Northern Campbell Plateau, 48°05.7′S, 168°32.5′E, CM, 396–406 m, in shells of *Iredalina* sp. and *Fusitriton* sp., 13 Sep 1987, coll. R. Stewart, NMNZ CR7513, 7515.

Description.—Shield (Figs. 1A, 2A) longer than broad; anterior margin between rostrum and lateral projections concave, anterolateral margins sloping; posterior margin truncate. Rostrum broadly triangular, acute, usually with tiny terminal spinule. Lateral projections obtusely triangular, unarmed or with small marginal spinule. Posterior carapace with area between cardiac sulci and sulci cardiobranchialis weakly calcified in anterior half; posteromedian plate frequently with transverse band of calcification adjacent to linea transversalis.

Ocular peduncles stout, short, half to ⅔ shield length, dorsomesial surface with row of stiff setae; corneae not dilated. Ocular acicles simple, triangular, usually with small marginal terminal spine; separated basally by width of rostrum, or approximately by ¼ to ½ basal width of 1 acicle.

Antennular peduncles moderately long, overreaching ocular peduncles by slightly less to more than entire length of ultimate segment; basal segment with small acute spine on lateral surface distally; penultimate segment with few scattered setae dorsally and ventrally; ultimate segment with few tufts or with row of setae on dorsal surface; flagellum shorter to slightly longer than ultimate peduncular segment.

Antennal peduncles exceeding ocular peduncles by ½ to ⅔ length of ultimate segment, but reaching only to distal half of ultimate segment of antennular peduncle. Fifth and fourth segments with few scattered setae; third segment with very strong spine at ventrodistal margin; second segment with dorsolateral distal angle strongly produced into broad, triangular process, terminating in acute simple or rarely bifid spine, mesial margin unarmed, lateral margin with 1 or 2 often widely-separated spines, dorsomesial distal angle with acute spine; first segment with small spine at laterodistal margin, ventral margin produced, with 2 or 3 spines laterally. Antennal acicle usually reaching at least to middle of ultimate peduncular segment, stout, slightly arcuate, with row of tufts of stiff setae on mesial margin and terminating in small spine. Antennal flagellum long, but not overreaching outstretched right cheliped, each article usually with 3 or 4 very short (< 1 article length) setae, and usually additional 2–4 longer setae at least on distal articles.

Maxillule (Fig. 2B) with 1 strong bristle on internal lobe of endopod, external lobe moderately well developed, articulated, not recurved. Maxilla (Fig. 2C) with endopod reaching to distal margin of scaphognathite; distal lobe of latter roundly triangular. First maxilliped (Fig. 2D) with basal segment of exopod generally subrectangular. Third maxilliped with very small spine at distal margin of merus.

Right cheliped (Fig. 3A, B) massive, operculate. Dactyl broad, slightly shorter to slightly longer than palm; cutting edge with calcareous margin faintly cusped, terminating in very small corneous claw and occasionally with few adjacent minute corneous teeth; dorsal surface slightly elevated in the midline proximally, smooth, slightly pitted, or with scattered low tubercles, granules or short transverse ridges, dorsomesial margin faintly or weakly crenulated and with 1 large, blunt tubercle proximally, mesial and ventral surfaces with very low, flattened, frequently corneous-capped, blister-like tubercles. Palm with maximum breadth greater than length, exceeding carpus by ¼ to ⅓ own length, dorsomesial distal angle markedly produced and armed with prom-

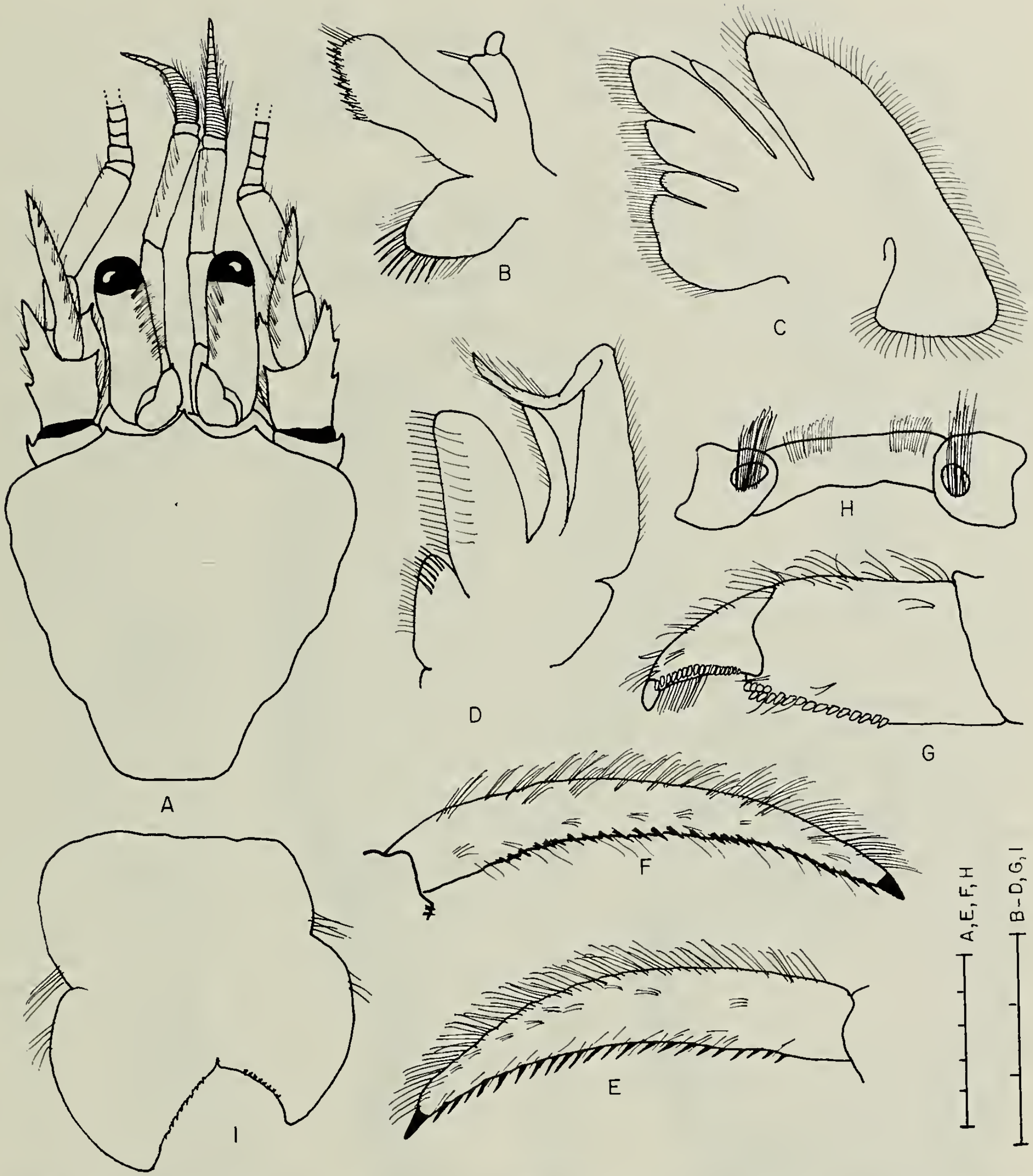

Fig. 2. *Bathypaguropsis yaldwyni,* new species, ♂ paratype (SL 10.0 mm), NMNZ CR8118. A, shield and cephalic appendages; B, left maxillule (external view); C, left maxilla (external view); D, left first maxilliped (external view); E, dactyl of right second pereopod (mesial view); F, dactyl of left third pereopod (mesial view); G, dactyl and propodus of left fourth pereopod (lateral view); H, sternite of male fifth pereopods; I, telson. Scales equal 5 mm (A, E, F, H) and 3 mm (B–D, G, I).

inent simple or multifid spine; dorsomesial margin with irregular row of 4 (rarely 2 or 3) blunt, tuberculate spines, frequently interspersed with smaller spines and/or tubercles, dorsal surface convex, smooth, faintly pitted, or covered with flattened granules and small tubercles, with 1 or 2 prominent tubercles at proximal margin;

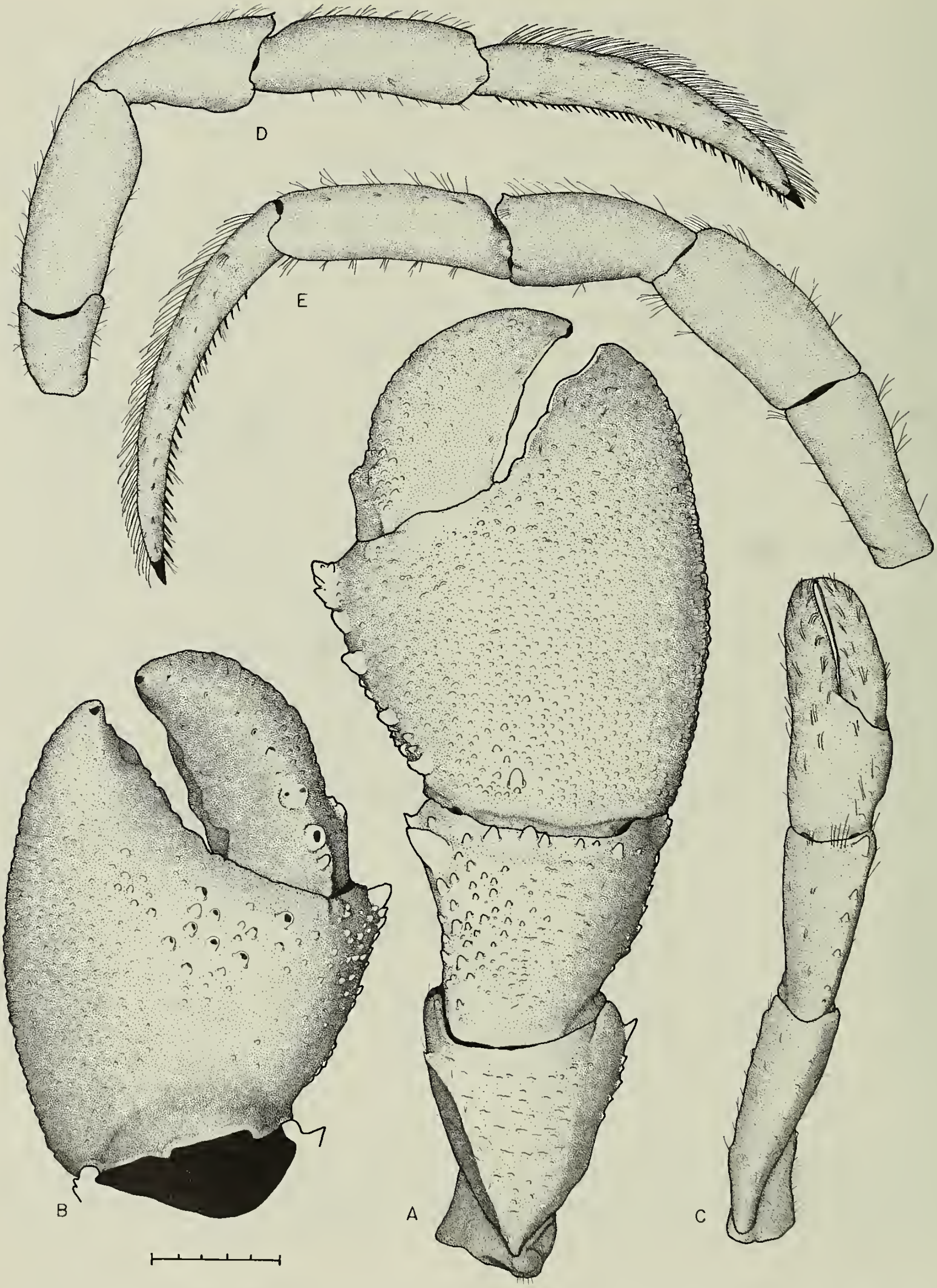

Fig. 3. *Bathypaguropsis yaldwyni,* new species, ♂ paratype (SL 10.0 mm), NMNZ CR8118. A, right cheliped (dorsal view); B, right chela (ventral view); C, left cheliped (dorsal view); D, right second pereopod (lateral view); E, left third pereopod (lateral view). Scale equals 5 mm.

dorsolateral margin not delimited or marked by single or double row of low, rounded, tubercles; mesial face with scattered low spinules, tubercles or granules; lateral face continuous with ventral surface, with scattered granules, low tubercles and/or short transverse ridges, ventral surface and several large, flattened, blister-like tubercles, often with corneous surfaces; ventral surfaces of dactyl and fixed finger with scattered granules or very small flattened, frequently corneous-capped tubercles; cutting edge of fixed finger with 2 or 3 weakly delineated calcareous teeth, terminating in very small corneous claw. Carpus equaling or only slightly longer than merus, subquadrate when viewed dorsally; dorsomesial distal angle depressed and with small spine, dorsomesial surface with 1 very strong, usually blunt spine distally and frequently single or double row of much smaller spines or tubercles proximally, dorsal surface with scattered low blunt or spinulose tubercles in mesial half, very short, transverse ridges in lateral half, distal margin with few to several blunt spines; dorsolateral margin not delimited, lateral and mesial surfaces with scattered blunt or spinulose tubercles or granules, ventral surface with scattered low tubercles or granules, strongest in lateral half, ventrodistal margin unarmed or weakly tuberculate. Merus broadly rounded and subtriangular laterally, with mesial face almost perpendicular; dorsomesial margin unarmed or occasionally with 1 or 2 small spines distally, dorsolateral margin not delimited, dorsal surface with low transverse, weakly granular ridges, lateral face smooth, slightly pitted, or with short, transverse ridges dorsally and scattered tubercles ventrally, ventrolateral margin with 1 or 2 strong acute spines at distal angle and few smaller spines or tubercles proximally; ventromesial margin unarmed or with 1 or 2 smaller spines at distal angle; ventral surface with scattered granules or tubercles, 2 or 3 moderately large tubercles on somewhat produced lateral protuberance. Ischium unarmed.

Left cheliped (Fig. 3C) not reaching to base of dactyl of right, slender; propodal carpal articulation approximately 45° from perpendicular. Dactyl slightly to half again longer than palm; surfaces unarmed but with scattered tufts of short setae; cutting edges of dactyl and fixed finger each with row of small corneous teeth in distal half to ⅔; terminating in small corneous claws. Palm ½ to ⅔ length of carpus; dorsomesial margin with 1–3 low protuberances or tubercles; surfaces all unarmed, but with few scattered setae, particularly on fixed finger. Carpus slightly shorter than merus; dorsomesial margin with 1 strong, acute or blunt spine on dorsomesial margin distally, and row of 3–5 small blunt or subacute spines or tubercles on dorsomesial margin; dorsolateral margin not delimited. Merus with unarmed dorsal margin; ventrolateral margin unarmed or with row of very small acute, simple or bifid spinules, ventral surface sometimes with 1 or 2 very small spinules and usually 1 moderately prominent tubercle proximally near mesial margin; dorsal and ventral surfaces with scattered short setae. Ischium often with 1 well developed tubercle on ventromesial margin distally and frequently also with row of moderately long setae.

Ambulatory legs (Figs. 2E, F; 3D, E) similar, but with left second and third pereopods slightly longer than right. Dactyls 1 and ⅓ to nearly twice length of propodi; in dorsal view, straight or very faintly twisted in distal third; dorsal margins each with row tufts of long, stiff setae, mesial faces each with 2 or 3 sparse rows of tufts of short to moderately long setae, sometimes replaced by short, stiff and spiniform bristles in large individuals (SL 10.0 mm); lateral face with few tufts of short setae; ventral margins each with row of 15–31 corneous spines and few tufts of setae. Propodi slightly longer than carpi, each with few scattered setae on dorsal surface, ventrodistal angles each with 1 or 2 small corneous spinules, ventral surfaces frequently with row of widely-spaced small corneous spinules, at least on second and with scattered setae. Carpi ⅔ to ⅘ length of meri; dorsodistal angles each with small spine, dorsal surface with sparse row of setae. Meri and ischia with scattered setae on dorsal and ventral margins. Fourth pereopods (Fig. 2G) with propodal rasp consisting of 1 long row and 1 or rarely 2 very short to moderately long rows of corneous scales; dactyl with small terminal claw, no preungual process detected. Fifth pereopods moderately elongate, chelate; chela with dense tuft of long setae ventrally.

Anterior lobe of sternite of third pereopods subrectangular, with central semicircle fringed with short setae. Sternite of fifth pereopods (Fig. 2H) broadly rectangular, with 2 prominent tufts of setae. Telson (Fig. 2I) with posterior lobes asymmetrical, left largest, separated by moderate median cleft, terminal margins each with row of very small spinules.

Habitat.—Occupying shells of *Fusitriton* sp. and occasionally *Iredalina* sp.

Distribution.—New Zealand. Off North Island to the east from north of North Cape to north of Mayor Island, and to the west and south of South Island from northwest of Westport to the Solander Trough and Northern Campbell Plateau; 272–573 m.

Etymology.—The species is named in honor of Dr. John Yaldwyn, retired director of the National Museum of New Zealand, in recognition of his many contributions to the decapod faunas of Australia and New Zealand.

Remarks.—One specimen indicated in the material examined as "?♀" was parasitized by an unidentified rhizocephalan. Although this was an adult individual (SL 9.6 mm) with female appearing pleopods, neither male nor female gonopores were present.

As is apparent from the description, *B. yaldwyni* exhibits considerable variability, particularly in chela morphology. In contrast to many pagurids where the strength of chela armature decreases with increasing animal size, tubercles and spines in *B. yaldwyni* increased in strength and number in large specimens of both sexes. Similarly, the number of spines on the ventral margins of the pereopodal dactyls increased from 15–18 in animals with shield lengths of 5 to 6 mm, to 25–31 in animals with shield length over 9.5 mm.

Bathypaguropsis marionensis, new species

Figs. 1B, 4, 5

Holotype.—♀♀ (SL 5.5 mm), Marion Plateau, Queensland, 19°32.85′S, 152°34.8′E, CSIRO sta 0685-30, 470–477 m, 23 Nov 1985, NTM CR006854.

Paratypes.—2 ♂ (SL 5.8; 4.7 mm), Marion Plateau, Queensland, 19°32.85′S, 152°34.8′E, CSIRO sta 0685-30, 470–477 m, 23 Nov 1985, NTM CR006854, USNM 267575.

Description.—Shield (Figs. 1B, 4A) subtriangular; as long or slightly longer than broad; anterior margin between rostrum and lateral projections somewhat concave; anterolateral margins slightly oblique; posterior margin truncate; dorsal surface with few tufts of setae. Rostrum long, reaching well beyond bases of ocular acicles, acute, with very small terminal spinule. Lateral projections triangular, usually with small terminal spinule.

Ocular peduncles stout, short, ½ to ⅔ shield length, dorsomesial surface with row of setae; corneae not dilated. Ocular acicles simple, triangular, unarmed or with tiny terminal spinule; separated basally by width of rostrum, or by half to ⅔ basal width of 1 acicle.

Antennular peduncles long, overreaching ocular peduncles by almost entire length of ultimate segment; basal segment with acute spine on lateral surface distally; penultimate segment with few scattered setae dorsally and ventrally; ultimate segment with row of setae on dorsal surface; flagellum longer than ultimate peduncular segment.

Antennal peduncles exceeding ocular peduncles by half to ⅔ length of ultimate segment, but reaching only to distal half of ultimate segment of antennular peduncle. Fifth and fourth segments with few scattered setae; third segment with very strong spine at ventrodistal margin; second segment with dorsolateral distal angle strongly produced into broad, triangular process, terminating in acute spine, usually 1 or 2 spines on mesial margin (absent in holotype) and 2–4 on lateral margin, dorsomesial distal angle with acute spine; first segment with small spine at laterodistal margin, ventral margin produced, with 1 or 2 spines laterally. Antennal acicle reaching slightly beyond proximal margin of ultimate peduncular segment, stout, slightly arcuate, with row of tufts of setae on mesial margin and terminating in small spine. Antennal flagellum long, but not overreaching outstretched right cheliped, each article usually with 3 or 4 very short (<1 article length) setae and occasionally 1–4 somewhat longer.

Maxillule (Fig. 4B) with 1 strong bristle on internal lobe of endopod, external lobe moderately well developed, articulated, not recurved. Maxilla (Fig. 4C) with endopod reaching distal margin of scaphognathite; distal lobe of latter subtriangular. First maxilliped (Fig. 4D) with basal segment subrectangular. Third maxilliped with small spine at distal margin of merus.

Right cheliped (Fig. 5A, B) massive, operculate. Dactyl broad, shorter than palm; cutting edge with 1 large fused or 2 or 3 distinct calcareous teeth, terminating in very small corneous claw; dorsal surface slightly elevated in midline, and with row of low tubercles, dorsomesial margin with 1 or 2 tubercles proximally, weakly crenulate, tuberculate, or with transverse ridges distally, mesial and ventral surfaces with low, flattened, sometimes corneous-capped, blister-like tubercles. Palm broader than long, exceeding length of carpus by ¼ to ⅓ own length, dorsomesial distal angle markedly produced and armed with 2 or 3 prominent tuberculate spines; dorsomesial margin with single or irregular double row of blunt, tuberculate spines, sometimes interspersed with small tubercles, dorsal surface convex, covered with flattened granules and small tubercles, with 1 or 2 prominent tubercles at proximal margin; dorsolateral margin rounded, tuberculate, becoming more distinct and crenulated on fixed finger; mesial face with scattered low tubercles, lateral face continuous with ventral surface, with scattered granules and few flattened, frequently corneous-capped, blister-like tubercles distally near articulation of dactyl; ventral surfaces of dactyl and fixed finger with scattered granules or very small, flattened tubercles; cutting edge of fixed finger with 2 or 3 calcareous teeth, terminating in very small corneous claw. Carpus equaling or only slightly longer than merus, subquadrate when viewed dorsally; dorsomesial distal angle depressed and armed with spine or tubercle, margin with strong spine distally and 1 or 2 tubercles or blunt spines in distal half, occasionally with oblique row of 4 or 5 spines in distal half and few low spinulose tubercles or blunt spines on or near dorsomesial margin proximally, dorsal surface with scattered low blunt or spinulose tubercles, often most prominent in distal half and very short, transverse ridges; dorsolateral margin not delimited, lateral and mesial surfaces with scattered blunt or spinulose tubercles, strongest near distal margins, ventrodistal margin with row of small, blunt or subacute spines or tubercles. Merus broadly and roundly triangular; dorsal margin not delimited, dorsal, mesial and lateral surfaces with low transverse, weakly granular ridges, ventromesial margin with 1 strong acute spine at distal angle and few low protuberances or tubercles proximally; ventrolateral margin with slightly smaller

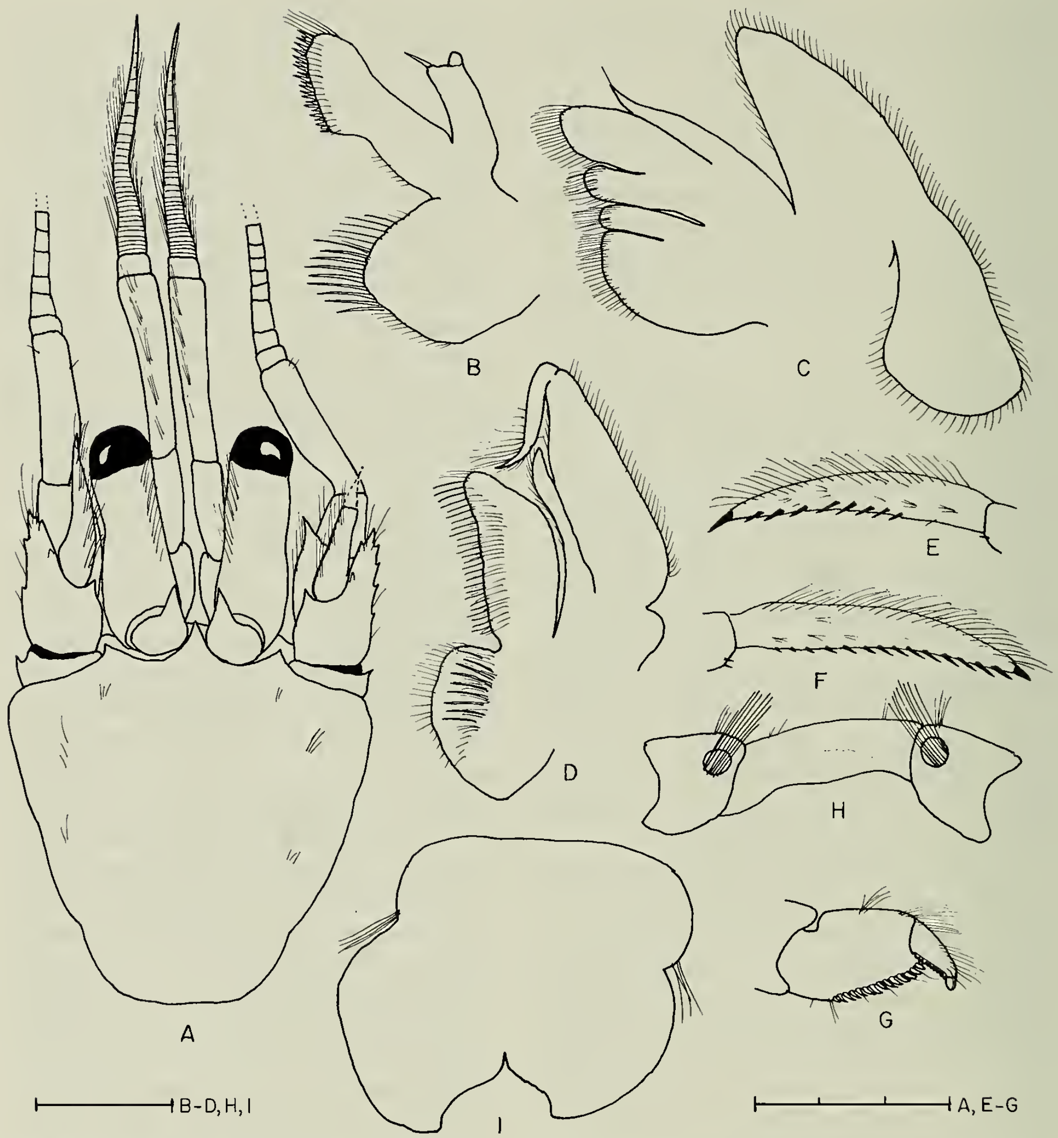

Fig. 4. *Bathypaguropsis marionensis,* new species, ♂ paratype (SL 5.8 mm), USNM 267575. A, shield and cephalic appendages; B, left maxillule (external view); C, left maxilla (external view); D, left first maxilliped (external view); E, dactyl of right second pereopod (mesial view); F, dactyl of left third pereopod (mesial view); G, dactyl and propodus of right fourth pereopod (lateral view); H, sternite of male fifth pereopods; I, telson. Scales equal 3 mm (A, E–G) and 1 mm (B–D, H, I).

spine near distal angle and few spinulose tubercles proximally; ventral surface with scattered granules or tubercles, 2 or 3 moderately large tubercles on somewhat produced mesial half. Ischium with few minute granules on ventromesial margin.

Left cheliped (Fig. 5C) not reaching to base of dactyl of right, slender; propodal-carpal articulation approximately 45° from perpendicular. Dactyl shorter to slightly longer than palm; surfaces unarmed or with 1 or 2 minute tubercles on dorsal surface

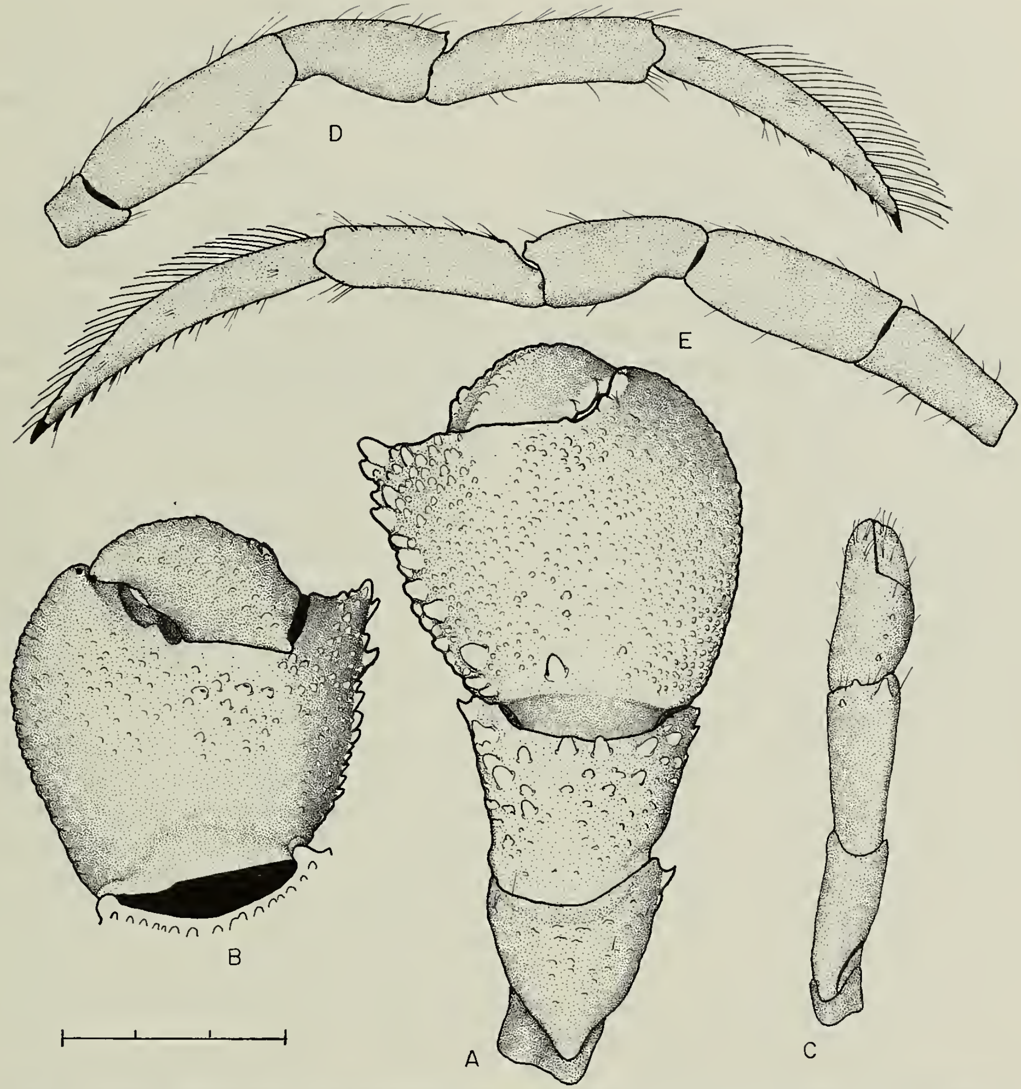

Fig. 5. *Bathypaguropsis marionensis,* new species, ♂ paratype (SL 5.8 mm), USNM 267575. A, right cheliped (dorsal view); B, right chela (ventral view); C, left cheliped (dorsal view); D, right second pereopod (lateral view); E, left third pereopod (lateral view). Scale equals 3 mm.

proximally, but with scattered tufts of setae; cutting edges of dactyl and fixed finger each with row of small corneous teeth; terminating in small corneous claws. Palm half to ⅔ length of carpus; dorsomesial margin with 2–4 small, acute or blunt spines, usually strongest proximally; surfaces all unarmed, but with few scattered setae, particularly on fixed finger. Carpus slightly longer than propodus; dorsomesial margin with 1 or 2 strong, acute or blunt spines on dorsomesial margin distally and also 2 or 3 spinules or low tubercles proximally, sometimes 1 small blunt spine on dorsodistal margin and 1 still smaller spine on dorsolateral surface distally; dorsolateral margin not delimited. Merus with few very small spines, tubercles or short transverse granular ridges on ventromesial and ventrolateral margins. Ischium unarmed or with 2 or 3 small tubercles on ventromesial margin.

Ambulatory legs (Figs. 4E, F; 5D, E) similar, but left second and third pereopods slightly longer than right. Dactyls longer than propodi by ⅓ to ½ own length; in dorsal view faintly twisted in distal third; dorsal margins each with row of long, stiff bristles; mesial faces each with row of tufts of setae and also frequently few corneous spinules dorsally in distal half; lateral face with few tufts of short setae, and occasionally faint indication of longitudinal sulcus; ventral margins each with row of 8–14 corneous spines, fewest usually on second pereopod. Propodi slightly longer than carpi, each with 1 or 2 small corneous spinules on ventrodistal margin; dorsal and ventral surfaces with scattered setae. Carpi ½ to ⅘ length of meri; dorsodistal angles each with small spine, dorsal and ventral surfaces with few setae. Meri and ischia with scattered setae on dorsal and ventral margins. Fourth pereopods (Fig. 4G) with 1 row of curved acute corneous scales on propodal rasp, sometimes second row of 2 or 3 scales distally; dactyl with small terminal claw, no preungual process detected. Fifth pereopods moderately elongate, chelate; chelae with fringe of long setae ventrally.

Sternite of third pereopods with anterior lobe subrectangular and central semicircle with short marginal setae. Sternite of fifth pereopods (Fig. 4H) broadly rectangular, with anterior marginal setae. Telson (Fig. 4I) with posterior lobes asymmetrical, left largest, separated by prominent median cleft, terminal margins unarmed or with very few minute tubercles.

Habitat.—The holotype occupied an unidentified gastropod shell.

Distribution.—At present known only from the type locality, off Queensland, Australia; 470–477 m.

Etymology.—The specific name is derived from the type locality, the Marion Plateau.

Remarks.—At first glance, *B. marionensis* and *B. yaldwyni* are extremely similar in overall morphology, and given the range of size-correlated variation that has been observed in *B. yaldwyni,* no single character can unequivocally assure accurate identification. For example, *B. marionensis* has only 8–14 corneous spines on the ventral margins of the ambulatory dactyls, whereas most specimens of *B. yaldwyni* are readily recognized by the larger number (22–31). However, in small specimens of this latter species (SL 5 to 6 mm) the number closely approximates that of *B. marionensis.* As *B. marionensis* is presently known from only three relatively small, albeit mature specimens; growth influenced variations cannot be adequately assessed. Nonetheless, when *B. marionensis* is compared with small representatives with *B. yaldwyni* it is immediately apparent that cheliped armature is appreciably stronger in the former species. Even in small specimens of *B. yaldwyni* the sternite of the fifth pereopods is marked by two moderately distinct tufts of setae, while there is only an anterior marginal fringe of setae in *B. marionensis.* The dorsolateral distal angle of the second antennal segment is broadly triangular in both species, but in *B. marionensis* the mesial margin may be unarmed or carry one or two small spines; the lateral margin is armed with two to four spines. In *B. yaldwyni* the mesial margin is consistently unarmed and the lateral margin has only one or two spines. Even though it may be necessary to utilize a suite of characters to distinguish between the taxa, there is amply morphological evidence to justify recognition of two distinct species.

Acknowledgments

Specimens for this study have been provided through the kindness of Drs. J. Yaldwyn, G. R. F. Hicks, and W. R. Webber, National Museum of New Zealand, and Dr. A. J. Bruce, Northern Territories Museum of Arts and Sciences, through Dr. R. Lemaitre, National Museum of Natural History, and to all I express my appreciation. This is a scientific contribution from the Shannon Point Marine Center.

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MARINE ISOPODS FROM THE LESSER ANTILLES AND COLOMBIA (CRUSTACEA: PERACARIDA)

Brian Kensley and Marilyn Schotte

Abstract.—Records of shallow-water marine isopods from Colombia, Tobago, and Dominica are listed. These are derived from recent collections as well as from published records. Several new species are described: *Joeropsis tobagoensis, Munna caprinsula, Anopsilana sinu, Paraimene charlesae* (the second known species in the genus), *Pseudocerceis latistylis* (the first record of the genus in the Atlantic), *Sphaeromopsis heardi,* and *Astacilla marna.*

While records of marine isopods from the overall Caribbean are relatively plentiful, the south-eastern region including the Lesser Antilles, Trinidad and Tobago, and Venezuela, is poorly represented (see Kensley & Schotte 1989). The work of H.-G. Müller in Colombia (see Table 1) has revealed the rich isopod fauna of the south-western Caribbean. With reference to marine isopods, the faunal ties with the shallow-water northern Brazilian region are slender, being about 3% of the Caribbean fauna (Kensley & Schotte 1989:262), but this figure almost certainly will change with increased collecting. This paper attempts to fill some of the gaps in the knowledge of the shallow-water isopod diversity of the southeastern Caribbean. Material was collected by both authors (BK & MS) on two separate occasions around the island of Dominica, and by the second author (MS) on a single field-trip to Tobago. Material from the latter island was also made available by Dr. R. W. Heard (RH), the result of two collecting trips sponsored by J. David Hardy, for a faunal survey requested by the Tobago House of Assembly. Material from two collecting trips to Colombia was made available by Dr. R. Lemaitre (RL) and Dr. Darryl Felder (DF). Much of the material from Dominica and Tobago represents either range extensions or new records, but no attempt has been made to indicate these in Table 1.

Systematics

Suborder Asellota

Family Joeropsidae

Joeropsis tobagoensis, new species

Fig. 1

Material.—Holotype, USNM 252761, ♂ tl 1.9 mm, Allotype, USNM 252762, ♀ tl 1.8 mm, Paratypes, USNM 252763, 5 ♂, 2 ovig. ♀, 11 ♀, sta 5, Sandy Bay, Tobago, sand and rock washings, intertidal to 1.5 m, coll. RH, 7 Apr 1992.—USNM 252764, 1 ♂, Pigeon Point, Tobago, coll. RH, 7 Apr 1992.—USNM 252765, 2 ♂, 2 ♀, sta 8, east side of Man o' War Bay, Tobago, rocky intertidal, coll. RH, 6 Apr 1992.—USNM 252766, 1 ♂, Goat Island, Tobago, sediment, 4–5 m, coll. RH, 14 Jan 1993.

Diagnosis.—Free margin of rostrum broadly convex. Lateral margins of cephalon entire. Lateral margins of pleotelson having 3 teeth. Dorsal cephalon with reticulated pigmentation.

Description.—Male: Body 3 times longer than wide. Cephalon width 1.4 times length. Rostrum evenly convex with fringe of transparent teeth, flanked by rounded lobes. Pigment reticulated, on cephalon only. An-

Table 1.—Records of marine isopods from Colombia, Dominica, and Tobago, compiled from the collections mentioned in the Introduction, plus the published Colombian records of Müller (1988a, 1988b, 1989, 1990a, 1990b, 1990c, 1990d, 1991, 1992, 1993a, 1993b, 1993c).

Species	Colombia	Dominica	Tobago
Anthuridea			
Family Anthuridae			
Amakusanthura paramagnifica	+		
Amakusanthura signata	+	+	
Amakusanthura tengo	+		
Amakusanthura vermiformis	+		
Apanthura cracenta			+
Apanthuroides millae		+	
Chalixanthura sp.			+
Cortezura confixa	+		
Licranthura amyle		+	
Mesanthura cf. brasiliensis	+		
Mesanthura fasciata			+
Mesanthura hopkinsi	+		
Mesanthura paucidens	+		+
Mesanthura pulchra	+	+	
Mesanthura punctillata	+	+	
Minyanthura corallicola	+	+	
Pendanthura hendleri			+
Family Hyssuridae			
Chalixanthura colombiana	+		
Eisothistos tayronae	+		
Kupellonura sp.			+
Stellanthura caribbica	+		
Xenanthura conchae	+		
Family Paranthuridae			
Accalathura crenulata		+	
Colanthura tenuis	+		
Paranthura infundibulata	+	+	+
Asellota			
Family Gnathostenetroididae			
Neostenetroides sp.			+
Family Janiridae			
Carpias algicola		+	+
Carpias brachydactylus			+
Carpias parvus	+		
Carpias punctatus		+	+
Carpias serricaudus	+	+	+
Carpias triton	+		
Janira gracilis	+		
Family Joeropsidae			
Joeropsis paradubia	+		
Joeropsis personata	+		
Joeropsis rathbunae	+		+
Joeropsis tayrona	+		
Joeropsis tobagoensis		+	

Table 1.—Continued.

Species	Colombia	Dominica	Tobago
Family Munnidae			
Munna caprinsula		+	
Uromunna sp. A			+
Uromunna sp. B			+
Uromunna sp. C			+
Family Paramunnidae			
Munnogonium wilsoni			+
Family Pleurocopidae			
Pleurocope floridensis			+
Family Santiidae			
Halacarsantia sp.			+
Santia milleri		+	+
Family Stenetriidae			
Stenetrium minocule	+		+
Stenetrium patulipalma			+
Stenetrium stebbingi	+	+	+
Family Incertae Sedis			
Mexicope kensleyi		+	
Flabellifera			
Family Aegidae			
Rocinela signata	+		+
Family Cirolanidae			
Anopsilana sinu	+		
Calyptolana hancocki	+		+
Cirolana kiliani	+		
Cirolana parva	+	+	+
Colopisthus parvus	+		
Eurydice personata			+
Excirolana brasiliensis			+
Excirolana mayana	+		+
Metacirolana agaricicola	+		
Metacirolana agujae	+		
Metacirolana halia	+		
Metacirolana sphaeromiformis		+	+
Neocirolana tayronae	+		
Family Corallanidae			
Alcirona krebsii			+
Excorallana delaneyi			+
Excorallana sexticornis	+		+
Excorallana tricornis tricornis	+		
Excorallana warmingii			+
Family Cymothoidae			
Cymothoa excisa			+
Family Limnoriidae			
Limnoria indica	+		+
Limnoria pfefferi	+		+

Table 1.—Continued.

Species	Colombia	Dominica	Tobago
Limnoria platycauda	+	+	+
Paralimnoria andrewsi	+		
Phycolimnoria clarkae			+
Family Serolidae			
Serolis mgrayi	+		
Family Sphaeromatidae			
Ancinus braziliensis			+
Cassidinidea ovalis		+	+
Dynamenella perforata			+
Exosphaeroma diminutum			+
Geocerceis barbarae		+	
Paracerceis caudata	+	+	+
Paradella plicatura		+	
Paraimene charlesae		+	+
Paraleptosphaeroma glynni		+	
Pseudocerceis latistylis		+	
Sphaeromopsis heardi		+	+
Gnathiidea			
Family Gnathiidae			
Gnathia beethoveni	+		+
Gnathia gonzalezi	+		
Gnathia magdalenensis	+		
Gnathia samariensis	+		
Gnathia vellosa	+		
Gnathia virginalis	+		
Oniscidea			
Family Ligiidae			
Ligia baudiniana			+
Family Philosciidae			
Littorophiloscia culebrae			+
Family Tylidae			
Tylos niveus		+	+
Tylos wegeneri			+
Valvifera			
Family Astacillidae			
Arcturella spinata	+		
Astacilla cymodocea	+		
Astacilla marna		+	
Astacilla tayronae	+		
Astacilla sp.			+
Edwinjoycea horologium	+		
Family Idoteidae			
Cleantioides occidentalis	+		
Cleantioides planicauda	+		
Edotia samariensis	+		
Erichsonella filiformis	+	+	+
Idotea metallica			+

terolateral angles of cephalon acute; eyes well-pigmented. Body nearly glabrous with few scattered setae on margins of pereonites. Pleotelson width 1.3 times length, lateral margins with 3 teeth and several setae, apex narrowly rounded.

Antennule, basal article longest and widest with transparent dentate flange on outer distal angle; articles 2–4 with few setae; terminal article with 2 aesthetascs and four simple setae. Antennal article 4 largest; transparent fringe on outer margins of articles 4 and 5; flagellum of 8 setose articles. Mandibular palp of 3 articles, article 2 having 3 distal fringed spines, article 3 with 5 distal fringed spines; spine row of 9 spines on both mandibles, blunt projection between 7th and 8th spines on left mandible only; molar slender, tapering. Maxilla 1, inner ramus with 3 slender terminal setae and several fine setules; outer ramus with 12 stout dentate spines. Maxilla 2, inner ramus with 3 simple setate and several setules distally; both lobes of outer ramus bearing one simple and 3 fringed setae. Maxillipedal endite broad, bearing 3 coupling hooks, distolateral margin weakly serrate, mediodistally emarginate with 2 widely separated flattened spines; palp of 5 articles, penultimate article longest. Pereopods typical for genus, except pereopod 7 having anterodistal margin of merus strongly serrate. Pleopods 1 and 2 as figured. Uropod with mediodistal angle curved and acute; inner ramus bearing 2 plumose and several simple setae; outer ramus shorter with long and short setae.

Female: Operculum, proximal half with broadly convex margins, distal half tapering to apex bearing 4 setae.

Remarks.—*Joeropsis tobagoensis* resembles the Caribbean species *J. coralicola* Schultz & McCloskey, 1967, and *J. rathbunae* Richardson, 1902. Both of these are much more setose than *J. tobagoensis,* have serrated margins of the pleotelson, and reticulated pigment over the entire body. The rostrum, which has an evenly convex anterior margin, differs from that of *J. coralicola* which has a slightly indented anterior margin.

Etymology.—The specific epithet derives from the type locality, Tobago.

Family Munnidae
Munna caprinsula, new species
Figs. 2, 3

Material.—Holotype, USNM 252767, ♂ tl 1.0 mm, Allotype, USNM 252768, ♀ tl 1.2 mm, Paratypes, USNM 252769, 7 ♀, Goat Island, Tobago, tube sponge, 4–5 m, coll. RH, 14 Jan 1993.—Paratypes, USNM 252770, 2 ♂, 2 ovig. ♀, 2 ♀, sta 8, east side of Man o' War Bay, Tobago, rocky intertidal, coll. RH, 6 Apr 1992.

Diagnosis.—Pleotelson longer than wide. Pereopod 1 in male carpochelate, carpus broad, with bidentate process at posterodistal angle. Pleopod 1 in male, mesial lobes of rami having very obtuse angle.

Description.—Male: Body almost 3 times longer than wide, pereonite 1 wider and longer than all other pereonites. Several setae on dorsum and lateral margins. Head with straight anterior margin bearing 6 setae; eyes on short stalks, with few ommatidia. Pleon of one short segment and globose pleotelson, longer than wide, dorsally sparsely setose, posteriorly rounded.

Antennule of 7 articles, single aesthetasc on distal 2 articles; article 2 with single setose spine distally. Antenna missing in all specimens. Mandibular palp 3-segmented, terminal article with 3 distal spines and two medial rows of combed spines; molar process distally truncate, nor serrate; spine row of 4 spines; lacinia mobilis with 4 cusps, incisor of 4 cusps. Maxillae typical of genus. Maxilliped, article 2 of palp largest, all articles bearing setae; endite with 3 retinaculae and several setae; distal margin truncate with 5 fringed spines, 3–4 submarginal feather setae, and 3 simple spines. Pereopod 1 carpochelate, length of propodus, carpus and merus combined somewhat less than ½

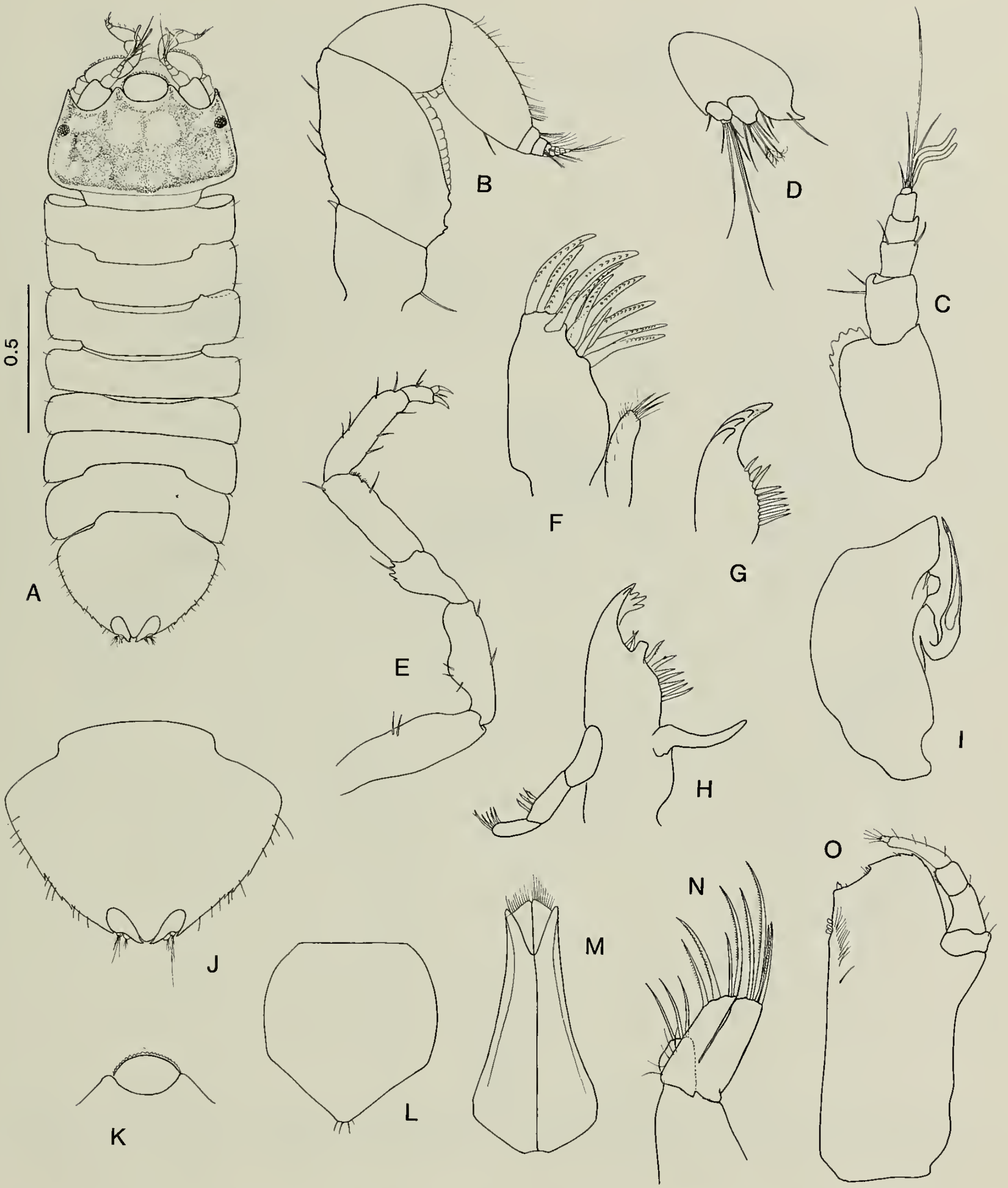

Fig. 1. *Joeropsis tobagoensis.* A, male in dorsal view; B, antenna; C, antennule; D, uropod; E, pereopod 7; F, maxilla 1; G, right mandible; H, left mandible; I, male pleopod 2; J, pleotelson; K, rostrum; L, female operculum; M, male pleopod 1; N, maxilla 2; O, maxilliped.

length of body; merus widening distally; carpus widening distally into bidentate process, single spines at anterodistal angle; propodus nearly as wide as long; dactylus about 3.5 times as long as wide, barely reaching distal margin of carpus, unguis long and slender. Pereopods 2–7 slender with sensory spines on margins of carpi and

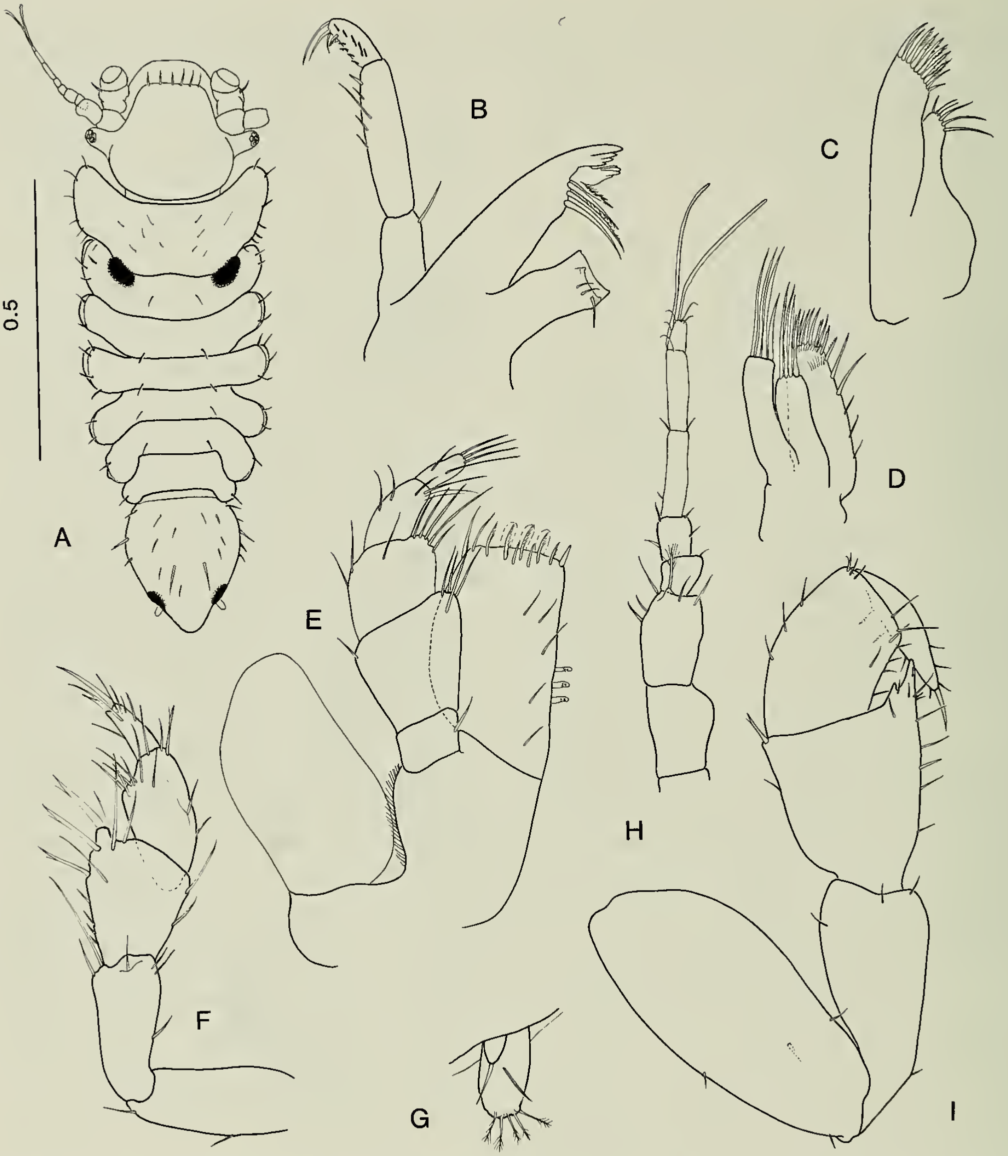

Fig. 2. *Munna caprinsula.* A, male in dorsal view; B, mandible; C, maxilla 1; D, maxilla 2; E, maxilliped; F, pereopod 1 ♀; G, uropod; H, antennule; I, pereopod 1 ♂.

propodi; dactyli biunguiculate with single seta between slender ungui. Pleopod 1, rami fused for about ⅔ of length, inner distal lobe bearing about 6 setae, outer lobe acute, triangular. Pleopod 2, outer ramus with about 12 simple setae on surface and fine fringe on outer margin; inner ramus tapering, extending just beyond apex of outer ramus. Pleopod 3, outer ramus with about 5 setae on surface, inner ramus much shorter and bearing 3 distal plumose setae. Pleopod 4, outer ramus broadly triangular, inner ramus slender with 2 distal plumose setae. Uropod, longer ramus parallel-sided with rounded apex bearing about 5 setae; smaller ramus much shorter with one seta.

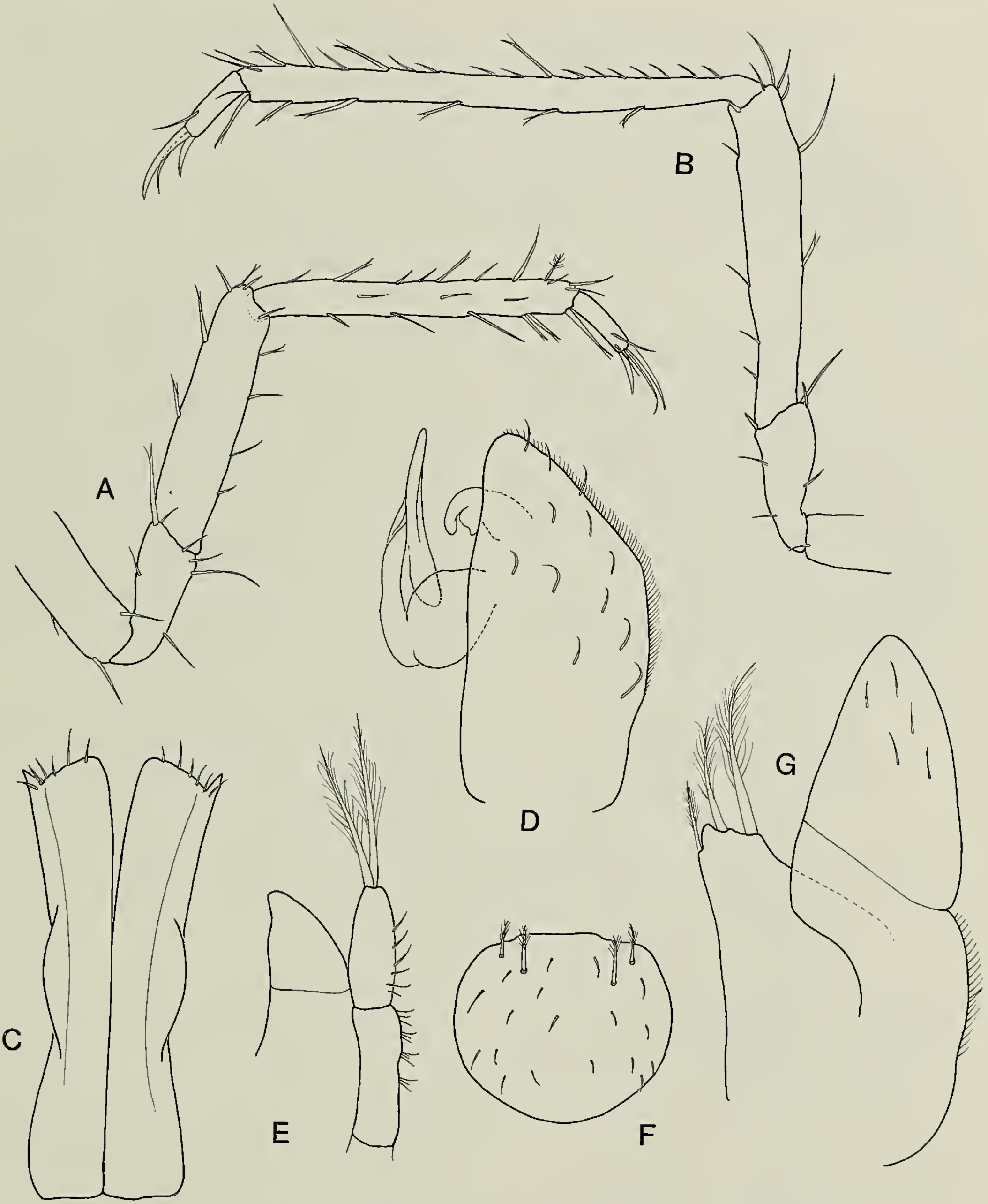

Fig. 3. *Munna caprinsula.* A, pereopod 2; B, pereopod 7; C, pleopod 1; D, pleopod 2; E, pleopod 4; F, operculum; G, pleopod 3.

Female: Body ovate, widest at pereonite 4; pereonite 1 not enlarged as in male. Pereopod 1 shorter than other legs; carpus extended distally with 3 sensory spines at or near anterodistal angle; propodus with single sensory spine at posterodistal angle; dactylus biunguiculate, anterior unguis longer than posterior. Operculum wider than long, almost oval, dorsal surface setose with two pairs of stout, setose spines near proximal margin.

Color.—Pigment somewhat variable; several specimens with large, brown pigment spots at anterior margin of pereonite 2; smaller patches on distolateral pleotelson near uropods; some specimens with pigment only on pleotelson, some with no coloration.

Remarks.—*Munna caprinsula* most closely resembles another Caribbean congener, *M. petronastes* Kensley, 1984, from Belize, but differs in pigment pattern and in the morphology of the first pereopod of the male. All other munnids from the western Atlantic are in the genus *Uromunna,* which lacks mandibular palps and has a single aesthetasc on the antennule.

Etymology.—The specific epithet is derived from the Latin, *capri,* goat, and *insula,* island, and refers to the type locality.

Suborder Flabellifera

Family Cirolanidae

Anopsilana sinu, new species

Figs. 4–6

Material.—Holotype, USNM 252771, 1 ovig. ♀ tl 6.0 mm, Allotype, USNM 252772, 1 ♂ tl 7.9 mm, Paratypes, USNM 252773, 79 ♂, 19 ovig. ♀, 100+ non-ovigerous ♀ & juv., from mussel-covered mangrove roots in drainage canal of Rio Sinu between Cienaga Soledad and Bahia de Cisputan, about 2 miles from seacoast, < 1 m depth in brackish water of 10–25 ppm, coll. RL & DF, 25 Oct 1992.

Diagnosis.—Body length more than 3 times greatest width. Frontal lamina rectangular, 1.7 times longer than wide. Uropodal exopod having 7 spines on lateral margin; uropodal endopod having 2 spines on lateral margin, 5 spines on mesial margin. Pleotelsonic apex having 10 spines.

Description.—Scattered pigment, frequently dense, on all somites and uropods, most concentrated toward posterior margins of pereonites and pleonites. Length of largest specimen 7.9 mm. Body length more than 3 times width. Anterior margin of cephalon produced into small rostrum separating bases of antennae 1, and ventrally, appearing to insert into anterior edge of frontal lamina. Latter rectangular, length about 1.7 times width. Cylpeus as deep as width of frontal lamina. Pereonite 1 longest, pereonites 2–6 gradually increasing in length, pereonite 7 somewhat shorter than 6. Posterior edges of coxae 2–3 rounded, 4–7 acute; coxa of pereonite 7 reaching beyond pleonite 1; all coxae with oblique carinae. Pleonites 1–4 subequal in length, 5 longest; pleonite 1 partly overlapped by pereonite 7; pleonite 5 overlapped laterally by pleonite 4; epimera of pleonites 1–3 pointed, of pleonite 4, rounded. Pleotelson triangular, slightly longer than wide, rounded apically, armed with 10 spines and many interspersing setae.

Antennule reaching to midpoint of pereonite 1, flagellum with 11 articles and 8 aesthetascs in male. Antenna nearly reaching pereonite 4, flagellum with 19 articles. Mandible as figured, tricuspid. Exopod of maxilla 1 with 12 spines, 2 with accessory spinules, endopod with 3 plumose spines. Maxilla 2 with 5 and 8 setae on palp and exopod respectively; endopod with 11 setae, some plumose. Maxilliped with one coupling hook. Pereopods as figured, with 1 plumose seta each on ischium and basis. Pereopod 7 as figured. Pleopod 1 with 4 hooks and 2 setae on protopod, stout simple seta on proximolateral margin of exopod; protopod of pleopod 2 bearing 3 hooks and 3 plumose setae, copulatory stylet tapering to rounded apex, nearly twice length of endopod. Pleopod 3 with 3 hooks, 3 plumose setae and 3 simple setae on protopod. Pleopod 4 having 3 hooks and 2 setae on protopod; pleopod 5 as figured. Uropods reaching beyond apex of pleotelson; exopod with 7 spines on lateral margin, 3 on mesial margin. Endopod longer than exopod, with 5 mesial and 2 lateral spines.

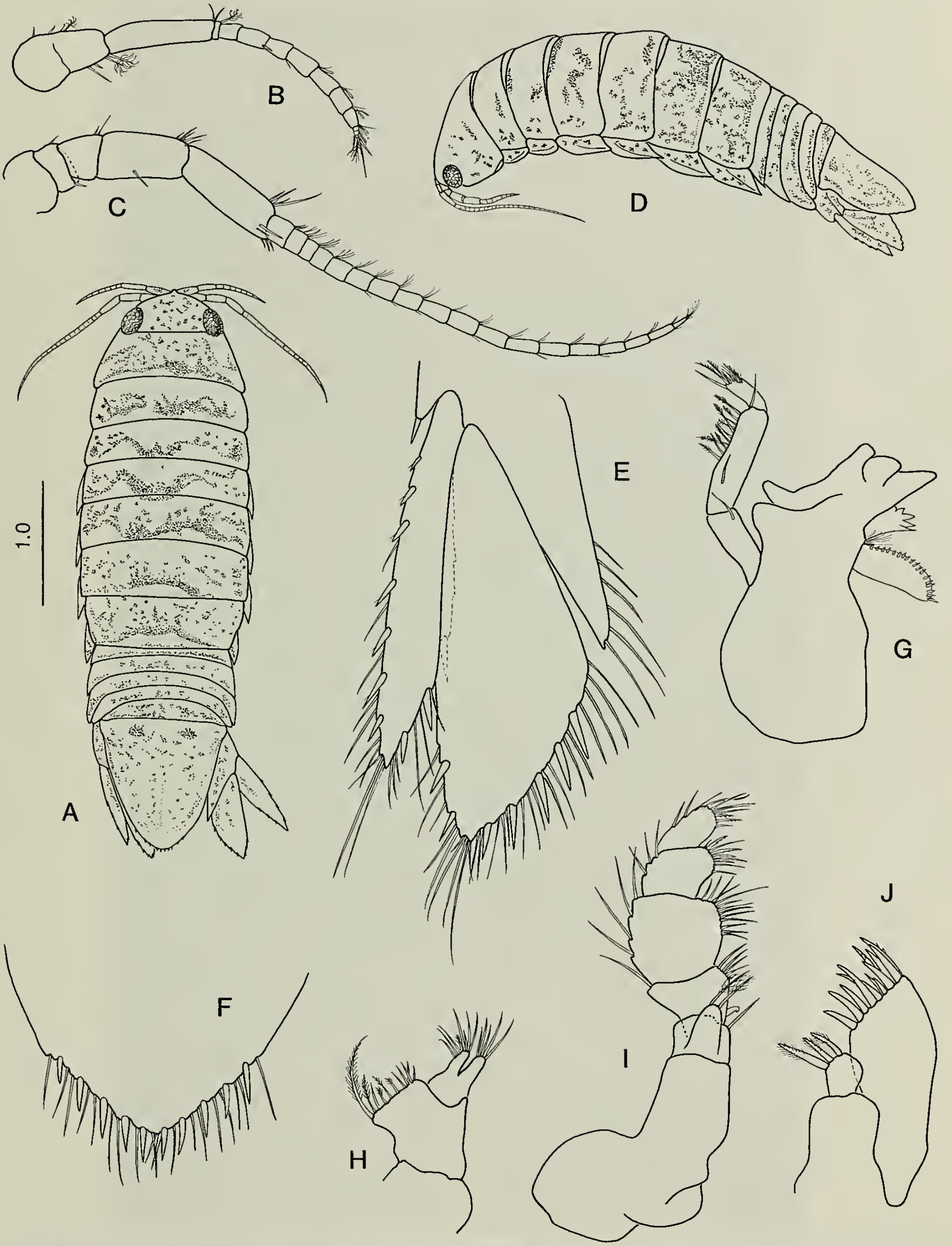

Fig. 4. *Anopsilana sinu.* A, male in dorsal view; B, antennule; C, antenna; D, male in lateral view; E, uropod; F, apex of pleotelson; G, mandible; H, maxilla 2; I, maxilliped; J, maxilla 1.

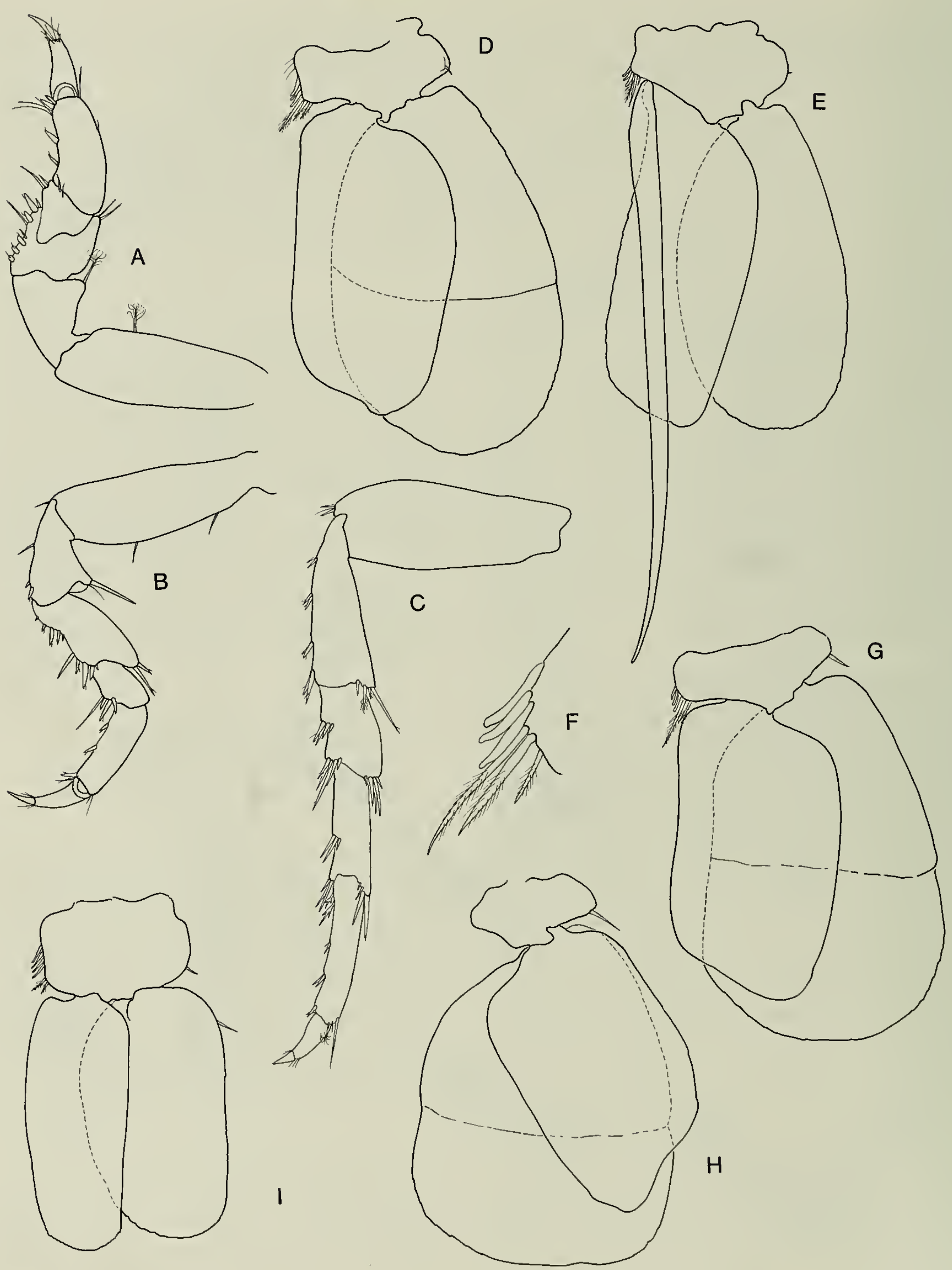

Fig. 5. *Anopsilana sinu.* A, pereopod 1; B, pereopod 2; C, pereopod 7; D, pleopod 3; E, pleopod 2 ♂; F, coupling hooks and setae of pleopod 1 protopod enlarged; G, pleopod 4; H, pleopod 5; I, pleopod 1.

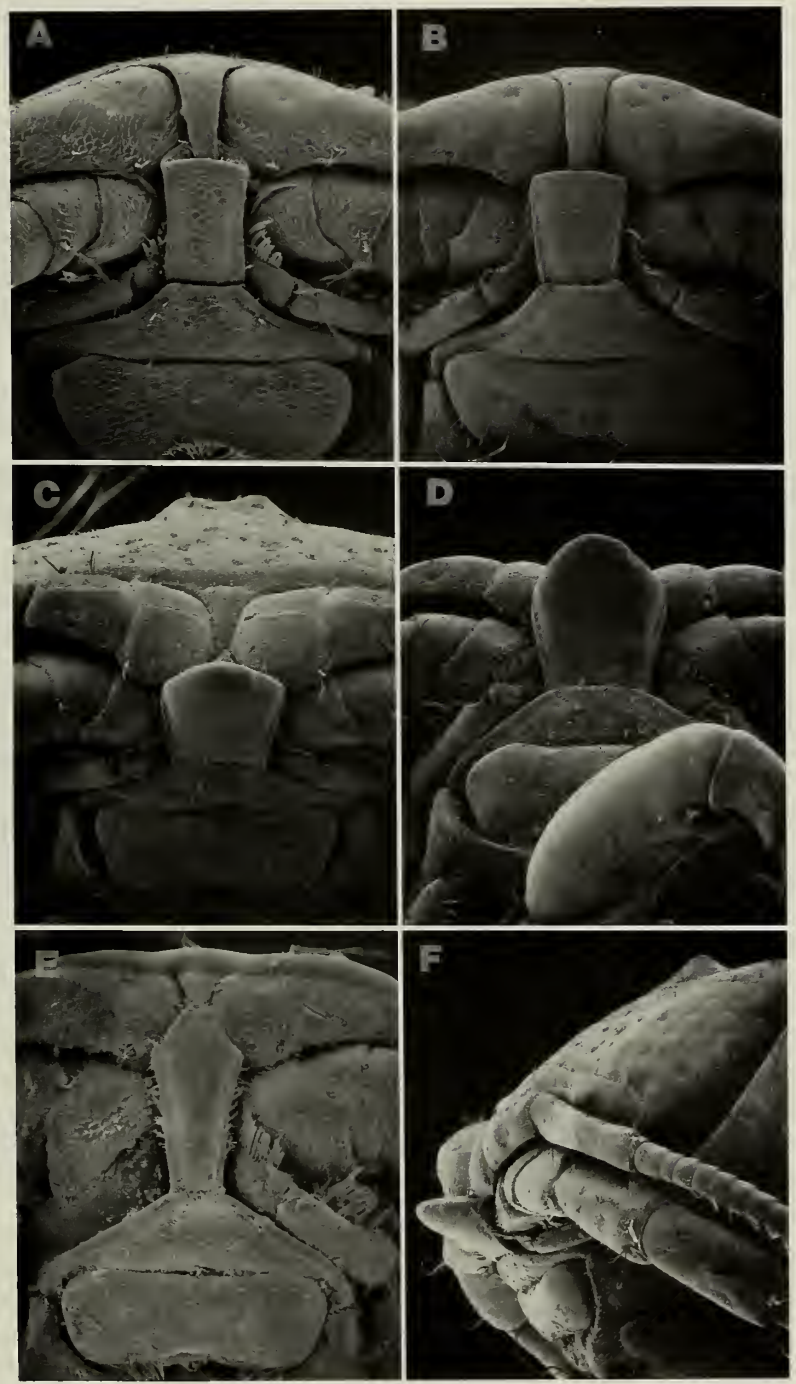

Fig. 6. A, *Anopsilana sinu,* frontal lamina and clypeus; B, *Anopsilana oaxaca,* frontal lamina and clypeus; C, *Anopsilana browni,* frontal lamina and clypeus; D, *Anopsilana browni,* frontal lamina and clypeus from more ventral position than in C; E, *Anopsilana jonesi,* frontal lamina and clypeus; F, *Anopsilana browni,* lateral view of anterior cephalon.

Remarks.—Of the 14 known species of *Anopsilana,* six are blind and are found in caves, wells, or springs. The present new species can be separated from the remaining non-anchialine Atlantic and eastern Pacific cogeners (except *A. oaxaca* Carvacho & Haasmann, 1984), by the morphology of the frontal lamina. In *A. jonesi* Kensley, 1987 (from Belize), the frontal lamina is pentagonal, while the projecting, rounded frontal lamina of *A. browni* (Van Name, 1936) (from Cuba, Belize, and Pacific Costa Rica) clearly identifies that species. The new species from the Caribbean is obviously very closely related to *A. oaxaca* from the Pacific coast of Mexico. The frontal laminae are similar when viewed with a light microscope. Scanning electron microscopy, however, reveals that the frontal lamina of *A. oaxaca* is nearly square, with a length/width ratio of 1.2 instead of 1.7, and is slightly widened distally. *Anopsilana oaxaca* is stouter in shape, with the body length 2.5 times the maximum width. Differences between the two species can be seen in spination of the uropods, the number of articles of the antennal and antennular flagellae (fewer in the new species in all cases), in the number of setae on maxilla 2, the shape of the apex of the pleotelson (more narrowly rounded in *A. oaxaca*) and in the general pigmentation pattern. The copulatory stylet is proportionately longer in *A. sinu*: 25–35% longer than the endopod in *A. oaxaca* and nearly twice the endopodal length in the new species. Given these subtle yet consistent differences, *Anopsilana oaxaca* and *A. sinu* may represent geminate species on either side of the Central American isthmus.

Etymology.—The specific epithet is taken from the type locality, the Rio Sinu, Colombia.

Family Sphaeromatidae
Paraimene charlesae, new species
Figs. 7, 8

Material.—Holotype, USNM 252774, ♂ tl 3.1 mm, Paratypes, USNM 252775, 2 ovig. ♀, tl 3.1 mm, 2 juv., sta K-DOM-19, Grand Bay, Dominica, algal turf including branching corallines and *Dictyota,* on boulders, 0.5 m, coll. BK & MS, 18 Nov 1992.—USNM 252776, 1 juv., sta K-DOM-1, Portsmouth, Dominica, encrusting algae on intertidal concrete blocks, coll. BK, 22 Mar 1989.—USNM 252777, ovig. ♀ tl 3.0 mm, sta K-DOM-4, Calabishie, Dominica, intertidal/shallow infratidal algal turf on beachrock platform, coll. BK, 22 Mar 1989.—USNM 252778, 4 ♀ tl 3.1 mm, sta K-DOM-15, Scots Head, Dominica, algal turf on subtidal boulders, coll. BK & MS, 17 Nov 1992.—USNM 252779, 7 juv., Man o' War Bay, Tobago, 1 m plankton tow, coll. R. Heard, 6 Apr 1992.

Diagnosis.—Pleotelson of male basally inflated with one pair of small, and 2 pairs large rounded tubercles. Pleotelson of female having only 2 pairs of rounded tubercles; apex narrower than in male. Accessory dactylar spine of pereopods bilobed. Copulatory stylet of pleopod 2 in male slender, reaching by half its length beyond apex of endopod. Uropodal endopod of female with short mesiodistal lobe.

Description.—Mature male: Body length about 1.9 times greatest width; dorsal integumental surface smooth, with few scattered short setae. Cephalon roughly semicircular, domed, lacking ridges, tiny rostral point not visible dorsally; epistome anteriorly broadly rounded, with short diverging arms embracing labrum; eyes large, dorsolateral. Pereonal tergites unornamented; pereonite 6 with posteriorly projecting trilobed narrow ridge; pereonite 7 unornamented, much shorter than, and overlapped laterally by 6. Pleon consisting of single short free pleonite plus pleotelson, latter anteriorly bulbous, bearing one small and 2 large tubercles on each side; posterior half tapering rapidly to narrowly rounded apex.

Antennule with broad basal article subequal in length to articles 2 and 3; flagellum of 7 articles, equal in length to 2 distal peduncle articles, second flagellar article with 2 aesthetascs, articles 3–5 each with single

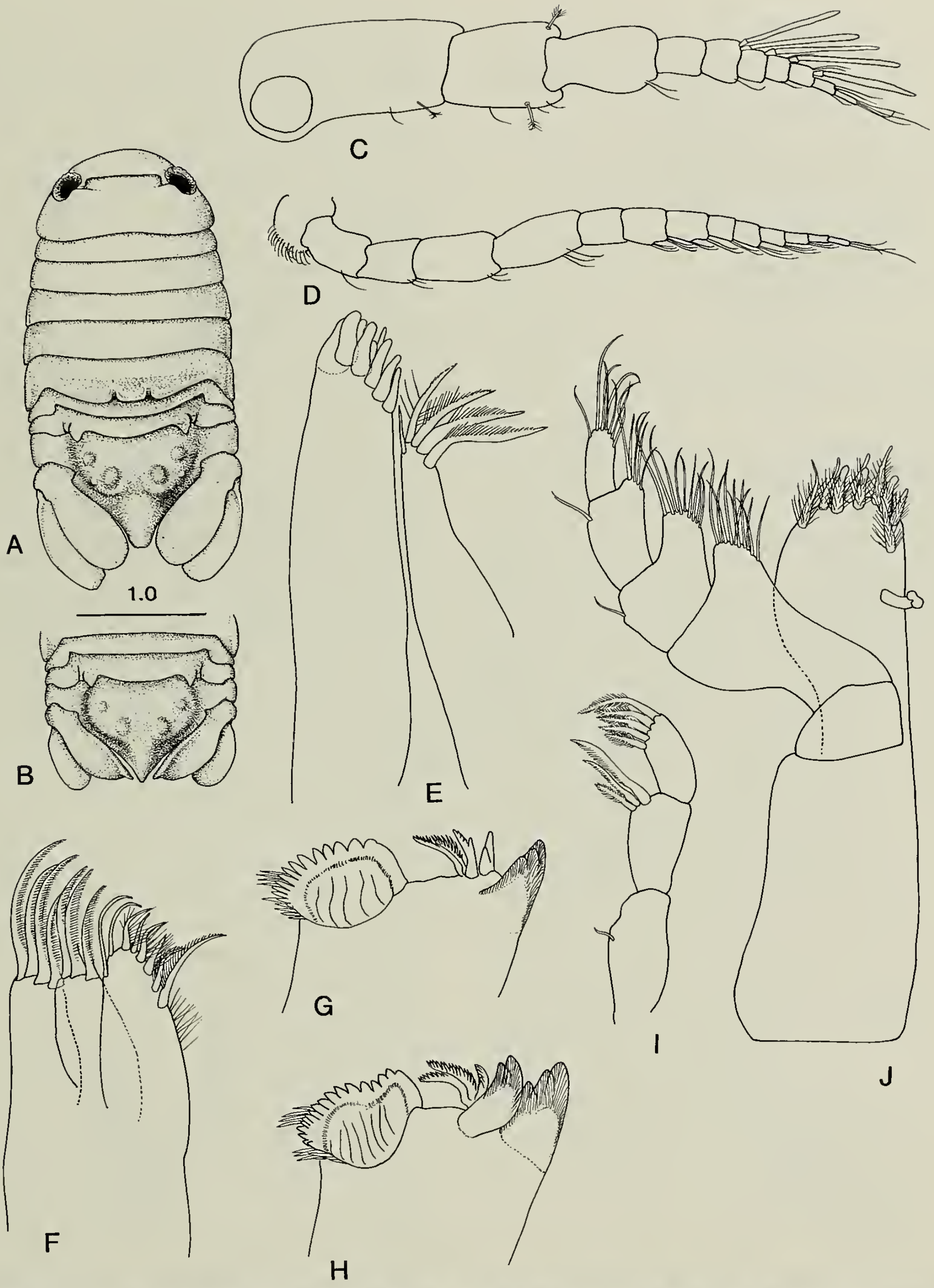

Fig. 7. *Paraimene charlesae*. A, male in dorsal view; B, female pleon in dorsal view; C, antennule; D, antenna; E, maxilla 1; F, maxilla 2; G, left mandible; H, right mandible; I, mandibular palp; J, maxilliped.

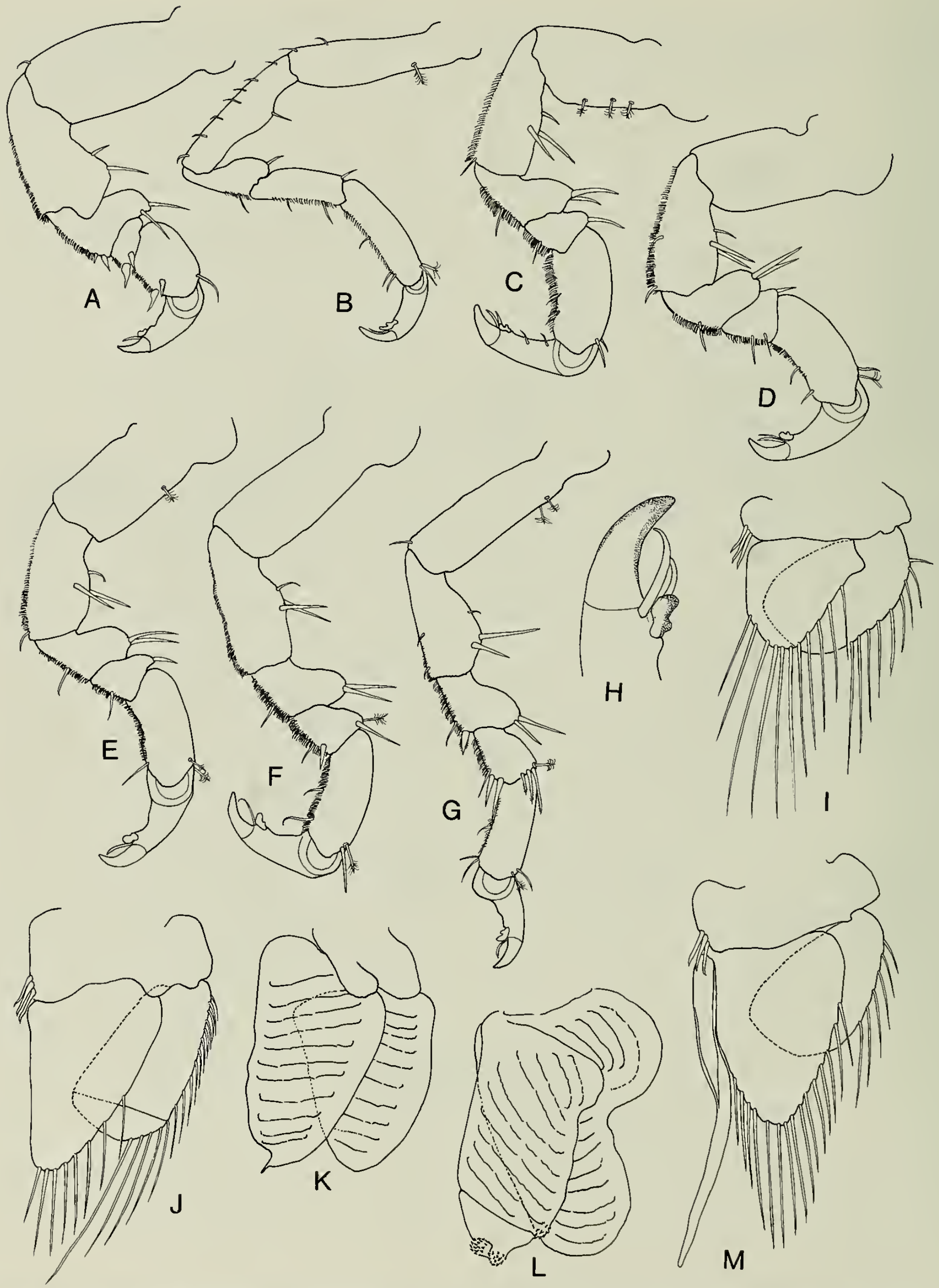

Fig. 8. *Paraimene charlesae.* A, pereopod 1; B, pereopod 2; C, pereopod 3; D, pereopod 4; E, pereopod 5; F, pereopod 6; G, pereopod 7; H, pereopodal dactylar unguis and accessory spine; I, pleopod 1; J, pleopod 3; K, pleopod 4; L, pleopod 5; M, pleopod 2.

aesthetasc. Antenna subequal in length to antennule, peduncular articles relatively slender, increasing in length distally; flagellum of 9 setose articles. Mandible with sclerotized incisor of 3 cusps; sclerotized lacinia mobilis of 2 cusps; spine row of 4 serrate to fringed spines; molar broad, truncate, with marginal teeth; palp of 3 articles, article with 3 distolateral fringed setae; article 3 with distolateral row of 5 fringed setae. Maxilla 1, inner ramus with 4 stout fringed setae; outer ramus bearing about 9 blunt nondentate spines. Maxilla 2, inner ramus with 6 fringed setae on distomesial margin and 2 simple setae distolaterally; both lobes of outer ramus bearing 4 curved fringed spines. Maxillipedal endite broad, with single coupling hook on mesial margin, distal margin bearing 9 stout fringed setae; palp of 5 articles, articles 2–4 each with well developed distomesial setose lobe. Pereopods increasing in length posteriorly, having short setulose pile on posterior surfaces of ischium, merus, carpus, and propodus. Pereopod 1 with merus, short carpus, and propodus each with 2 squat setae posterodistally; squat, broadly bilobed accessory spine at base of dactylus. Pereopod 2 markedly more slender than pereopods 1 or 3. Pereopods 3–7 essentially similar, with 3 setae on anterior surface of ischium, 2 on merus, one on carpus. Penes on sternite 7 short, stubby, distally rounded. Pleopod 1, basis short, with 3 distomesial coupling hooks; endopod roughly triangular, mesial margin straight; exopod elliptical. Pleopod 2, basis roughly rectangular, with 3 distomesial coupling hooks; endopod triangular, with narrow, tapering copulatory stylet articulating basally, twice length of ramus; exopod elliptical. Pleopod 3 basis broadly rectangular, with 3 distomesial coupling hooks; endopod triangular; exopod roughly elliptical with transverse suture in distal fifth. Pleopod 4, both rami membranous, having transverse pleats, endopod distally acute. Pleopod 5, both rami membranous, with transverse pleats, exopod with distal transverse suture and 3 spinulose bosses. Uropodal rami subequal, distally rounded, reaching well beyond pleotelsonic apex.

Ovigerous female: Differing from male in lacking trilobed ridge on tergite of pereonite 6; bulbous anterior region of pleotelson with 2 rather than 3 tubercles on each side; pleotelsonic apex more narrowly acute than in male; uropodal endopod distomesially slightly lobed and upturned against pleotelson.

Color.—Dorsally with mottled or reticulate grey-brown pigment, pleotelson often solidly pigmented.

Remarks.—The present material agrees in several features with the diagnosis of *Paraimene* Javed & Ahmed, 1988, and with its single species *P. tuberculata* recorded from the coast of Pakistan. This agreement is seen in the mouthparts structure, the coxa of pereopod 6 almost completely overlapping that of 7, the bifid accessory dactylar spine of the pereopods, the structure of the penes, the pleotelsonic structure, the pleopods (including the structure of the copulatory stylet, the transverse suture of the exopod of pleopod 3, and the acute apex of the exopod of pleopod 4), and the uropods. Apart from specific differences in the pleotelsonic tuberculation, and the structure of the tergite of pereonite 6, two features that could be considered of generic importance require comment. In *P. tuberculata* the coxa of pereopod 7 is described as forming a dorsally curved narrow tubular structure overlapped by the coxa of pereopod 6. In the present species, the coxa of pereopod 7 is subtriangular, with its narrow apex just visible beyond the coxa of pereopod 6. The second pereopod in both male and female is markedly more slender and less sclerotized than either pereopods 1 or 3. This condition is less marked in juveniles. What the function of this modification can be, is unknown.

Each of the four samples of this species from Dominica came from dense algal turfs growing on concrete blocks, boulders, or flat beachrock in the intertidal or shallow infratidal zone.

Etymology.—The species is named for The Honorable Mrs. Eugenia Charles, Prime Minister of Dominica, and strong supporter of nature conservation.

Pseudocerceis latistylis, new species
Figs. 9, 10, 11

Material.—Holotype, USNM 252780, ♂ tl 3.9 mm, Paratypes, USNM 252781, 3 ♂, tl 3.9 mm, sta K-DOM-11, Portsmouth, Dominica, algal turf on boulders, 2–3 m, coll. BK & MS, 16 Nov 1992.—Paratypes, USNM 252782, ♀ tl 3.4 mm, sta K-DOM-1, Portsmouth, Dominica, algal turf on intertidal concrete blocks, coll. BK, 22 Mar 1989.—Paratypes, USNM 252783, ♂ tl 3.6 mm, ♀ tl 3.9 mm, 4 juv., sta K-DOM-10, Portsmouth, Dominica, coral rubble between coral heads and boulders, 2–3 m, coll. BK & MS, 16 Nov 1992.—USNM 252784, 6 juv., sta K-DOM-21, Grand Bay, Dominica, rubble and coarse sediments between boulders, 2–3 m, coll. BK & MS, 18 Nov 1992.

Diagnosis.—Rounded apex of frontal lamina dorsally visible. Pleotelson in male basally inflated, bearing 3 ridges; apex notched. Pleotelson in female basally inflated, bearing 3 ridges; posterior region less expanded than in male, apex broadly rounded. Copulatory stylet of pleopod 2 in male basally broad, folded on itself. Uropodal exopod in male much longer than endopod, tapering to narrowly rounded apex. Uropodal exopod in female lamellar, subequal to endopod.

Description.—Mature male: Body length about 2.5 times greatest width; dorsal integumental surface irregularly rugose. Cephalon roughly semicircular, somewhat flattened, with low rounded lateral, and faint anteromedian ridge; epistome of cephalon anteriorly narrowing to subcircular dorsally-visible apex; eyes large, dorsolateral. Pereonal tergites lacking ridges or ornamentation; pereonite 1 about twice length of 2; pereonites 2–7 subequal in length. Pleon having 2 lateral incisions demarking fused pleonites; broad anterior half having series of low rounded lateral and submedial ridges posteriorly, median region unridged; posterior half having low rounded median, and pair of smaller lateral bosses. Pleotelson with anterior half broadly rounded, with median and two lateral ridges defining central area; posterior half having narrow rounded raised area, posterior margin broadly notched.

Antennule with broad basal article subequal in length to following 3 articles, article 3 narrow-elongate; flagellum of 7 articles, articles 4–6 each having single aesthetasc, terminal article bearing 2 aesthetascs. Antenna subequal in length to antennule, peduncular articles relatively slender, increasing in length distally; flagellum of 8 articles. Mandible with sclerotized incisor of 3 cusps; sclerotized lacinia mobilis of 3 cusps; spine row of 5 stout serrate spines; molar broad, truncate, with marginal teeth; palp of 3 articles, article 2 bearing 4 fringed distal setae, article 3 bearing row of 10 fringed setae increasing in length distally. Maxilla 1, inner ramus bearing 4 stout fringed apical setae; outer ramus bearing about 9 dentate apical spines. Maxilla 2, inner ramus with 7 fringed setae distally; inner and outer lobe in outer ramus each with 6 distal dentate spines. Maxillipedal endite broad, with single coupling hook on mesial margin, distal convex margin bearing about 7 short fringed setae; palp of 5 articles, 2–4 with well developed mesiodistal lobes bearing distal setae. Pereopods increasing in length posteriorly; pereopod 1, merus having pile of short setules and single fringed seta on posterior surface; carpus having almost no free anterior margin, having 2 fringed setae on posterior margin; propodus bearing 2 fringed setae on posterior margin; dactylus having short strong tooth at base of unguis. Pereopods 2–7 similar, with merus, carpus and propodus having pile of short setules and 2 more elongate setae on posterior margins; dactyli

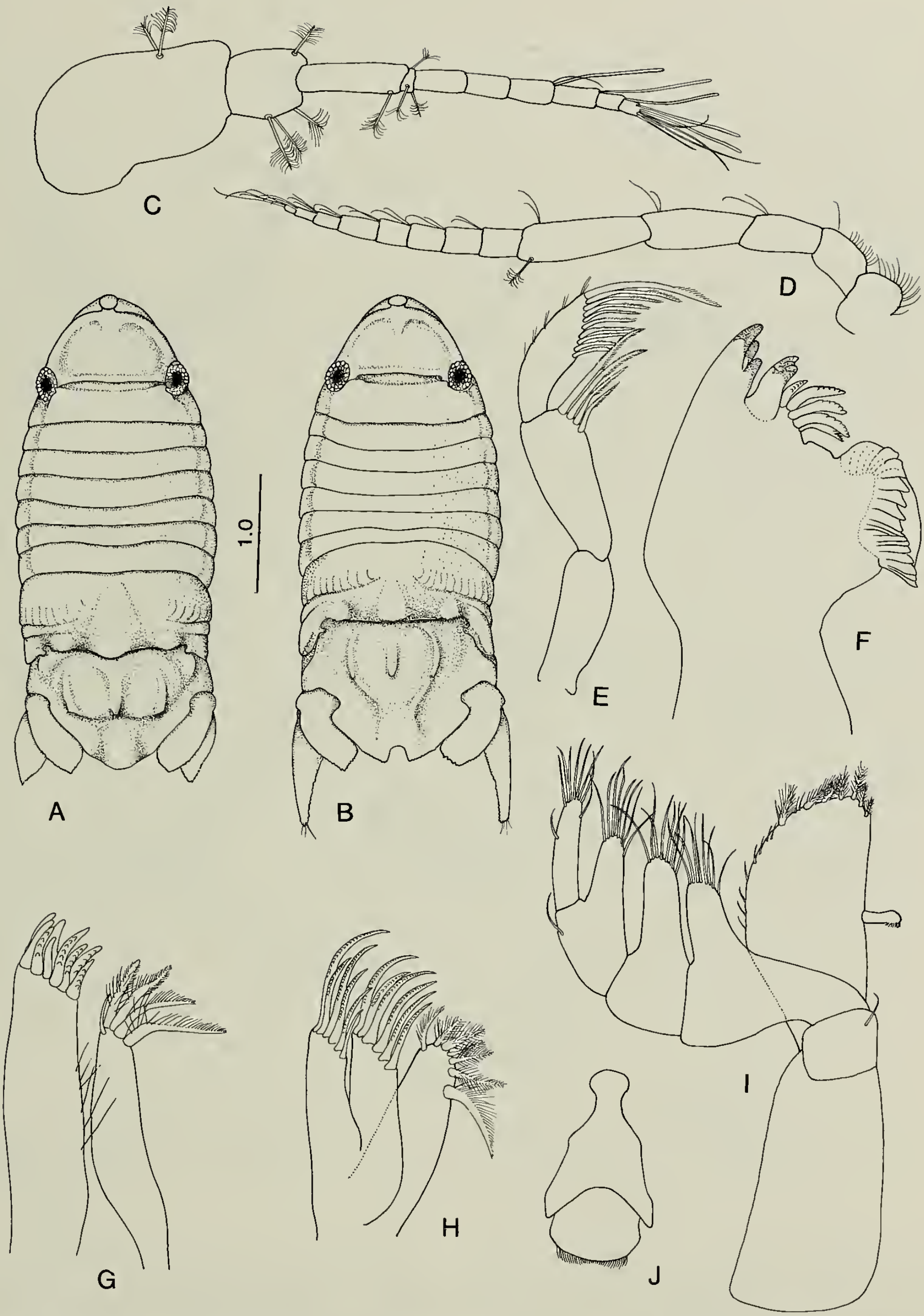

Fig. 9. *Pseudocerceis latistylis.* A, female in dorsal view; B, male in dorsal view; C, antennulae; D, antenna; E, mandibular palp; F, mandible; G, maxilla 1; H, maxilla 2; I, maxilliped; J, frontal lamina and clypeus.

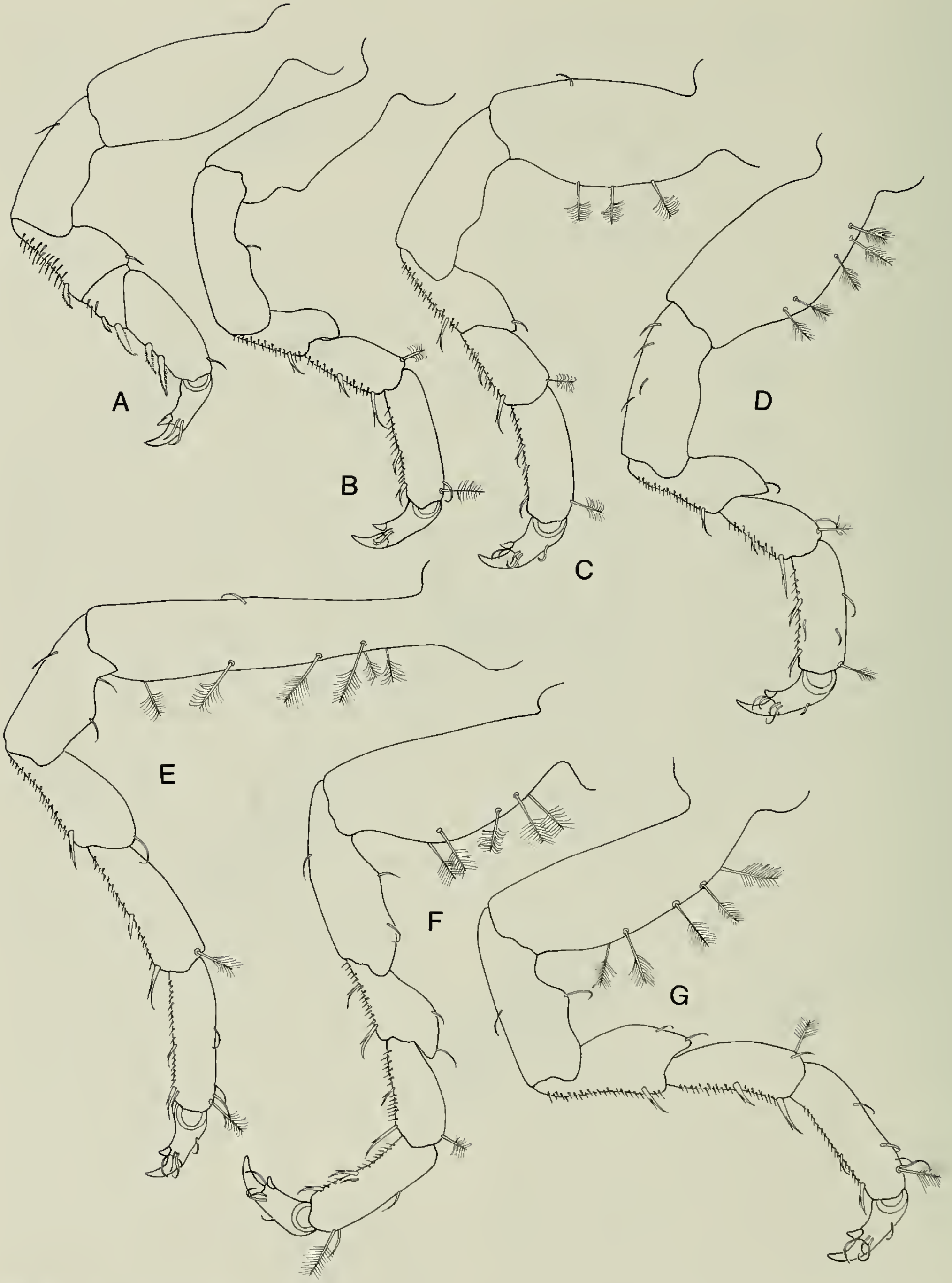

Fig. 10. *Pseudocerceis latistylis.* A, pereopod 1; B, pereopod 2; C, pereopod 3; D, pereopod 4; E, pereopod 7; F, pereopod 5; G, pereopod 6.

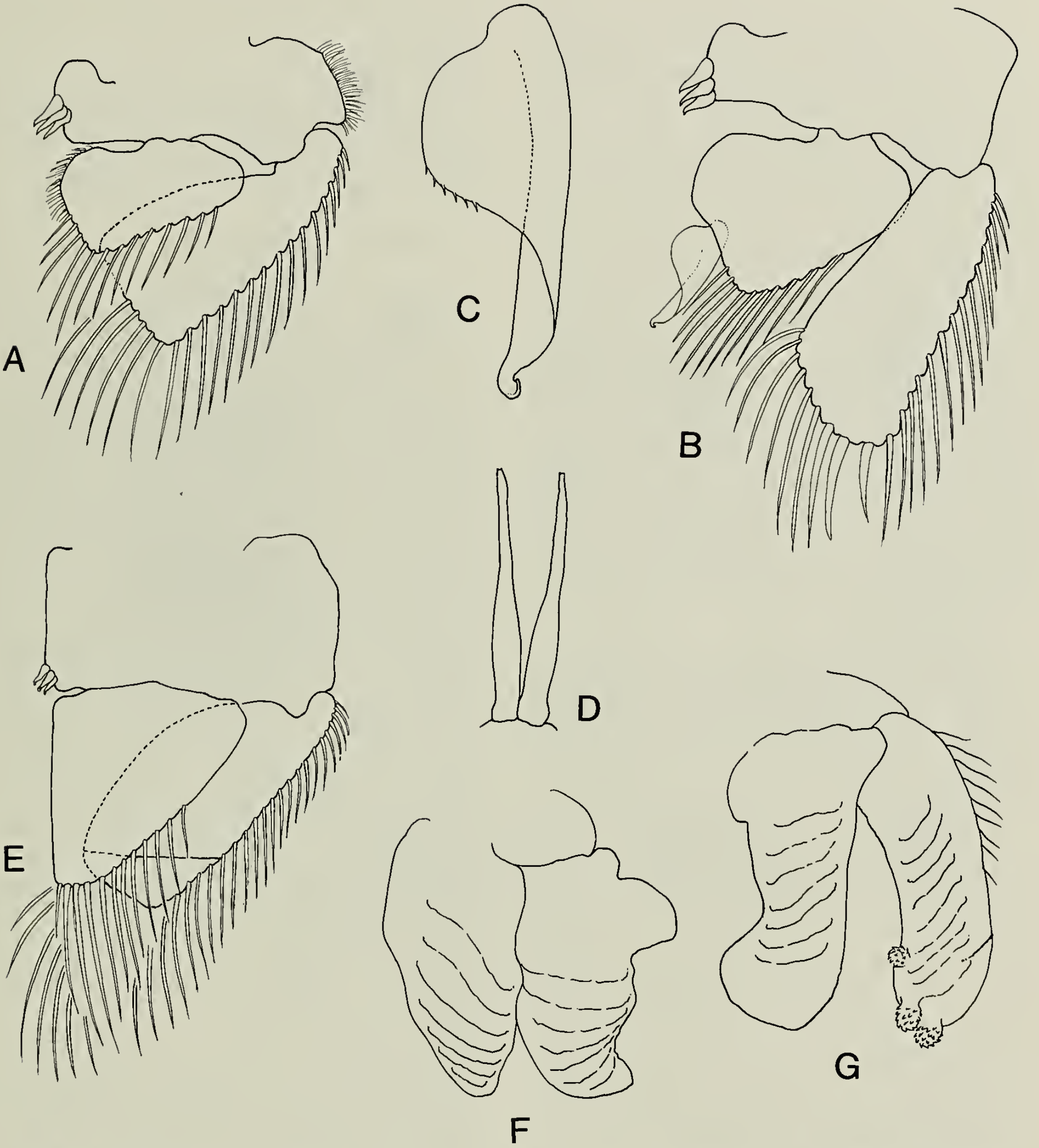

Fig. 11. *Pseudocerceis latistylis.* A, pleopod 1; B, pleopod 2 ♂; C, copulatory stylet enlarged; D, penes; E, pleopod 3; F, pleopod 4; G, pleopod 5.

having short strong accessory tooth at base of unguis. Penes on sternite of pereonite 7 elongate-slender, tapering, basally contiguous, separated from bases of pleopod 1 by transverse band of cuticle bearing elliptical region on each side of midline. Pleopod 1, basis broadly rectangular, with 3 mesiodistal coupling hooks; endopod triangular, mesial margin straight; exopod elliptical, with oblique distal suture. Pleopod 2, basis with 3 mesiodistal coupling hooks; endopod bearing copulatory stylet at midlength of mesial margin, stylet having broad basal flap folding over open gutter of stylet, apex rounded, slightly sclerotized; exopod elliptical, lacking transverse suture. Pleopod 3, basis with 3 mesiodistal coupling hooks; endopod much smaller than exopod, roughly elliptical but mesially truncate; exopod with mesial margin truncate, lacking transverse suture. Pleopod 4, both rami membranous, having transverse pleats. Pleopod 5, both rami membranous, having transverse pleats, exopod with incomplete distal transverse suture, bearing one subterminal and 2 terminal spinose bosses. Uropodal basis fused with endopod, latter distally flattened, reaching beyond level of pleotelsonic apex, distal margin somewhat truncate and finely but irregularly denticulate; exopod basally flattened, somewhat scooped, tapering distally, mesial margin finely denticulate, reaching by more than half its length beyond pleotelsonic apex.

Non-ovigerous female: Differing from male only in pleotelson, which lacking apical notch, and in uropod, in which flattened exopod not elongate as in male but subequal in length to endopod, distally acute, margins denticulate.

Remarks.—Using Harrison and Ellis's 1991 key to the sphaeromatid genera, the present species falls into the *Cerceis* group, characterized by the possession of a sternal cuticular band with submedial elliptical areas between the penes and the bases of pleopod 1. The character of the epistome being visible in dorsal view leads to the genus *Pseudocerceis.* The species does possess moderately dentate margins of pleopods 1–3, and generally agrees with the generic diagnosis (Harrison & Holdich 1982:428). The unusual structure of the copulatory stylet of pleopod 2, with its basally broadened and overlapping flap, is not seen in *Pseudocerceis.* Whether this feature is of sufficient strength to warrant the creation of a separate genus is unclear. *Pseudocerceis* is known from four species, from the intertidal of eastern and southern Australia, and East Africa. If indeed a *Pseudocerceis,* this is the first record of the genus from the Atlantic Ocean.

Etymology.—The specific epithet is derived from the Latin *latus*—broad, plus *stylus,* referring to the broad-based copulatory stylet of the male second pleopod.

Sphaeromopsis heardi, new species
Figs. 12, 13

Material.—Holotype, USNM 252785, ♂ tl 2.0 mm, Paratypes, USNM 252786, 3 ♀ tl 1.7–1.9 mm; 2 juvs., sta K-DOM-1. Portsmouth, Dominica, algal turf on intertidal concrete blocks, coll. BK, 22 Mar 1989.—Paratype, USNM 252787, ♂ tl 2.0 mm, sta K-DOM-9, Portsmouth, Dominica, rubble between coral heads and boulders, 1–2 m, coll. BK & MS, 16 Nov 1992.—Paratypes, USNM 252788, ovig. ♀ tl 2.0 mm, sta K-DOM-26, Calibishie, Dominica, algal turf on intertidal beach rock, coll. BK & MS, 19 Nov 1992.—USNM 252789, 5 ♀ tl 1.9 mm, 4 juv., sta K-DOM-25, Calibishie, Dominica, rubble between boulders, 0.5 m, coll. BK & MS, 19 Nov 1992.—USNM 252790, 9 juv., Man o' War Bay, Lovers Beach, Tobago, coll. R. Heard, 6 Apr 1992.—USNM 252791, 26 juv., Buccoo Reef, Tobago, 1 m, coll. R. Heard, 11 Jan 1993.—USNM 252792, 40+ juv., Pigeon Point, Tobago, sand, 1 m, coll. R. Heard, 15 Jan 1993.

Diagnosis.—Cephalon and pereonites having somewhat rounded, strongly pitted ridge close to posterior margin. Pleotelson in male and female similar, basal half having 2 roughly rectangular raised areas bearing low scattered tubercles; posterior area smooth, apex evenly rounded.

Description.—Mature male: Body length about 1.9 times greatest width. Cephalon broader than long, moderately convex, rounded rostral projection visible in dorsal view; epistome linguiform, with apex contiguous with rostrum, dorsally visible; posterior margin between large pigmented eyes

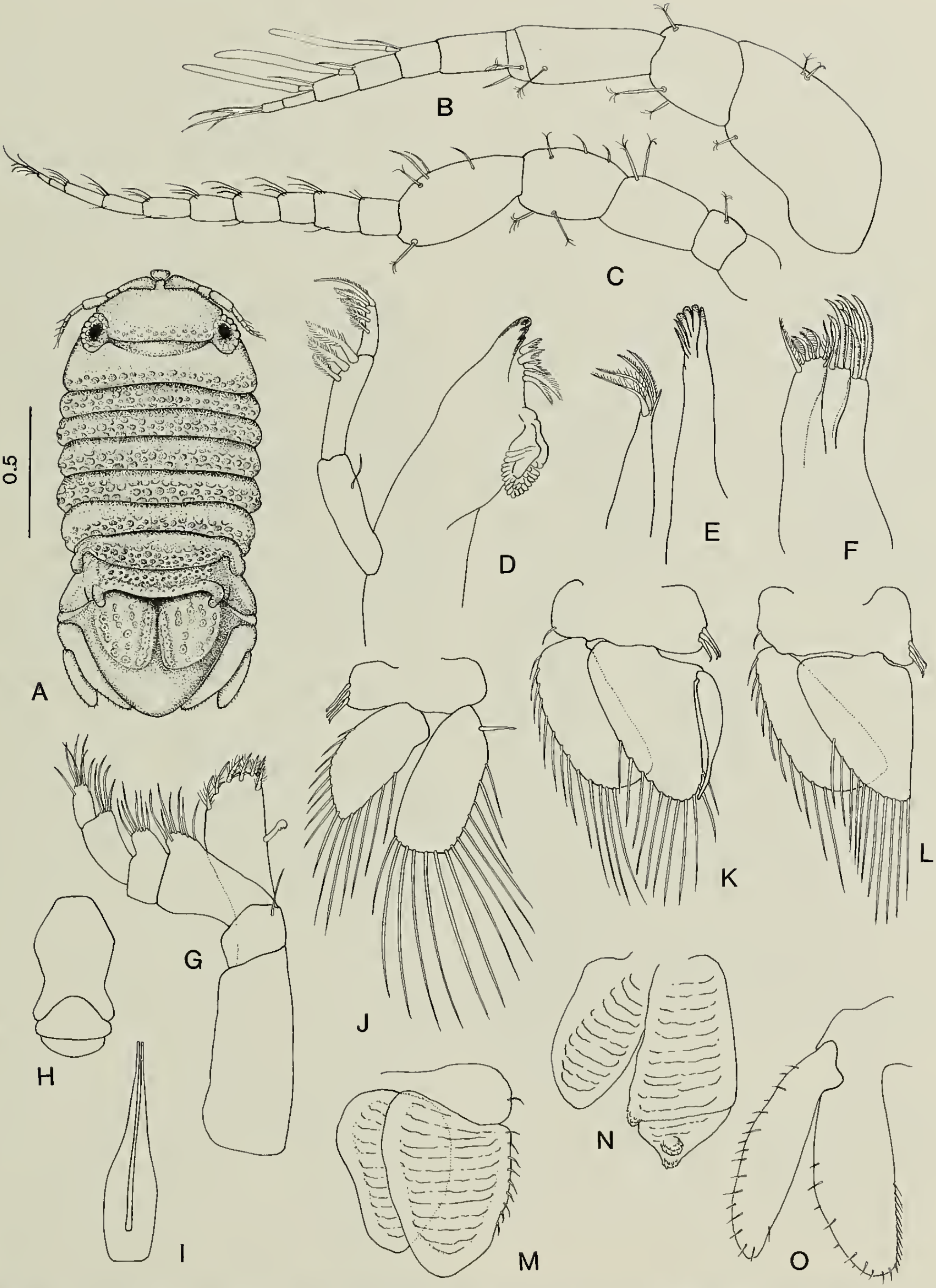

Fig. 12. *Sphaeromopsis heardi.* A, male in dorsal view; B, antennule; C, antenna; D, mandible; E, maxilla 1; F, maxilla 2; G, maxilliped; H, frontal lamina and clypeus; I, penes; J, pleopod 1; K, pleopod 2; L, pleopod 3; M, pleopod 4; N, pleopod 5; O, left uropod.

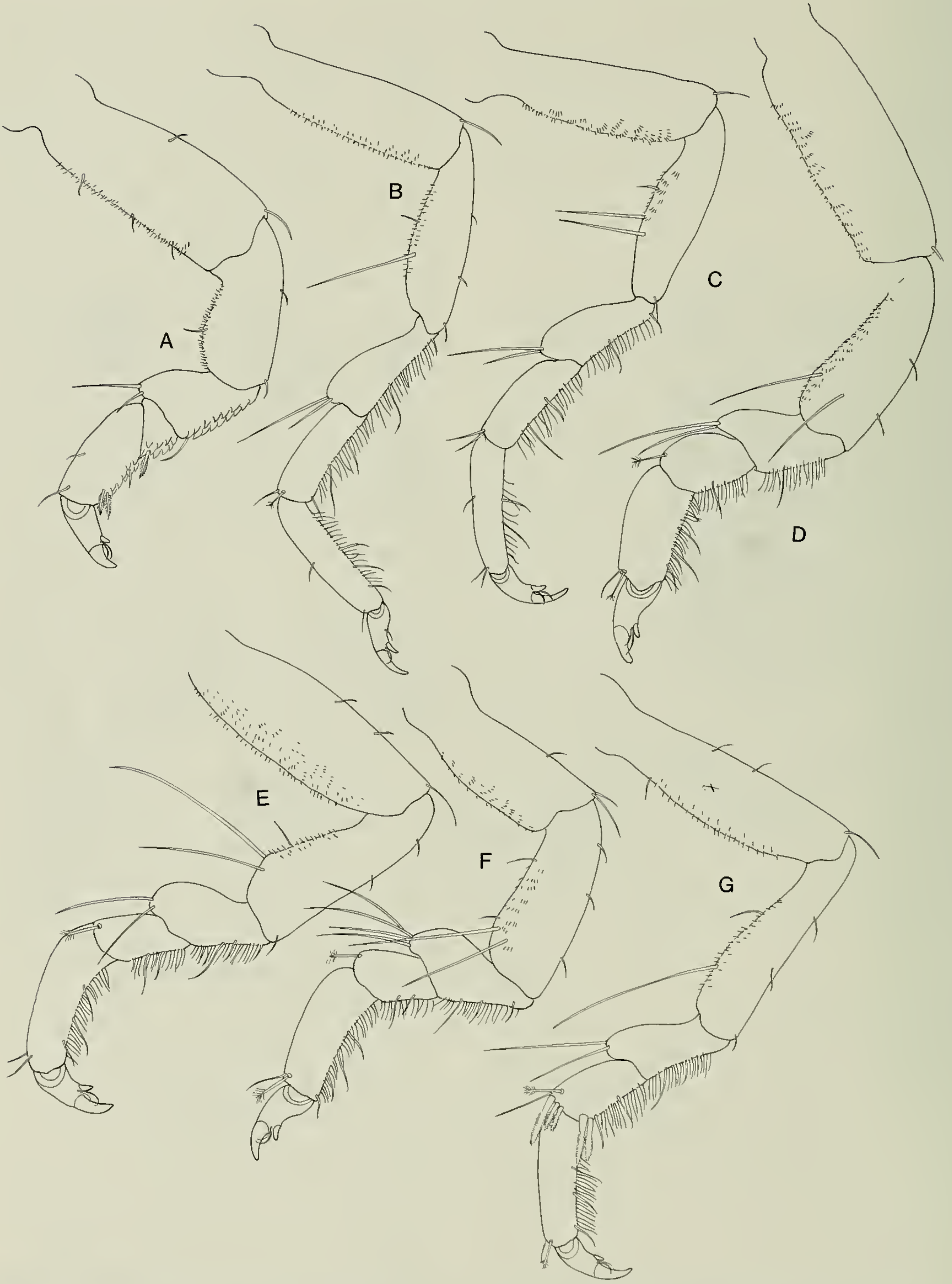

Fig. 13. *Sphaeromopsis heardi.* A, pereopod 1; B, pereopod 2; C, pereopod 3; D, pereopod 4; E, pereopod 6; F, pereopod 5; G, pereopod 7.

rounded, pitted. Pereonal tergites each with transverse rounded and pitted ridge near posterior margin. Pleon with single free pleonite having 2 short suture lines reaching posterior margin, bearing two transverse pitted ridges. Pleotelson broadly triangular, apex broadly rounded; dorsally with 2 broad, raised subrectangular areas bearing scattered low pitted tubercles.

Antennule with broad basal article, proximally slightly flexed, subequal in length to articles 2 and 3 together; flagellum of 7 articles; articles 3–6 each bearing single aesthetasc. Antenna with peduncle articles 1 and 2 short, subequal, together subequal to article 3; articles 3 and 4 subequal, slightly shorter than article 5; flagellum of 10 setose articles. Mandible with sclerotized incisor of 3 cusps, spine row of 5 fringed spines, molar with numerous marginal teeth; palp with 3 distal fringed setae on article 2, 5 fringed setae on article 3. Maxilla 1, inner ramus with 4 fringed setae; outer ramus bearing 4 distally blunt spines plus several slender fringed spines. Maxilla 2, inner ramus with 7 setae on distal margin; both lobes of outer ramus bearing 4 curved fringed spines. Maxillipedal endite broad, with single coupling hook on mesial margin, distal margin bearing 7–9 stout fringed setae; palp of 5 articles, articles 2–4 each with low rounded setose distomesial lobe; article 5 short, setose. Pereopods increasing in length posteriorly, having short scattered setules on anterior margins of basis and ischium; pereopods 2–7 having pile of fine relatively elongate setules on posterior margins of merus, carpus and propodus. Pereopod 1, merus, carpus, and propodus with acute scales on posterior surface; carpus triangular, with very short free anterior margin, single posterodistal fringed seta; propodus with 2 posterodistal fringed setae; dactylus with short blunt accessory spine at base of unguis. Pereopod 2 longer and more slender than pereopod 1; pereopods 2–7 similar, ischium with 1 or 2 elongate setae on anterior margin; merus with 2–4 elongate setae on anterior margin. Pereopod 7, carpus having several anterodistal and posterodistal stout fringed setae. Penile rami on sternite 7 basally fused, rami tapering to narrow apices. Pleopod 1, basis short, with 3 distomesial coupling hooks; endopod narrowly triangular, exopod roughly rectangular, with stout stiff seta proximally. Pleopod 2, endopod triangular, with narrow tapering copulatory stylet articulating basally, just reaching apex of ramus; exopod roughly rectangular. Pleopod 3, basis broadly rectangular, with 3 coupling hooks; endopod triangular; exopod roughly ovate. Pleopod 4, both rami having transverse pleats, basally broad, gently tapering to rounded apices. Pleopod 5, both rami having transverse pleats, exopod longer than endopod, with transverse suture distally, bearing 3 spinulose bosses. Uropodal rami subequal in length, endopod narrower than endopod, both rami apically rounded.

Female: Cephalon, pereon, and pleon as in male.

Remarks.—The genus *Sphaeromopsis* Holdich & Jones, 1973, contains four species, only one of which is from the Atlantic, viz. *S. mourei* (Loyola e Silva 1960) from Brazil (see Holdich & Harrison 1981). While agreeing with the Brazilian species in almost all details of the frontal lamina, mouthparts, and appendages, the present species, which is about half the size of *S. mourei*, can immediately be distinguished by the very distinctive ornamentation of the pleotelson, and by the pitted transverse ridges of the pereonal tergites.

Etymology.—The species is named for Dr. Richard Heard of the Gulf Coast Research Laboratory, Ocean Springs, Mississippi, respected colleague and indefatigable collector.

Suborder Valvifera
Family Astacillidae
Astacilla marna, new species
Figs. 14, 15

Material.—Holotype, USNM 252793, ♂ tl 3.5 mm, Paratypes, USNM 252794, 3 ♂

tl 3.5 mm, 2 ovig. ♀ tl 4.4 mm, ♀ tl 4.0 mm, 3 juv., sta K-DOM-20, Grand Bay, Dominica, algal turf with sponges on boulders, 3–5 m, coll. BK & MS, 18 Nov 1992.—Paratypes, USNM 252795, ♂ damaged, ovig. ♀ tl 4.9 mm, sta K-DOM-11, Portsmouth, Dominica, algal turf on boulders, 3–5 m, coll. BK & MS, 16 Nov 1992.

Diagnosis.—Male and female having single strong medial tubercle on cephalon. Pereonite 4 in male elongate, unarmed; in female having raised tuberculate area at about midlength. Pleon lacking free anterior pleonites. Antennal flagellum consisting of 3 spinose articles.

Description.—Male: Body elongate-cylindrical, geniculate, between pereonites 4 and 5. Integument sparsely setose. Cephalon with anterior margin concave, anterolateral lobes well produced, rounded in lateral view; dorsolateral eyes large, well pigmented, subcircular; strong conical dorsal tubercle present above eye. Pereonite 1 fused with cephalon, line of fusion marked by slit in ventral margin. Pereonites 2 and 3 unornamented. Pereonite 4 cylindrical, about 4 times longer than wide, lacking ornamentation. Pereonites 5–7 decreasing in length posteriorly, irregularly rugose but lacking clearly defined tubercles or spines. Pleotelson with 2 anterior fused pleonites weakly indicated dorsally; apex rounded.

Antennule of 4 articles, basal article longer and broader than articles 2 and 3, with blunt conical tubercle dorsally; flagellum subequal in length to three basal articles, bearing row of about 15 pairs of aesthetascs along ventral surface. Antenna with 2 basal articles short, articles 3–5 elongate-cylindrical, unornamented; flagellum of 3 articles, each bearing row of flattened spines on ventral surface, terminal article also bearing strong curved terminal spine. Mandibular incisor of 4 cusps; lacinia mobilis dentate, distally noticeably bifid; spine row having 2 fringed spines; molar broadly truncate with strong marginal teeth. Maxilla 1, inner ramus bearing 4 distal fringed setae; outer ramus with about 8 sparsely toothed stout spines, feathery setae on mesial margin. Maxilla 2, inner ramus with about 10 mesiodistal fringed setae; inner lobe of outer ramus bearing 2 distal elongate setae, outer lobe with 3 elongate setae. Maxillipedal palp of 5 articles, article 1 short, article 3 longest and widest, articles 2–5 each bearing several fringed setae mesiodistally; endite distally rounded-truncate, with 4 short fringed setae, mesial margin bearing single strong coupling hook, inner surface of mesial area bearing 2 elongate setae. Pereopod 1 with carpus bearing row of finely fringed setae on posterior margin; propodus bearing 5 fringed setae on posterior margin plus several groups of setae on outer surface, single strongly dentate seta distally; dactylus with single elongate finely fringed terminal seta. Pereopods 2–4 similar, lacking dactylus, with propodi, carpi, and meri bearing elongate setae on posterior margins. Pereopods 5–7 stout, prehensile, dactylus strongly biunguiculate. Pleopod 1, basis with 3 retinaculae; exopod subequal in length to endopod, with strong notch in lateral margin having 2 elongate fringed setae; distal margins of both rami bearing 5 or 6 elongate plumose setae. Pleopod 2, basis with 3 retinaculae; exopod shorter than endopod, with 7 plumose setae on distal margin; endopod having 4 plumose setae on distal margin; copulatory stylet stout, articulating near base of endopod, grooved for most of its length, distal third consisting of slender sinuous styliform structure. Pleopod 3, endopod elliptical, lacking marginal setae; exopod shorter than endopod, bearing 2 distal fringed setae. Pleopods 4 and 5 similar, endopod elliptical, lacking marginal setae; exopod shorter than endopod, with single laterodistal fringed seta. Uropod with outer ramus triangular, margins setulose; inner ramus half length and one-third basal width of outer, bearing single strong apical seta.

Female: Integument relatively more tuberculate than in male. Cephalon with strong conical middorsal tubercle, submedian pair

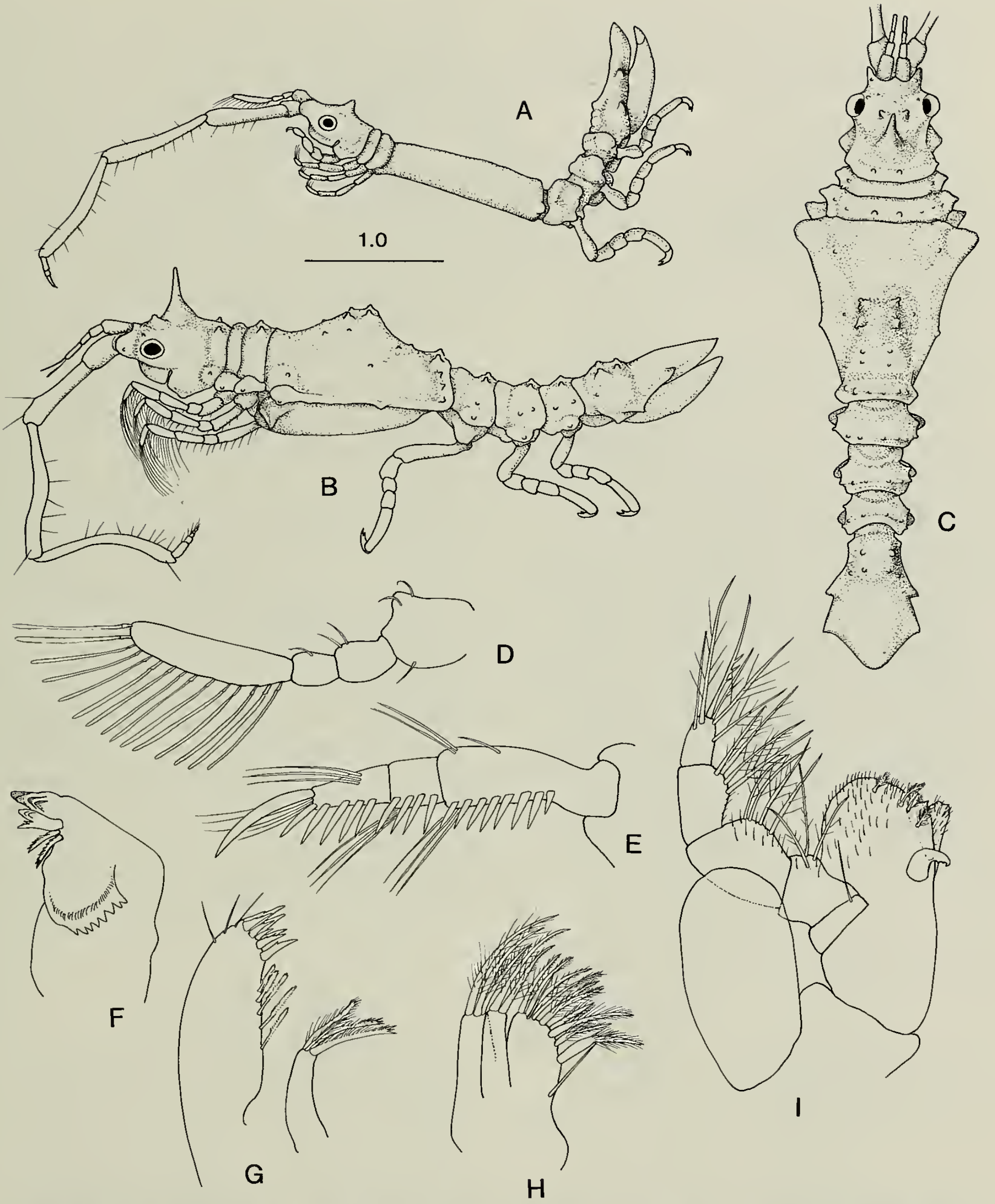

Fig. 14. *Astacilla marna.* A, male in lateral view; B, female in lateral view; C, female in dorsal view; D, antennule; E, flagellum of antenna; F, mandible; G, maxilla 1; H, maxilla 2; I, maxilliped.

of smaller tubercles between eyes; fused pereonite 1 with submedian dorsal pair of small tubercles. Pereonites 2 and 3 with few small scattered tubercles. Pereonite 4, anterior width subequal to midlength, tapering posteriorly in dorsal view, anterolateral corners rounded, with triangular anteroventral tubercle visible in dorsal view; raised area at

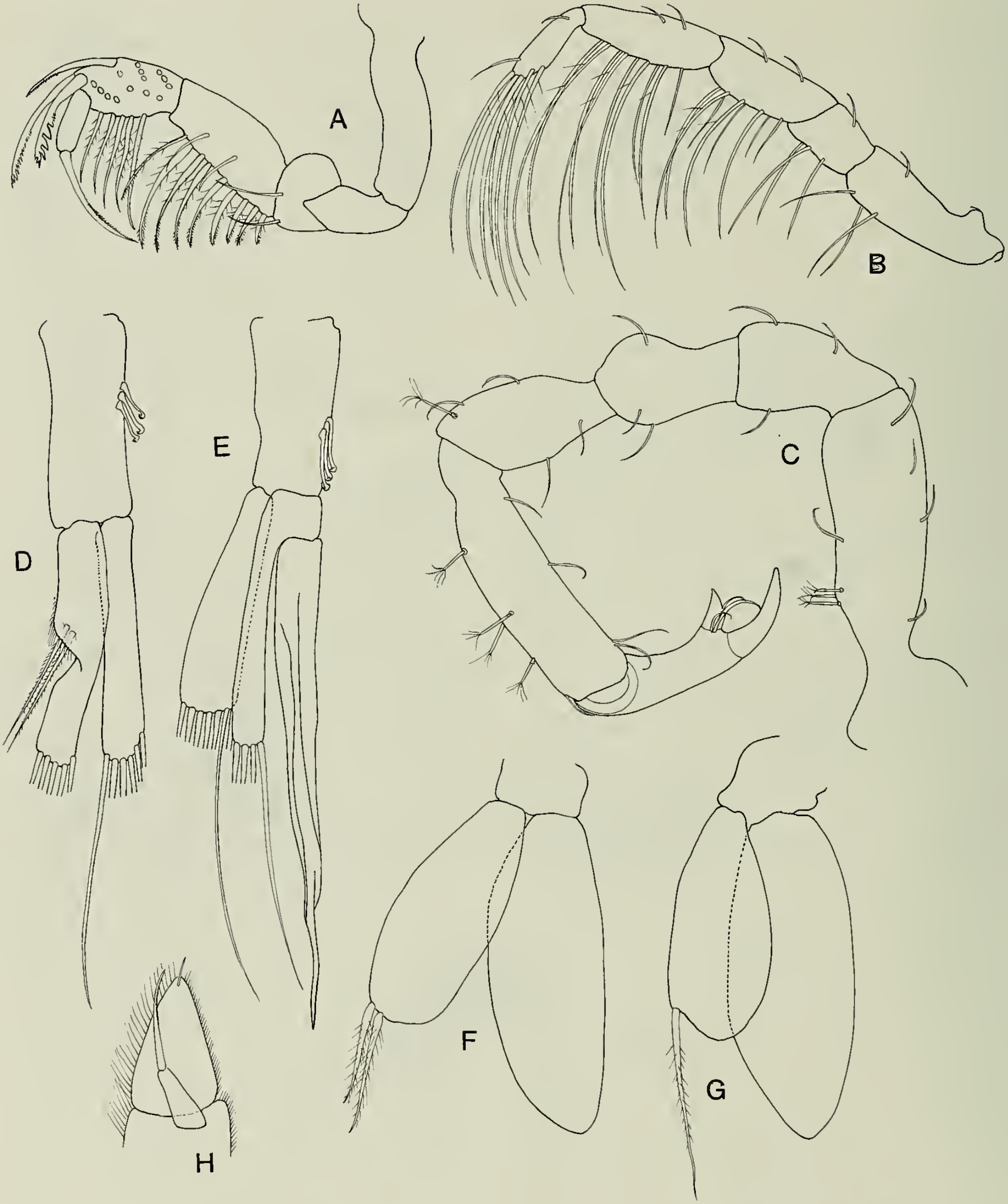

Fig. 15. *Astacilla marna.* A, pereopod 1; B, pereopod 2; C, pereopod 7; D, pleopod 1; E, pleopod 2; F, pleopod 3; G, pleopod 4; H, apex of uropod.

about middle of dorsal surface formed by 4 tubercles arranged in square; several small scattered tubercles on irregular surface of tergum; row of small tubercles along posterior margin. Pereonites 5–7 similar, decreasing in length posteriorly, more tuberculate than in male. Pleotelson as in male.

Remarks.—Of the three species of *Astacilla* known from the Caribbean area, *A. marna* most closely resembles *A. spinata*

(Menzies & Kruczynski, 1983) (=*A. regina* Kensley, 1984, known from Belize, Barbados, and St. Lucia; see Müller 1993c). Many differences separate these two species, most notably in size (*A. spinata* is roughly twice as large as *A. marna*), general body proportions of the male and ovigerous female as well as in ornamentation. Differences in the appendages, e.g., the antennal flagellum (2 non-spinose articles in *A. spinata,* 3 spinose articles in *A. marna*), the setation of the notch of the exopod of pleopod 1 (3 long setae in *A. spinata,* 2 in *A. marna*), copulatory stylet of the male pleopod 2 (apically bifid in *A. spinata,* with a single stylet in *A. marna*), uropodal setation (endopod with two apical setae in *A. spinata,* one in *A. marna*), also easily differentiate these two species.

Arcturella sawayae Moreira, 1973, from the São Paulo region of Brazil and known only from a single ovigerous female, has a strong pair of tubercles on the cephalon, a single strong spinose tubercle on each of pereonites 1–3, lacks middorsal tubercles on pereonite 4, and is over twice the length of *Astacilla marna.*

Etymology.—The species is named for Ms. Marna Disbrow of Vancouver, Canada, whose generosity made the second Dominica fieldtrip possible.

Acknowledgments

We thank Dr. Darryl Felder, University of Southwestern Louisiana, Dr. Richard W. Heard, Gulf Coast Research Laboratory, Mississippi, and Dr. Rafael Lemaitre, Smithsonian Institution, for making material available for study. Ms. Marna Disbrow of Vancouver, Canada, made funds available for a visit to Dominica, as did the Office of the Director, National Museum of Natural History, in support of its membership in the consortium overseeing the Archbold Tropical Research Center. We gratefully acknowledge logistical help from the Marine Fisheries Section of Tobago Fisheries in Scarborough, Tobago. A draft of this paper was read by R. W. Heard; we are grateful for his suggestions for improvements.

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NEW SPECIES OF *ECHINISCUS* (HETEROTARDIGRADA: ECHINISCOIDEA: ECHINISCIDAE) FROM KOREA

Seung Y. Moon and Won Kim

Abstract.—*Echiniscus cheonyoungi,* a new tardigrade species is described. The present new species mainly differs from the other species of the genus *Echiniscus* in the following characteristics: lack of spurs at the base of the internal claws, presence of all lateral cirri and dorsal cirri C^d, D^d, and cuticular plates with double sculpturing consisting of irregular pores and minute closely spaced polygons.

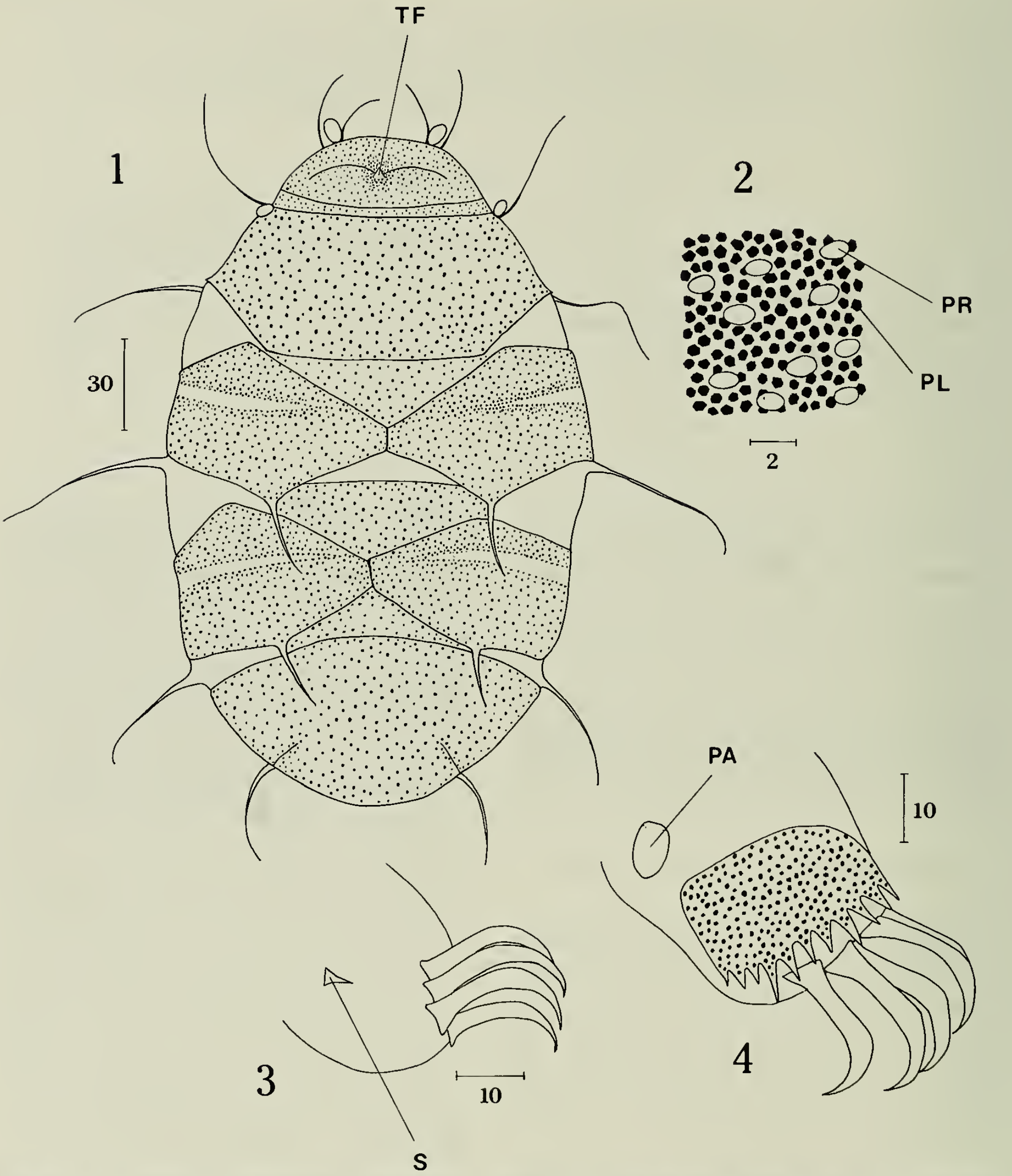
A new species of *Echiniscus* was identified during an investigation of the tardigrades collected from lichens on shaded rocks and the bark of live trees in Korea. Holotype and one paratype are deposited in the Zoological Museum, University of Copenhagen (ZMUC), Denmark, and two paratypes are deposited in the Moon collection, Department of Molecular Biology, Seoul National University, Korea.

Echiniscus cheonyoungi, new species
Figs. 1–4

Material examined.—Holotype (ZMUC TAR 00101) and three paratypes (one paratype, ZMUC TAR 00102). All the type specimens were collected from lichens on shaded rocks and the bark of trees on 27 Jul 1988 from Wŏlch'ulsan (126°42′N, 34°46′E), Chŏllanam-do, Korea.

Description.—Holotype. Body (Fig. 1) light yellow, with length 218 μm. Internal buccal cirri of head 27.5 μm long; external buccal cirri, 31.7 μm long; buccal papillae prominent, 7.3 μm long by 3.3 μm wide, larger than clavae. Cuticular plates (Fig. 2) with double sculpturing consisting of minute, closely spaced polygons and irregular pores except for head and leg plates having only polygons; polygons similar in size (0.3–0.5 μm), but slightly smaller on head and leg plates; pores larger than polygons (0.6–1.6 μm), and more distinct on scapular and terminal plates. Head plate (Fig. 1) having small triangular middorsal field without sculpture. Paired plates 1, 2 (Fig. 1) with transverse stripe of clear zone separating smaller anterior part from posterior part of plate. Median plates undivided. Cuticular sculpture of median plates similar to that of other plates; median plate 3 somewhat subsided compared with other dorsal plates. Terminal plate (Fig. 1) with rather shallow lateral incisions, without terminal facetting. Delineation of all cuticular plates distinct. All lateral cirri A, B, C, D and E (Fig. 1) present. Cirrus A (50 μm) thinner than any other cirri on body, about 0.2 times as long as body length; cirrus B (50 μm) as long as cirrus A; cirrus C (62 μm) longest of all lateral cirri; cirrus D (41 μm) slightly longer than cirrus E; cirrus E (35 μm) shortest of all lateral cirri. Dorsal cirri, C^d (26 μm) and D^d (24 μm) also present and similar in length. Spine (Fig. 3) on leg I a short thorn. Large sized papilla (Fig. 4) on leg IV. Dentate fringe on leg IV (Fig. 4) with about 11 sharp teeth of irregular size, and very finely sculptured without pores. Internal and external claws of legs (Figs. 3, 4) without basal spur; internal claws slightly longer than external claws on all legs.

Variation.—The cirrus C^d was very re-



Figs. 1–4. *Echiniscus cheonyoungi,* new species, holotype. 1, whole animal, dorsal view (TF, triangular middorsal field); 2, surface pattern of cuticle (PR, pore; PL, polygon); 3, spine and claws of leg I (S, spine); 4, dentate fringe and claws of leg IV (PA, papilla). Scales in μm.

duced on the right side of body and absent on the left in one specimen of the three paratypes. The other two paratypes showed no variation.

Etymology.—It is our pleasure to name this species for Dr. Cheon Young Chang, who provided an opportunity for the first author to study tardigrade systematics.

Remarks.—The minute, closely spaced polygons situated under the larger, irregular pores of the cuticle are observed only at the higher magnification with phase-contrast microscopy. Otherwise, they may appear to be just irregular granules.

The sculpture of dorsal plates, the location of cirri or spines on the surface of body, and the claw morphology, particularly the presence and location of secondary or tertiary spurs of claws are considered to have high taxonomic value for identifying species of the genus *Echiniscus* (see Kristensen 1987). The present new species is close to *Eschiniscus quadrispinosus* Richters, 1902 and *E. merokensis suecicus* Thulin, 1911, especially in the location of cirri (see Thulin 1911, Ramazzotti & Maucci 1983). The present new species can be distinguished from *E. quadrispinosus* and *E. merokensis suecicus* by the following major differences: (1) The basal spur of internal claws is absent in the present new species, but is present in *E. quadrispinosus* and *E. merokensis suecicus.* (2) In the present new species, the head and leg plates lack the irregular pores that are present in the other cuticular plates, whereas the head and leg plates also have pores as the other cuticular plates in *E. quadrispinosus* and *E. merokensis suecicus.* (3) The small triagular middorsal field without sculpture on the head plate is found in the present new species, but is absent in *E. quadrispinosus* and *E. merokensis suecicus.*

Acknowledgments

We thank Dr. Hoon Soo Kim, who encouraged the first author to study tardigrade systematics nine years ago, and Dr. Reinhardt Møbjerg Kristensen for reviewing the manuscript and suggestions on the related species *Echiniscus quadrispinosus* and *E. merokensis suecicus.* This work was supported by a research grant from the Korea Science and Engineering Foundation through the Research Center for Cell Differentiation (93-4-3).

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DORYPHORIBIUS KOREANUS, A NEW SPECIES OF TARDIGRADA FROM KOREA

Seung Y. Moon, Won Kim, and Roberto Bertolani

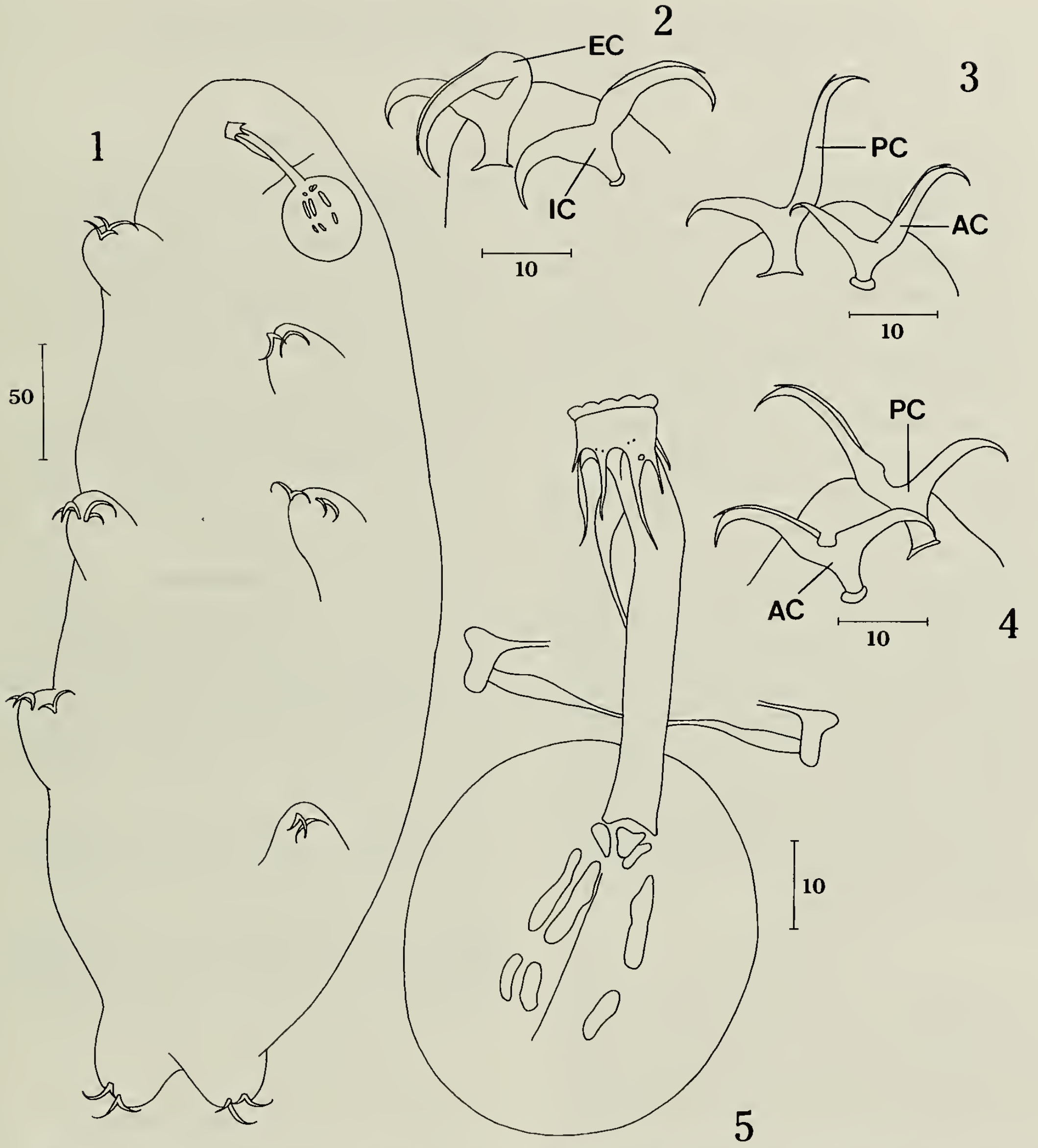
Abstract.—*Doryphoribius koreanus,* a new tardigrade species collected from terrestrial mosses and freshwater habitats in Korea, is described. The present new species mainly differs from the other species of the genus *Doryphoribius* in the following characteristics: smooth cuticle, two macroplacoids, presence of lunules only in the internal or anterior claws of legs, and very reduced buccal armature.

Since the genus *Doryphoribius* in the Eutardigrada was established (Pilato 1969), eleven species have been reported (Pilato 1971, Binda et al. 1980, Bertolani 1983, Ramazzotti & Maucci 1983, Beasley & Pilato 1987, Biserov 1988, Pilato & Binda 1990). A new species of *Doryphoribius* was identified during an investigation of the tardigrades collected from terrestrial mosses and benthic samples from freshwater habitats in Korea. The specimens were mounted on a microscope slide with Hoyer's medium. Examination and drawings were made with a phase-contrast compound microscope. The holotype and two paratypes are deposited in the Moon collection, Department of Molecular Biology, Seoul National University, Korea. One paratype is deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C., U.S.A., and the other paratype in the Bertolani collection, Department of Animal Biology, University of Modena, Italy.

Doryphoribius koreanus, new species
Figs. 1–5

Material examined.—Holotype-Myŏngam reservoir, Ch'ŏngju, Kyŏnggi-do, collected by Cheon Y. Chang, 8 Oct 1986; four paratypes-three specimens, Pŏmŏ temple (moss), Yangsan, Kyŏngsangnam-do, collected by Seung Y. Moon, 25 May 1986; one specimen (USNM 259663), Sŏgwip'o (pond), Chejudo, collected by Cheon Y. Chang, 23 Apr 1987.

Description.—Holotype. Body (Fig. 1) yellowish, with length 456 μm. Eye spots absent (or not preserved) in holotype but present in paratypes. Cuticle smooth. Mouth subterminal, positioned rather anteroventrally. Buccal armature (Fig. 5) almost not existent, consisting of few posterior teeth, 2–4 minute ventral teeth, and single slightly larger dorso-medial tooth. Peribuccal lamellae absent. Buccal tube (Fig. 5) moderately wide (internal diameter 5 μm), rigid, but slightly curved dorsally and anteriorly; ventral lamina of buccal tube present. Pharyngeal bulb (Fig. 5) round (length : width, about 1.2:1), containing well-developed apophyses and two rod-like macroplacoids; first macroplacoid with slight median constriction 10.1 μm long, about 1.7 times as long as second macroplacoid (6.0 μm long); macroplacoids arranged in somewhat arcuate line; microplacoid absent. Double claws (Figs. 2–4) clearly of *Isohypsibius* type, moderately large, similar in size and shape on the same leg and on the first three pairs of legs; on the fourth pair of legs, anterior double claw similar in length to internal ones of other pairs, whereas posterior double claw somewhat longer than anterior one of same leg and external claws of other pairs; main



Figs. 1–5. *Doryphoribius koreanus,* new species, holotype. 1, whole animal, ventro-lateral view; 2, claws of third pair of legs (EC, external claw; IC, internal claw); 3 & 4, claws of fourth pair of legs (PC, posterior claw; AC, anterior claw); 5, buccopharyngeal apparatus. Scales in μm.

branch of double claw with 2 minute accessory points; basal branch of external (posterior) double claw moderately long and rather robust, with its basal end expanded laterally; basal branch of internal (anterior) double claw somewhat shorter than that of external double claw, without basal expanding; lunules of internal double claws more distinct on claws of fourth pair of legs; lunules absent on external double claws.

Etymology.—The specific name is based on Korea, the type locality of the new species.

Remarks.—The present new species differs from seven [*Doryphoribius bertolanii* Beasley & Pilato, 1987; *D. flavus* (Iharos 1966); *D. gibber* Beasley & Pilato, 1987; *D. mariae* Pilato & Binda, 1990; *D. polynettae* Biserov, 1988; *D. zappalai* Pilato, 1971; *D. zyxiglobus* (Horning, Schuster, & Grigarick, 1978)] of the eleven previously described species by its smooth cuticle and/or by the number of macroplacoids. The other species with a smooth cuticle and two macroplacoids are *D. doryphorus* (Binda & Pilato 1969), *D. evelinae* (Marcus 1928), *D. macrodon* Binda, Pilato, & Dastych, 1980, and *D. pilatoi* Bertolani, 1983. The present new species, *D. koreanus,* differs from *D. doryphorus* by having the external claws with laterally expanded basal end, the internal claws surrounded by a lunule, and a wider buccal tube. It differs from *D. evelinae* by the presence of longer claws and the absence of tubercles on the legs. It differs from *D. macrodon* by the presence of lunules around the basal ends of the internal (anterior) claws and by the very reduced buccal armature. Lastly, it differs from *D. pilatoi* which has reduced claws on the fourth pair of legs.

The present new species is found both in terrestrial and aquatic habitats as well as *D. evelinae* and *D. zappalai.*

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AMPHITRITE LOBOCEPHALA, A NEW SPECIES (POLYCHAETA: TEREBELLIDAE) FROM TAIWAN

Hwey-Lian Hsieh

Abstract.—A new terebellid polychaete species is described from a sandflat on the west coast of Taiwan. *Amphitrite lobocephala,* new species, lives in U-shaped tubes and is gregarious. The new species is similar to *Amphitrite edwardsii* (Quatrefages). Both species have 17 thoracic setigers and three pairs of well developed branchiae. Uncini are present from uncinigerous segments 7–16. The new species differs markedly from *A. edwardsii* and other species of *Amphitrite* that have been recorded from Pacific and adjacent waters by the presence of lateral lobes on the peristomium. A key is provided to the species of *Amphitrite* from the western Pacific, East Indies, Red Sea, Mediterranean and northern Australia.

Studies on polychaete communities from the intertidal areas on the west coast of Taiwan have recently been conducted (Hsieh & Chang 1991). A new terebellid species is one of the dominant tube-dwellers on the sandflats. This species is described herein and compared with related species. The types are deposited in the Institute of Zoology, Academia Sinica, Taipei, Taiwan (ASIZIP); the Australian Museum, Sydney, Australia (AM) and the National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A (USNM).

Family Terebellidae
Genus *Amphitrite* Müller
Amphitrite lobocephala, new species
Figs. 1–5

Material examined.—Intertidal sandflat at Hsiang Shan (24°50′N, 120°54′E), Hsin Chu Hsien, northwest coast of Taiwan, 22 Aug 1990: holotype (ASIZIP7), complete, female, 144 setigers, 80 mm long, 3.3 mm maximum width. 10 paratypes: 3 females (ASIZIP8, ASIZIP15, ASIZIP17), complete, 124–130 setigers, 73–80 mm long, 2.7–2.8 mm wide; 2 males (ASIZIP9, ASIZIP13) complete, 131–166 setigers, 75 mm long, 3.3–3.4 mm wide; 3 males (ASIZIP10, ASIZIP11, ASIZIP12) incomplete, 28–49 setigers, 30–47 mm long, 2.8–3.0 mm wide; 2 sex indeterminable (ASIZIP14, ASIZIP16), incomplete, 24–71 setigers, 25–48 mm long, 3.3 mm wide. 27 Nov 1990: 4 paratypes (ASIZIP18), complete with tubes, 42–80 mm long, tubes 140–210 mm long. 16 Apr 1991: 2 paratypes (ASIZIP19), complete with tubes, 75–90 mm long, tubes 140–160 mm long. 1 Feb 1993: 2 paratypes (ASIZIP20), juveniles, 38–47 setigers. May 1990: 1 paratype (ASIZIP21), incomplete, about 2.5 mm wide. 29 Sep 1990: 3 paratypes (AM W 20887), 1 complete, 150 setigers, 23 mm long, 2.5 mm wide; 2 incomplete, 29–56 setigers, 25 mm long, 1.5–2.5 mm wide. 10 Aug 1991: 4 paratypes (AM W 20888), 90–105 setigers, 27–45 mm long, 2–3.5 mm wide. 1 Feb 1993: 9 paratypes (USNM168062), complete with tubes, tubes about 120–170 mm long.

Description.—Found in U-shaped tubes made of sand grains and shell debris. Tube length about twice that of an individual. One of two tube openings fringed. Live specimens with anterior dorsum pale green, ventral glandular pads red, edge of thoracic uncinigerous podia brownish in color; al-

Fig. 1. *Amphitrite lobocephala,* new species, paratype (ASIZIP9). a. dorsal view of anterior body. Part of buccal tentacles was removed to show peristomium and peristomial lateral lobes. Branchiae also were cut off from the bases to show the 2nd pair of lateral lobes. b. ventral view of anterior body. Arabic numerals 3, 4 indicating segments 3, 4.

cohol preserved material pale cream. Prostomium with large anteriorly projecting U-shaped upper lip and small tongue-like lower lip. Anterior margin of peristomium thickened and collar-shaped, from where numerous filiform buccal tentacles arise (Fig. 1a). Peristomium (=segment 1) shorter than segment 2 dorsally. Lateral lobes on segments 1 and 3. Peristomial lateral lobes on segment 1 bluntly pointed, triangular, overlapping base of tentacles, margin of lobes less glandular than rest of lobe. Lobes connected mid-ventrally, forming V-shaped glandular structure (Fig. 1b). Inner surface of peristomial lateral lobes mottled and crenulated. Lateral lobes on segment 3 rectangular with thin glandular margins; dorsolateral margins convoluted and folded posteriorly, whole lateral lobe inserted at slight angle, terminating ventrally at margins of ventral pads (Figs. 1b, 2a). Peristomial lobe larger than lateral lobes of segment 3. Eyespots absent in holotype and large specimens but present in juveniles, two or three red eyespots distributed on outer anterior regions of the peristomium.

Three pairs of branchiae on segments 2–4 originating from mid-dorsal region of segments, those on segment 4 arising from about line of notopodia (Figs. 1a, 2a). Branchiae delicate, finely branched, main stem wide but not thickened or ridged. Branchiae with numerous, fine, multiple branches, arising spirally around the main stem, strongly arborescent (Fig. 3).

Thoracic setigers with well-developed, white, oval, glandular structures around notopodial bases. Areas anterior and posterior to neuropodia also glandular with additional glandular areas present along dorsal-lateral and lateral surface of anterior thoracic setigers. Notopodia 17 pairs, from segment

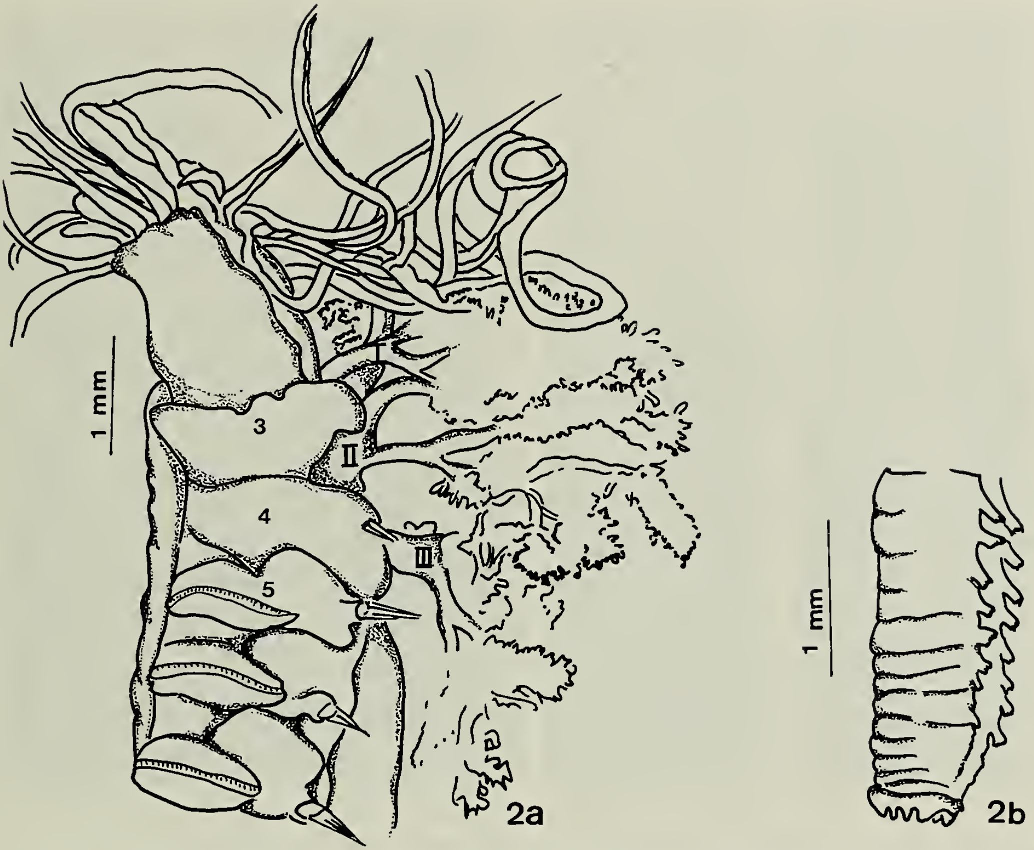

Fig. 2. *Amphitrite lobocephala,* new species, holotype. a. lateral view of anterior body. Arabic numerals 3, 4, 5 indicating segments 3, 4, 5. Roman numerals I, II, III indicating 3 pairs of branchiae. b. lateral view of posterior end.

4 and on following 16 segments. Notopodia rectangular, non-glandular structures. Notosetae within fascicle graded in length, limbate capillaries with very finely serrated tips (Figs. 4a, 5a–c). Thoracic uncini avicular with spur on posterior basal portion (Fig. 4b, c). Neuropodia present from setiger 2 (segment 5) continue to pygidium, initially uncini arranged in single rows, from uncinigerous segment 7 (segment 11) arranged in double rows back to back on remaining thoracic segments. Uncini of abdominal segments (from segment 21) arranged again in single rows. Neuropodia low ridges, transversely elongated on thoracic setigers (Figs. 1b, 2a), whereas those of abdominal setigers longitudinally elongated, paddle-like with uncini inserted on margins (Fig. 2b). Dental formulae of thoracic uncini MF:1–2:1–2:1–4:1–2, and abdominal uncini MF: 2:1:2–3:2–3.

Ventral pads forming an elongate V-shaped structure, anterior margins rounded, extending from segment 3 to end of thorax and then continuing as mid-ventral stripe along anterior abdomen (Fig. 1b). Pygidium terminal with margins convoluted (Fig. 2b).

Nephridial papillae small and rectangular, located just below and posterior to notopodia and above segmental boundary of segments 6–9. Papillae enlarged, oval-shaped in gravid individuals.

Variation. —The material examined

Fig. 3. *Amphitrite lobocephala,* new species, paratype (ASIZIP9). Posterior view of right branchia of the first pair.

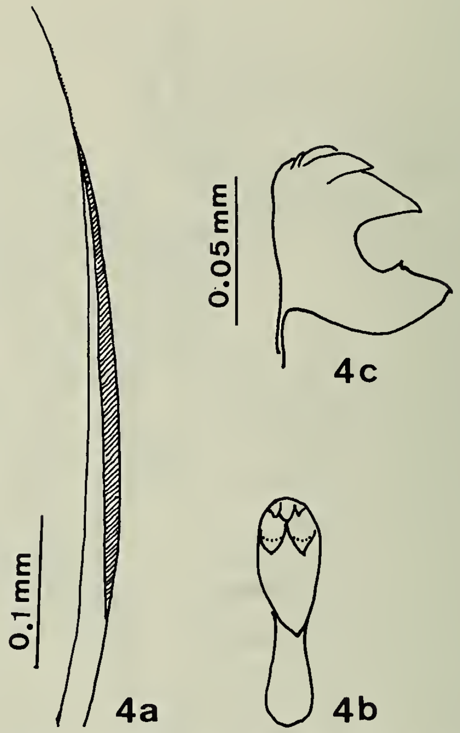

Fig. 4. *Amphitrite lobocephala,* new species. a. limbate capillary notoseta from setiger 7. b. uncini from setiger 7, frontal view. c. same as b, lateral view. a & c paratype ASIZIP12, b paratype ASIZIP8.

shows the following variation: branchiae differ in size with the first pair often larger than the subsequent two pairs. Numbers of parapodia on each side of the body may vary within an individual. Unequal development occurs within thoracic segments where one notopodium may be missing from one side of the corresponding podia. Such development more often occurs in posterior abdominal segments where 4 or 5 neuropodia may be absent. Additionally, an abdominal neuropodium may split into two lobes. Red eyespots are present in young juveniles but are absent in larger individuals.

Remarks.—Eighteen species of *Amphitrite* have been previously recorded (see Hartman 1959, 1965; Day 1967; Hutchings & Glasby 1988). Among these species, ten were reported from regions of the western Pacific, East Indies, Red Sea, Mediterranean and northern Australia. They are *A. cirrata* Müller, 1771, *A. edwardsii* (Quatrefages 1865), *A. leptobranchia* Caullery, 1944, *A. malayensis* Caullery, 1944, *A. oculata* Hessle, 1917, *A. pachyderma* Hutchings & Glasby, 1988, *A. ramosissima* Marenzeller, 1884, *A. rubra* (Risso 1826), *A. scylla* (Savigny 1820), and *A. variabilis* (Risso 1826). The remaining eight species were recorded from arctic and antarctic regions. Thus, only the new species *A. lobocephala* and the above ten species are included for further discussion. In some of these species characters used for comparisons are based on the original description and also on subsequent redescriptions including these of Okuda (1937) and Imajima & Hartman (1964) on *A. cirrata,* Imajima & Hartman (1964) on *A. edwardsii,* Hutchings & Glasby (1988) and Hutchings (1990) on *A. oculata,* Imajima & Hartman (1964) on *A. ramosissima,* Fauvel (1927), Okuda (1937) and Imajima & Hartman (1964) on *A. rubra* (Risso) and Fauvel (1927) on *A. variabilis.* As regards *A. rubra,* Hutchings & Glasby (1988) noted that all records of this species from Australia had been referred to either *A. pachyderma* or

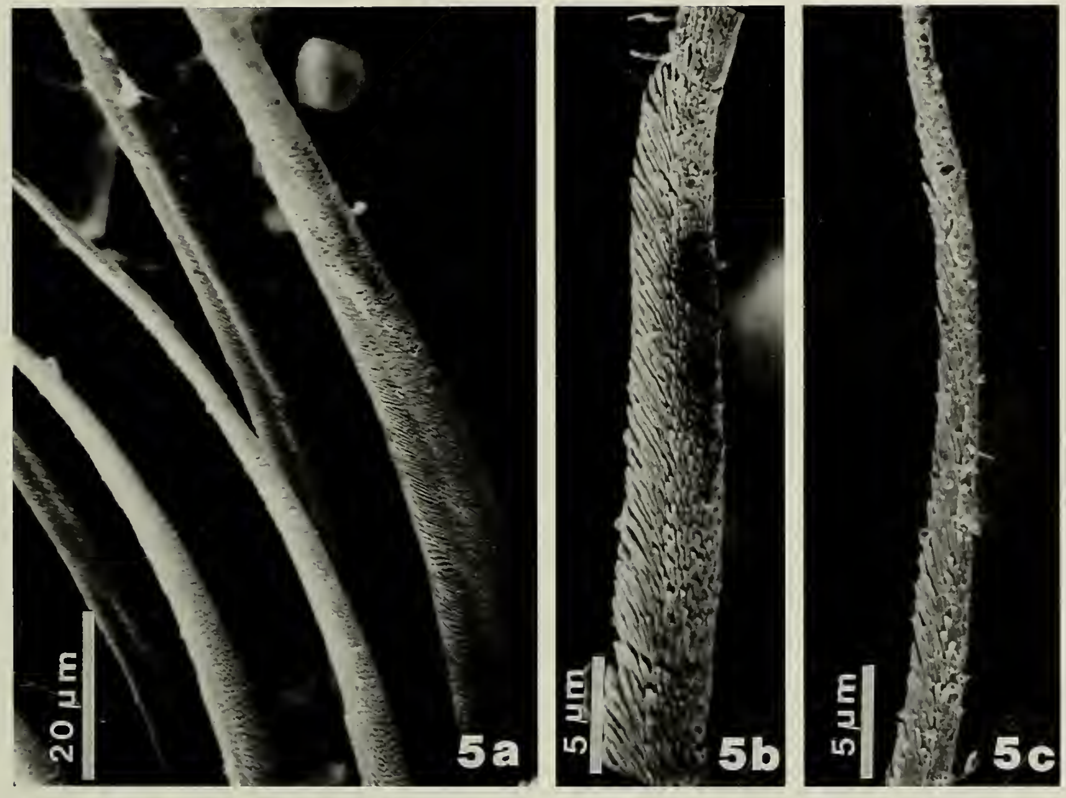

Fig. 5. *Amphitrite lobocephala,* new species. a. SEM (1570×) showing fine serration of limbate capillaries from setiger 5. b. SEM (4715×) showing serration at distal end of limbate capillary from setiger 5. c. SEM (4550×) showing hispid serration at the tip of limbate capillary from setiger 3. a–c paratype ASIZIP21.

Longicarpus. They also found that the type specimen of *A. rubra* was not a species of *Amphitrite.*

Amphitrite lobocephala has capillary notosetae with very fine serrated tips that may be characterized as faintly hispid using Kritzler's terminology in the classification of the genus (Kritzler 1984). *Amphitrite lobocephala* differs markedly from the other described species of *Amphitrite* in that the lateral lobes are first present on the peristomium (segment 1), rather than from segment 2. *Amphitrite lobocephala* resembles *Amphitrite edwardsii* in that both species have 17 thoracic setigers, three pairs of ramified branchiae that are well-developed, and uncini are present from uncinigerous segments 7–16. *Amphitrite lobocephala* differs from *A. edwardsii* in the number and distribution of lateral lobes (on segments 1 and 3 vs. on segments 2, 3 and 4) and the number of pairs of nephridial papillae present (4 pairs vs. 9 pairs). In addition, *A. lobocephala* differs from the other species in such features as branchial morphology, number of thoracic setigers, arrangement of uncini, dentition of uncini, and the segments on which nephridial papillae occur. The following key reflects these differences.

Key to species of *Amphitrite* recorded in western Pacific, East Indies, Red Sea, Mediterranean and northern Australia

1a. Lateral lobes absent; 2 pairs of branchiae on segments 2 and 3 .... *A. leptobranchia*

1b. Lateral lobes present, 1–3 pairs .. 2
2a. 1 pair of lateral lobes on segment 2; 19 thoracic setigers .... *A. scylla*
2b. 2 or 3 pairs of lateral lobes, various thoracic setigers 3
3a. Lateral lobes first present from peristomium (segment 1); a second pair on segment 3 .... *A. lobocephala*
3b. Lateral lobes first present from segment 2 4
4a. 2 pairs of lateral lobes on segments 2 and 3 5
4b. 3 pairs of lateral lobes on segments 2, 3 and 4 6
5a. Branchiae poorly branched with filaments arising directly from short stem .... *A. malayensis*
5b. Branchiae dendritically branched with short stem and very bushy tops ....*A. ramosissima*
6a. Branchiae filiform with short stem 7
6b. Branchiae dendritically branched 8
7a. Eyes absent; uncini in double rows from uncinigerous segments 7–16; nephridial papillae on segment 3 and segments 6–11 ...... *A. cirrata*
7b. Eyes present; uncini in alternating rows from uncinigerous segments 7–19, arranged face to face; nephridial papillae on segment 3 and segments 5–8 .... *A. oculata*
8a. 17 thoracic setigers 9
8b. 20 or more thoracic setigers ... 10
9a. Lateral lobes well developed; uncini with 3 or 4 rows of teeth above main fang; nephridial papillae on segments 3–11 .... *A. edwardsii*
9b. Lateral lobes poorly developed; uncini with numerous rows of fine teeth above main fang; nephridial papillae on segments 3–8 .... *A. variabilis*
10a. 20–24 thoracic setigers; uncini in double rows from uncinigerous segments 7–19; 12–14 pairs of nephridial papillae on segments 3–15 .... *A. rubra*
10b. 24 thoracic setigers; uncini in alternating rows, face to face, from uncinigerous segments 7–40; 7 pairs of nephridial papillae on segments 3–9 ...... *A. pachyderma*

Etymology.—The specific name, *lobocephala,* is derived from the Greek adjective, *lobos,* lobe and *cephala,* head referring to the first appearance of lateral lobes on the peristomium.

Habitat.—The type locality is a fine sand flat. The median grain size of the flat range from 0.17–0.18 mm in diameter with modal grain size ranging from 0.15–0.21 mm in diameter (Hsieh & Chang 1991). On the southwest side of the flat, the oyster *Crassostrea gigas* is cultured, supported above the sediment by bamboo sticks. Tubes of the terbellid *Amphitrite lobocephala,* the onuphid *Diopatra bilobata* Imajima and chaetopterids are the most obvious polychaete tubes seen on the flat.

Biology.—*Amphitrite lobocephala* is dioecious with a sex ratio of approximately 1:1. The species constructs sand tubes. Larger particulate materials, such as fragments of shells, are often incorporated onto the tubes. Sizes of particles in the tubes are generally larger than those in the surrounding area, suggesting that the worms select larger particles for tube construction (Hsieh & Chang 1991). The sizes of individuals in the benthic population range from about 10 segments to 150 segments. Largest oocytes are about 180 μm in diameter. Oocytes larger than 150 μm in diameter are present in the coelom from September to October and from March to May. Aulophore larvae (planktonic larvae with mucous tube, see Bhaud 1988) having one tentacle were found in the water column from late spring to summer (Hsieh, unpublished data).

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TWO NEW SPECIES OF *CIRROPHORUS* (POLYCHAETA: PARAONIDAE) FROM THE NORTHERN GULF OF MEXICO

Jerry A. McLelland and Gary R. Gaston

Abstract.—Two new species of paraonid polychaetes, *Cirrophorus perdidoensis* and *C. perkinsi,* are described from coastal waters off Perdido Key, Florida. The two species co-occur in moderately coarse sand substrate at depths from 1.6 to 7.0 m. *Cirrophorus perdidoensis* has slender, lyrate forked notosetae that are slightly asymmetrical; *C. perkinsi* has stout, acicular forked notosetae that are bayonet-shaped. The two new species and *C. juvenalis* (Hartmann-Schröder) are distinguished from other members of the genus by their small size, less than 4 mm, four or fewer pairs of branchiae, and by having two or more posterior segments reduced and represented only by dorsal podial lobes.

Specimens of two undescribed species of *Cirrophorus* occurred in benthic samples collected at Perdido Key (Escambia County), Florida, between October, 1989, and December, 1991. Sampling took place within the Gulf Islands National Seashore as part of a study on the effects of beach renourishment on shallow (1.6–7.0 m) nearshore sediments. Four transects (A–D), each consisting of nine stations ranging from 0 to 800 m from the beach, were established at 3 km intervals along the key. Samples were hand collected by SCUBA divers using 0.016 m^2 (12.5 cm sided) stainless steel box corers and screened through 0.5 mm mesh sieves. A more complete description of the study area and collecting methods was published by Rakocinski et al. (1993). Additional material from the Florida east coast and the Florida Keys is included. All material is associated with high salinity (28–35 ppt), highly oxygenated water (5.5–8.0 mg/l) and coarse sand substrate with the silt-clay composition not greater than 9%.

In his monograph of the Paraonidae, Strelzov (1973) combined the genera *Paraonides* Cerruti, 1909, and *Paradoneis* Hartman, 1965, with the genus *Cirrophorus* Ehlers, 1908, accounting for 10 species. He defined the genus *Cirrophorus* as those species with forked setae, either lyrate, acicular, or both, present in some of the notopodial fascicles. The presence or absence of an unpaired cephalic antenna, previously the chief distinguishing character separating *Cirrophorus* from *Paradoneis,* was deemed less significant because of its age-related variability. The present work follows Strelzov's general definition of the genus except for the exclusion of *Paraonides,* as discussed below.

Some works published since Strelzov's 1973 revision retain the genus *Paradoneis* as distinct from *Cirrophorus.* This view apparently originated with Laubier & Ramos' opinion (1973:1141) that Strelzov, in his 1968 paper, mis-identified specimens of *C. lyriformis* collected in the Barents Sea and failed to cite Glémarec's (1966) description of *Paradoneis armata.* They felt that Strelzov probably had a mixture of species, including *P. armata,* in his Barents Sea material, some with and some without a prostomial antenna. Thus, his justification for synonymizing *Paradoneis* with *Cirrophorus* based on the insignificance of the antenna was unfounded. Katzmann & Laubier (1975:569) referred to this interpretation of Strelzov's 1968 work as rationale for rejecting the synonymy of the two genera, and papers that have since retained *Paradoneis* have cited Katzmann & Laubier (Hartley 1981, Castelli 1988, Mackie 1991). Strelzov (1973), however, upon re-examining specimens from two north Pacific collections, synonymized *C. lyriformis* with *C. branchiatus,* and included *Paradoneis armata* Glémarec, 1966, (as *Cirrophorus armata*), which differs from *C. branchiatus* mainly by the number of prebranchial setigers.

Strelzov included *Paraonides* under the genus *Cirrophorus* after observing lyrate notosetae in a specimen of *Paraonis* (*Paraonides*) *neopolitana* identified by Glémarec from the Bay of Biscay. This, the type species for the genus, was originally described by Cerruti (1909) from one specimen from the Gulf of Naples. Strelzov interpreted Cerruti's (1909) illustrations of leaf-shaped modified limbate notosetae as distorted lyrate setae caused by the specimen's orientation in the mounting medium; thus his conclusion that the species belonged to *Cirrophorus.* This opinion was disputed as circumstantial by Katzmann & Laubier (1975) and Castelli (1988) mainly because Strelzov did not use specimens from the type locality in his analysis. *Paraonides neopolitana* was redescribed as lacking lyrate notosetae by Fauvel (1927) and Laubier & Paris (1962); the species was reported from Mediterranean waters by Laubier & Paris (1962), Castelli (1988), and Katzmann & Laubier (1975). A short review of *Paraonides* listing six species was presented in the latter work.

Another species listed by Strelzov, *Cirrophorus harpagoneus,* was regarded as a junior synonym of *Paradoneis* (=*Cirrophorus*) *armata* by López-Jamar et al. (1987) after comparison of the holotype of *C. harpagoneus* with para- and topotype material of *C. armata.*

Since Strelzov's 1973 monograph, three additional species of Paraonidae with notopodial forked setae were described that should be transferred to the genus *Cirrophorus*: *Paraonis* (*Paradoneis*) *juvenalis* Hartmann-Schröder, 1974, *Paradoneis ilvana* Castelli, 1985, and *Paradoneis eliasoni* Mackie, 1991. An updated list comparing species belonging to *Cirrophorus* is presented in Table 1.

Few records exist of *Cirrophorus* in the Gulf of Mexico. Gaston (1984) reported scattered occurrences of *Cirrophorus branchiatus, C.* cf. *forticirratus,* and *C. americanus* in the northeastern Gulf and off Texas. Taylor (1971) reported *C. furcatus* from a few stations in lower Tampa Bay, Florida. It is possible that because of their small size (i.e., less than 4 mm long) the two species described herein have been confused with juveniles of larger species; however, most specimens contained large eggs or sperm masses in their abdominal segments, indicating that they were mature.

Holotypes, paratypes, and additional material from the type locality are deposited in the National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C. Other specimens are deposited in the museum of the Gulf Coast Research Laboratory (GCRL), Ocean Springs, Mississippi, the Marine Invertebrate Collection of the Florida Marine Research Institute, Department of Natural Resources (FSBC I), St. Petersburg, Florida, and in the personal collections of the authors.

Family Paraonidae Cerruti, 1909

Genus *Cirrophorus* Ehlers, 1908

Cirrophorus perdidoensis, new species

Fig. 1

Type material.—Northwest Florida, Perdido Key (30°17′31″N, 87°25′12″W). Holotype (USNM 168090), thirty paratypes (20, USNM 168091; 10, GCRL 1303), Station A9, 6 Oct 1989, 5.5 meters depth, sediment type: 99.7% sand, 0.3% silt-clay.

Additional material examined.—Perdido Key: 51 specimens from 19 collections, made between 20 Sep 1990 and 3 Dec 1991, 2.1–7.0 m depth, sediment type and hydrographic conditions similar to type material

Table 1.—List of species in the genus *Cirrophorus* with some comparative morphological characteristics for worms of maximum size. Includes data published by Glémarec (1966), Strelzov (1973), Hartmann-Schröder (1974), Castelli (1985), and Mackie (1991).

Species	Forked notosetae		Cephalic antenna	Acicular neurosetae	Prebranchial setigers (no.)	Branchiae (pairs)	Setigers (no.)
	Type	Start setiger					
Cirrophorus perkinsi n.sp.	acicular	2	absent	absent	3	3–4	37
C. juvenalis (Hartmann-Schröder, 1974)	acicular	4	absent	absent	3	1	36
C. lyra (Southern, 1914)	lyrate	1–6	absent	absent	3	12–14	108+
C. perdidoensis n.sp.	lyrate	3	absent	absent	3	3–4	42
C. forticirratus Strelzov, 1973	lyrate	4–6	absent	absent	3–4	17	104
C. abranchiatus (Hartman, 1965)	lyrate	7–17	absent	absent	0	0	75
C. eliasoni (Mackie, 1991)	lyrate	4–8	absent	present	3	12	86+
C. americanus Strelzov, 1973	lyrate	2–3	present	present	3	46	90+
C. furcatus (Hartman, 1957)	lyrate	3	present	absent	3	33	70+
C. brevicirratus Strelzov, 1973	lyrate	6	present	absent	3	14–15	97
C. armatus (Glémarec, 1966)	both	3–10, lyrate 17–18, acicular	absent	absent	3	19	140
C. ilvana (Castelli, 1985)	both	4, lyrate 12–13, acicular	absent	absent	3	10	80
C. branchiatus Ehlers, 1980	both	5–8, lyrate 8–18, acicular	present	absent	4–5	25	140+

(USNM 168092, USNM 168093, USNM 168094, USNM 168095, USNM 168096, USNM 168097, USNM 168098, USNM 168099, USNM 168100, USNM 168101, USNM 168102, GCRL 1304, GCRL 1305, GCRL 1306, GCRL 1307, GCRL 1308, FSBC I 54472, FSBC I 54473, FSBC I 54474, FSBC I 54475). Florida Keys: Pigeon Key (24°50′N, 80°45′W), 1 specimen in seagrass kicknet sweeps, 1 m, coarse coralline sand, collected 17 Oct 1991 by J. McLelland.

Description.—Holotype 2.9 mm total length, 39 setigers, maximum body width 0.12 mm. Body circular in cross section. Prostomium approximately 1.5 times longer than wide, rounded anteriorly, lacking antenna (Fig. 1B). Pair of small, subdermal, reddish-orange eye spots, distinct but faint in preserved specimens. Two ciliary bands on head, anteriormost limited to dorsal surface anterior to eye spots, posterior band emerging laterally from nuchal slits and circumscribing ventral surface. Ciliary bands present on dorsum of prebranchial and branchial segments. First segment setigerous. Branchiae three (rarely four) pairs, beginning on setiger 4, each as long as segment width, lateral margins ciliated. Dorsal podial lobes (postsetal) short, tuberculate on prebranchial setigers, prominent and uniform in length on setigers 4 through 9; becoming tuberculate and reduced in size on setigers 10–31, then progressively longer toward end of body beginning 3–5 setigers from end. Pygidial region (Fig. 1C, D) with nine cirri consisting of three pairs arranged dorsolaterally to ventrolaterally, apparently representing dorsal podial lobes of three reduced segments, and three anal cirri, a single ventromedial one and a lateral pair; posterior cirri of nearly equal length, longer than pygidium, approximately as long as dorsal podial lobes of last setiger. Forked setae relatively slender, asymmetrically lyrate (Fig. 1E), one tine up to twice length of other, tines of equal thickness; occurring singly in inferior notopodial position from setiger 3 to at least 4th setiger from end. Remaining notosetae and all neurosetae simple capillaries.

Remarks.—Among the additional material examined, the number of setigers varied between 30 and 42; the largest specimen observed was 3.5 mm long. A few specimens were observed with four pairs of branchiae. In the posterior regions of several specimens, large eggs, nearly equal to the body width in diameter, occurred and dark granular material (sperm masses?) was observed in some presumed males. Similar gonadal conditions were also observed for *C. perkinsi* except that the eggs appeared proportionally smaller.

Cirrophorus perdidoensis is unique among members of the genus for its combination of small size, lyrate forked setae, and four or fewer pairs of branchiae. Among *Cirrophorus* species having lyrate forked setae, *C. perdidoensis* is similar to *C. furcatus* and *C. lyra* by having such setae beginning on the 3rd setiger, and by having podial lobes in the branchial region of uniform length and substantially longer than those of the prebranchial and most of the postbranchial lobes (Strelzov 1973, Mackie 1991). *Cirrophorus perdidoensis* differs from the former species, however, by lacking a cephalic antenna, and from both species by having substantially fewer setigers and pairs of branchiae (Table 1).

Etymology.—The specific name refers to the type locality, Perdido Key, Florida.

Cirrophorus perkinsi, new species
Fig. 2

Type material.—Northwest Florida, Perdido Key (30°17′31″N, 87°25′12″W). Holotype (USNM 168103), two paratypes (USNM 168104), station A9, 12 Dec 1990, 6.1 meters depth, sediment type: 95.4% sand, 4.6% silt-clay.

Additional material examined.—Perdido Key: 58 specimens from 11 collections made between 6 Oct 1989 and 3 Dec 1991, 1.6–

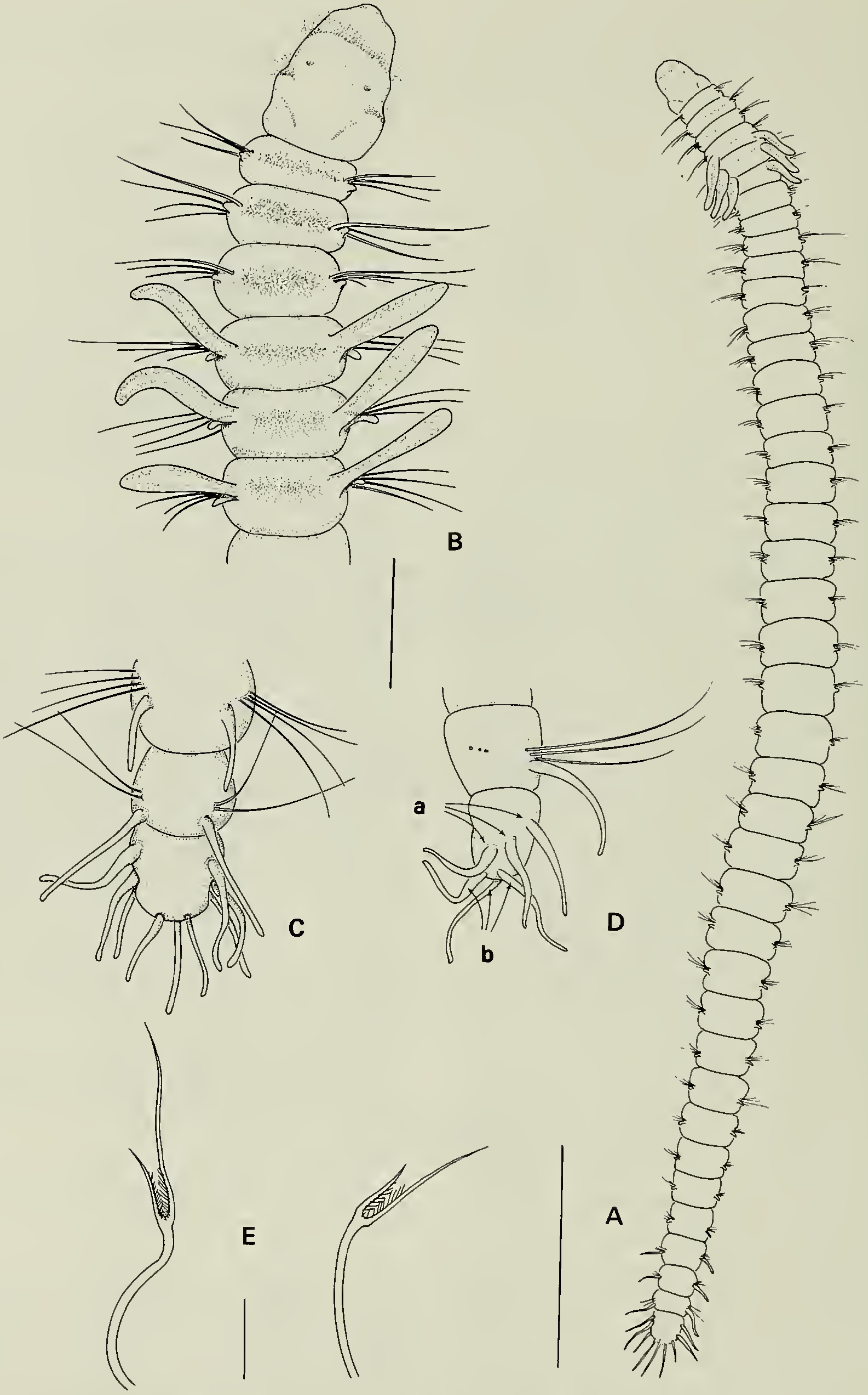

Fig. 1. *Cirrophorus perdidoensis,* new species. A. Entire animal, dorsal view. B. Anterior end, dorsal view. C. Posterior end, dorsal view. D. Posterior end, lateral view, neurosetae and cirri from right side omitted (a, podial lobes of reduced segments; b, anal cirri). E. Lyrate forked notosetae. Scales: A = 0.5 mm, B, C, and D = 0.1 mm, E = 0.01 mm.

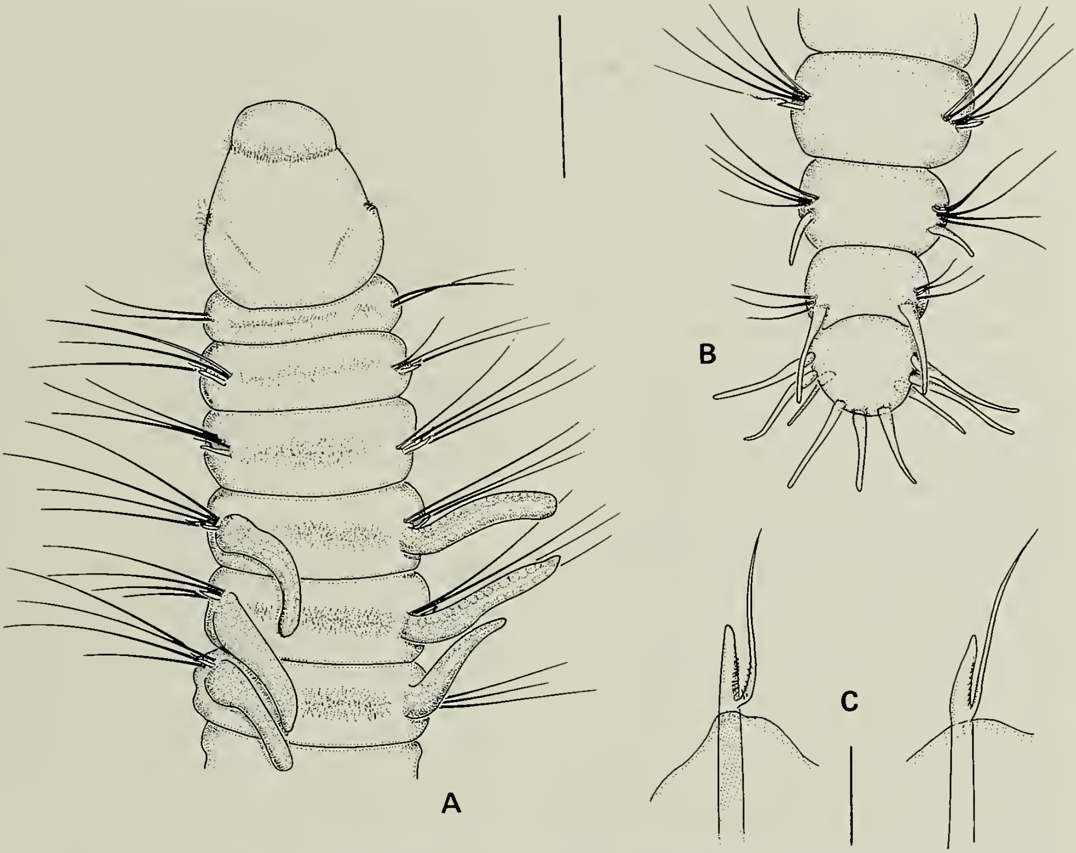

Fig. 2. *Cirrophorus perkinsi,* new species. A. Anterior end, dorsal view. B. Posterior end, dorsal view. C. Acicular forked notosetae. Scales: A, B = 0.1 mm, C = 0.01 mm.

7.0 m depth, sediment type and hydrographic conditions similar to type material (USNM 168105, USNM 168106, USNM 168107, USNM 168108, GCRL 1309, GCRL 1310, GCRL 1311, GCRL 1312, GCRL 1313, GCRL 1314, FSBC I 54476, FSBC I 54477). Florida east coast: six specimens from three collections off Hutchinson Island, St. Lucie County (27°21′N, 80°13′W), 10 May 1972 (USNM 54571), 2 Nov 1972 (FSBC I 39860) and 14 Mar 1977 (FSBC I 39861), all 10.9 m depth.

Description.—Holotype 2.5 mm total length, 37 setigers, maximum body width 0.18 mm. Body circular in cross section. Prostomium approximately 1.7 times longer than wide, rounded anteriorly, lacking antenna; eye spots absent (Fig. 2A). Two ciliary bands on head, anteriormost limited to dorsal surface, posterior band emerging laterally from nuchal slits and circumscribing ventral surface. Ciliary bands present on dorsum of prebranchial and branchial segments. First segment setigerous. Branchiae simple, three to four pairs, beginning on setiger 4, each longer than width of segments, lateral margins ciliated. Dorsal podial lobes absent or reduced to small, indistinct tubercles on all but posterior two setigers where they are well-developed. Pygidial region (Fig. 2B) with nine cirri consisting of three pairs arranged dorsolaterally to ventrolaterally, apparently representing dorsal podial lobes of three reduced segments, and three anal cirri, a single ventromedial one and a lateral pair; posterior cirri of nearly equal length, longer than pygidium, approximately as long as dorsal podial lobes of last setiger. Forked setae stout, acicular, bayonet-shaped (Fig. 2C), slender tine about twice as long as stout tine; occurring singly in inferior notopodial position from setiger 2 posteriorly to last fully developed setiger. Remaining notosetae and all neurosetae simple capillaries.

Remarks.—The holotype was the largest specimen observed. Other Perdido Key specimens ranged from 1.5 to 2.5 mm long, had 23–37 setigers, and had three or four pairs of branchiae. Of the Hutchinson Island specimens, one (USNM 54571), although in poor condition, was observed with about 45 setigers and five pairs of branchiae; the others had 30–35 setigers and four pairs of branchiae.

Among the species having acicular bayonet type modified setae, *Cirrophorus perkinsi* is distinguished from *C. branchiatus* and *C. armatus* by being much smaller, having fewer pairs of branchiae, by lacking lyrate notosetae in the branchial region, and by having tuberculate or reduced dorsal podial lobes throughout the body except for the pre-anal region. *Cirrophorus perkinsi* further differs from *C. branchiatus* by having three prebranchial segments instead of 4 or 5. *Cirrophorus juvenalis,* a small species from southern Africa, is similar to *C. perkinsi* in having only acicular type specialized notosetae and undeveloped notopodial postsetal lobes on all but the last two setigers, but *C. juvenalis* differs from *C. perkinsi* in having the specialized notosetae beginning on the 4th setiger rather than the 2nd setiger and having only one pair of branchiae rather than three or more (Table 1).

A reduction of three pre-anal segments, resulting in two remnant podial lobes per segment and a disappearance of setae, apparently occurs in *C. perkinsi* and in *C. perdidoensis,* giving the appearance of a pygidial region with nine anal cirri rather than the characteristic three. A similar reduction of segments also apparently occurs in *C. juvenalis,* which Hartmann-Schröder (1974) described and illustrated as having seven filamentous cirri surrounding the anus. This profusion of cirri at the posterior ends of these three small species, along with the lengthened dorsal podial lobes of the last two or three setigers, could represent an adaptation for an interstitial coarse sand habitat (T. H. Perkins, in litt.).

Etymology.—The species is named for Thomas H. Perkins honoring his many significant contributions to the study of polychaetes and for his helpful suggestions in producing this manuscript.

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TWO NEW SCALE-WORMS (POLYNOIDAE: POLYCHAETA) FROM THE LAU BACK-ARC AND NORTH FIJI BASINS, SOUTH PACIFIC OCEAN

Tomoyuki Miura

Abstract.—*Thermopolynoe branchiata,* a new genus and species of branchiate polynoid polychaete from the Lau Back-Arc and the North Fiji Basins, South Pacific Ocean, is described. The new species belongs to the subfamily Lepidonotopodinae in having well-developed notopodial bracts. It, however, differs from the other species of the subfamily in having arborescent branchiae. *Thermiphione fijiensis,* a new species of the subfamily Iphioninae from the North Fiji Basin, differs from *T. tufari* by the first occurrence of hooked neurosetae: segment 3 instead of segment 4 of the latter.

The hydrothermal community of the central part of the North Fiji Basin was found by bottom observations using a deep towed camera system during the R/V *Kaiyo* cruise conducted under the French-Japanese project in 1988. A series of cruises named STARMER were realized in the same project in succeeding years by the French submersible *Nautile* and its mother ship R/V *Nadir* (Azuende et al. 1989).

The objective of the second cruise, STARMER II, was the study of biology and ecology of organisms associated with the active vents of the North Fiji Basin. Beds of deep-sea mussels, numerous galatheid crabs, colonies of tiny anemones, and hundreds of gastropods were observed during these surveys (Jollivet et al. 1989). Close to the North-Fiji Basin, other hydrothermal fields occur at the spreading center of the Lau Back-Arc Basin west of the Tonga Islands (Fouquet et al. 1991). A scientific team from France, Germany, and Tonga explored the Lau Basin in 1989 and numerous organisms were collected using *Nautile* and *Nadir* (the NAUTILAU group 1991). Among the animals collected from the above two basins, were numerous specimens of polynoid polychaetes. These collections were provided to me for study. Nine species were identified and some were found in both basins. In the present study two new species are described. One is thought to belong to the subfamily Lepidonotopodinae and occurs in both basins. Another species from the North-Fiji Basin is attributed to the subfamily Iphioninae. The types are deposited in the Museum National d'Histoire Naturelle à Paris (MNHN), the National Museum of Natural History, Smithsonian Institution (USNM), and Japan Marine Science and Technology Center (JAMSTEC). Some specimens were used for SEM or histological observation at Kagoshima University (KU).

Family Polynoidae
Subfamily Lepidonotopodinae Pettibone, 1983, emended

The subfamily is emended to include *Thermopolynoe branchiata,* new species. There may be parapodial arborescent branchiae instead of lacking branchiae.

Thermopolynoe, new genus

Type species.—*Thermopolynoe branchiata,* new species.

Gender.—Feminine.

Diagnosis.—Body flattened; 27 segments (first achaetous). Elytra 11 pairs, on large elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, and 21. Dorsal cirri on non-elytrigerous segments; dorsal tubercles large. Branchiae well developed, arborescent. Prostomium bilobed; anterior lobes cylindrical, with frontal filaments; median antenna with short ceratophore and subulate style, inserted in anterior notch; palps with slender tips. First or tentacular segment not distinct dorsally; tentaculophores achaetous lateral to prostomium with two pairs of tentacular cirri. Segment 2 with first pair of elytrophores, biramous parapodia, and buccal cirri. Parapodia biramous, with notopodia shorter than neuropodia. Notopodia subconical, with large bracts. Neuropodia truncate, with fimbriated margins. Notosetae and neurosetae numerous, spinous. With or without ventral segmental papillae on middle segments. Pygidium bulbous, wedged between posterior parapodia, with pair of anal cirri. Pharynx with seven pairs of papillae and two pairs of jaws.

Etymology.—The generic name is from Greek, *Thermos,* hot and *Polynoe,* genus name of a polynoid worm.

Thermopolynoe branchiata, new species
Figs. 1–4

Material examined.—White Lady, North Fiji Basin, DSRV *Nautile* Dive 16, 11 Jul 1989, STARMER II Station 4, 16°59.5′S, 173°55.5′E, 2000 m, Holotype (MNHN UD 264), 14 paratypes (MNHN UD 262, JAMSTEC, KU). Same site, Dive 13, 8 Jul 1989, paratype (MNHN UD 265). Same site, Dive 20, 15 Jul 1989, 4 paratypes (USNM 168325). Vailili, Lau Basin, DSRV *Nautile* Dive 10, 22 May 1989, BIOLAU Station 2, 23°13′S, 176°38′E, 1750 m, 2 paratypes (MNHN UD 261).

Description.—Holotype 36 mm long, 12 mm wide including parapodia, with 27 segments including first achaetous tentacular segment. Largest paratype 53 mm long, 20 mm wide, with 27 segments. Body sturdy, slightly tapered anteriorly and posteriorly, flattened ventrally, slightly arched dorsally (Fig. 1a, b). Integument smooth. Preserved specimens brownish to tan.

Elytra 11 pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, and 21, large, covering dorsum, oval, stiff, rough with numerous brownish papillae on white bases (Figs. 1a, 2d–g). Elytra on segments 2–19 oval, wider than long (Fig. 2d, f); last pair on segment 21 subreniform, longer than wide (Fig. 2e). Dorsal cirri on non-elytrigerous segments with short cylindrial cirrophores, and short styles with slender tips, extending to tips of neurosetae; dorsal tubercles nodular (Figs. 3c, f, 4a–c). Branchiae arborescent, present on segments 3–26, around bases of dorsal tubercles and elytrophores; separated into two groups on anterior and posterior sides of notopodia on segments 3 and on some less-developed posterior segments; forming single large branchial areas encircling central parts of notopodia on other fully developed parapodia with about 20 tufts of branchiae; each tuft with 1–15 filaments; each parapodium maximally with about 80 branchial filaments (Figs. 3f–g, 4a, b).

Prostomium bilobed. Anterior lobes prominent, cylindrical, extending anteriorly, with small frontal filaments; median antenna, inserted in anterior notch, with short cylindrical ceratophore and subulate style extending to about tip of palp; palps thick, slightly wrinkled, extending beyond prostomium, with slender tips. Tentacular segment not distinct dorsally; tentaculophores lateral to prostomium achaetous, with two pairs of tentacular cirri slightly shorter than palps (Fig. 3a, b).

Segment 2 with first pair of elytrophores and biramous parapodia; ventral or buccal cirri attached basally on prominent cirrophores lateral to mouth, with styles similar to tentacular cirri, longer than following ventral cirri (Fig. 3a, b, e). Mouth opening situated between segments 1 and 2. Muscular pharnyx encircled by seven pairs of

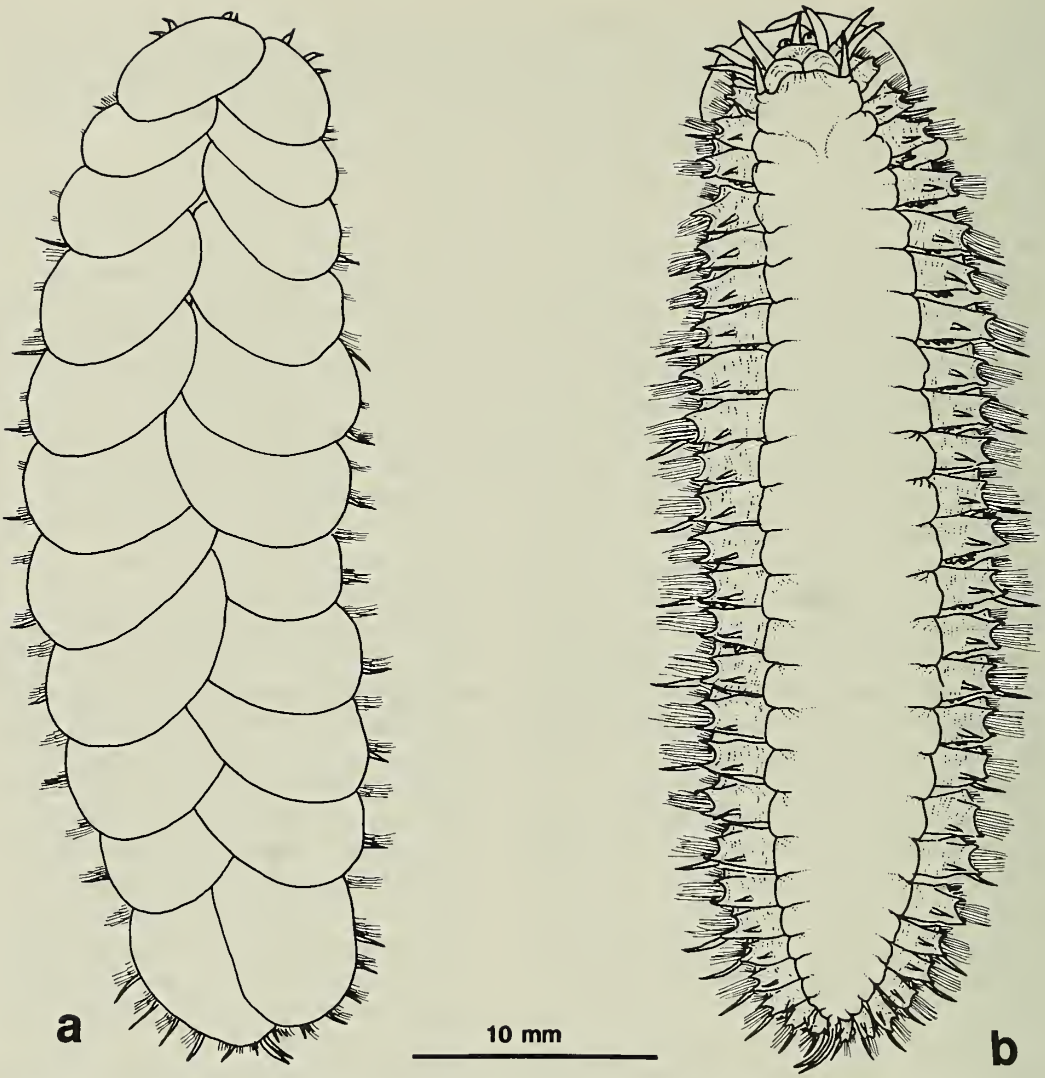

Fig. 1. *Thermopolynoe branchiata,* new species. Paratype (MNHN UD 265): a, Dorsal view; b, Ventral view.

bulbous papillae, subequal in size; dorsal and ventral pairs of jaws fused medially, each with 5–7 teeth on basal sides (observation on dissected paratypes).

Segment 3 with first pair of arborescent branchiae, dorsal cirri, short ventral cirri, and setal lobes similar to segment 2 (Fig. 3a, b, f). Following parapodia biramous, with short notopodia on anterodorsal sides of large neuropodia (Fig. 3g). Notopodia subconical, with projecting acicular lobes hidden by numerous notosetae, and enclosed antero-dorsally by well-developed large flaring bracts (Figs. 3e–g, 4a–c). Neuropodia diagonally truncate, deeply notched on upper part; distal margins fimbriated with slender filaments covered with numerous filamentous bacteria (Fig. 2a–c).

Notosetae numerous, forming radiating bundles, much stouter than neurosetae, serrated on distal margins; tips bare, blunt, tapered (Fig. 4d). Neurosetae numerous,

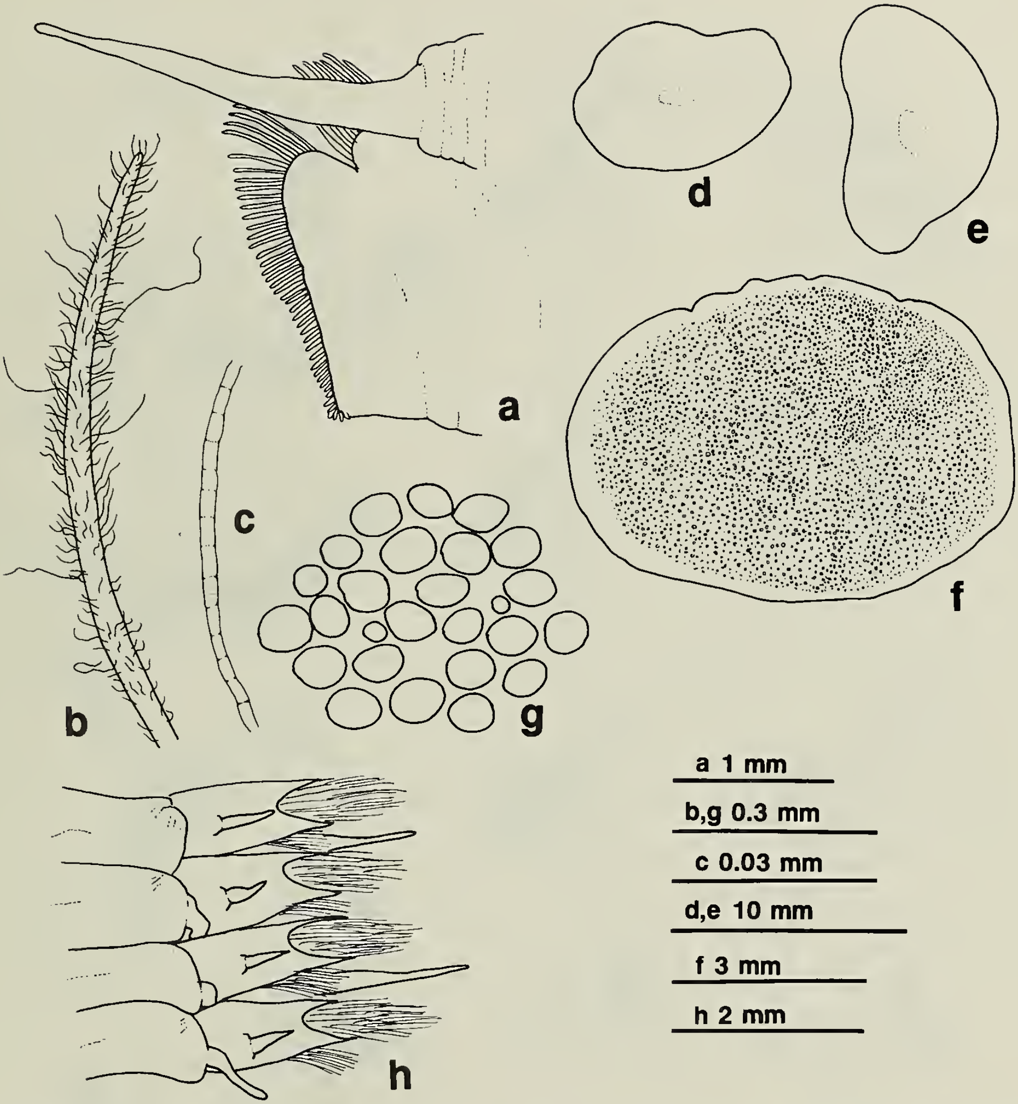

Fig. 2. *Thermopolynoe branchiata,* new species. Paratype (MNHN UD 265): a, Left cirrigerous parapodium from segment 10, anterior view; b, Filament of neuropodium from same, with filamentous bacteria; c, Bacterial filament; d, Left (5th) elytron from segment 9, papillae eliminated; e, Left (11th) elytron from segment 21, papillae eliminated; f, Left (1st) elytron from segment 2, surface micropapillae illustrated; g, Papillae from same; Paratype (MNHN UD 262): h, Left halves of segments 10–13, ventral view.

forming fan-shaped bundles. Supraacicular neurosetae with numerous prominent spines in two rows; tips bare, tapered (Fig. 4e). Subacicular neurosetae with numerous prominent spines in single rows; tips bare, slightly hooked (Fig. 4f).

Ventral segmental papillae long, attached to bases of neuropodia, and extending to bases of ventral cirri; three pairs present on segments 12, 13, and 14 (Fig. 2h), or lacking in half of large specimens (Fig. 1b). Pygidium visible dorsally as bulbous lobe, wedged between parapodia of posterior smaller segments (26–27), with pair of long ventral anal

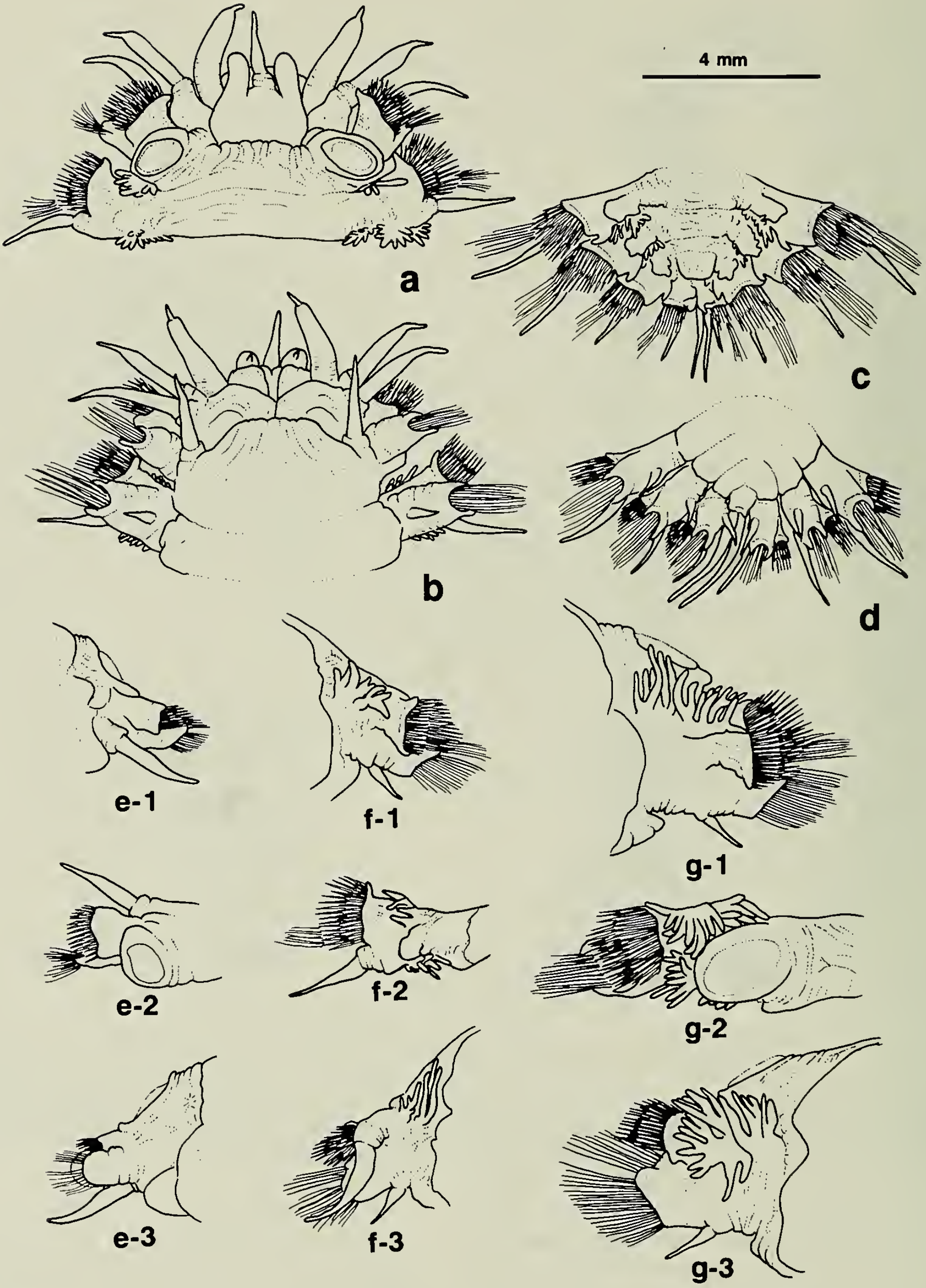

Fig. 3. *Thermopolynoe branchiata,* new species. Paratype (MNHN UD 265): a, Anterior end, dorsal view; b, Same, ventral view; c, Posterior end, dorsal view; d, Same, ventral view; e-1, Left elytrigerous parapodium from segment 2, elytron removed, anterior view; e-2, Same, dorsal view; e-3, Same, posterior view; f-1, Left cirrigerous parapodium from segment 3, anterior view; f-2, Same, dorsal view; f-3, Same, posterior view; g-1, Left elytrigerous parapodium from segment 9, elytron removed, anterior view; g-2, Same, dorsal view; g-3, Same, posterior view.

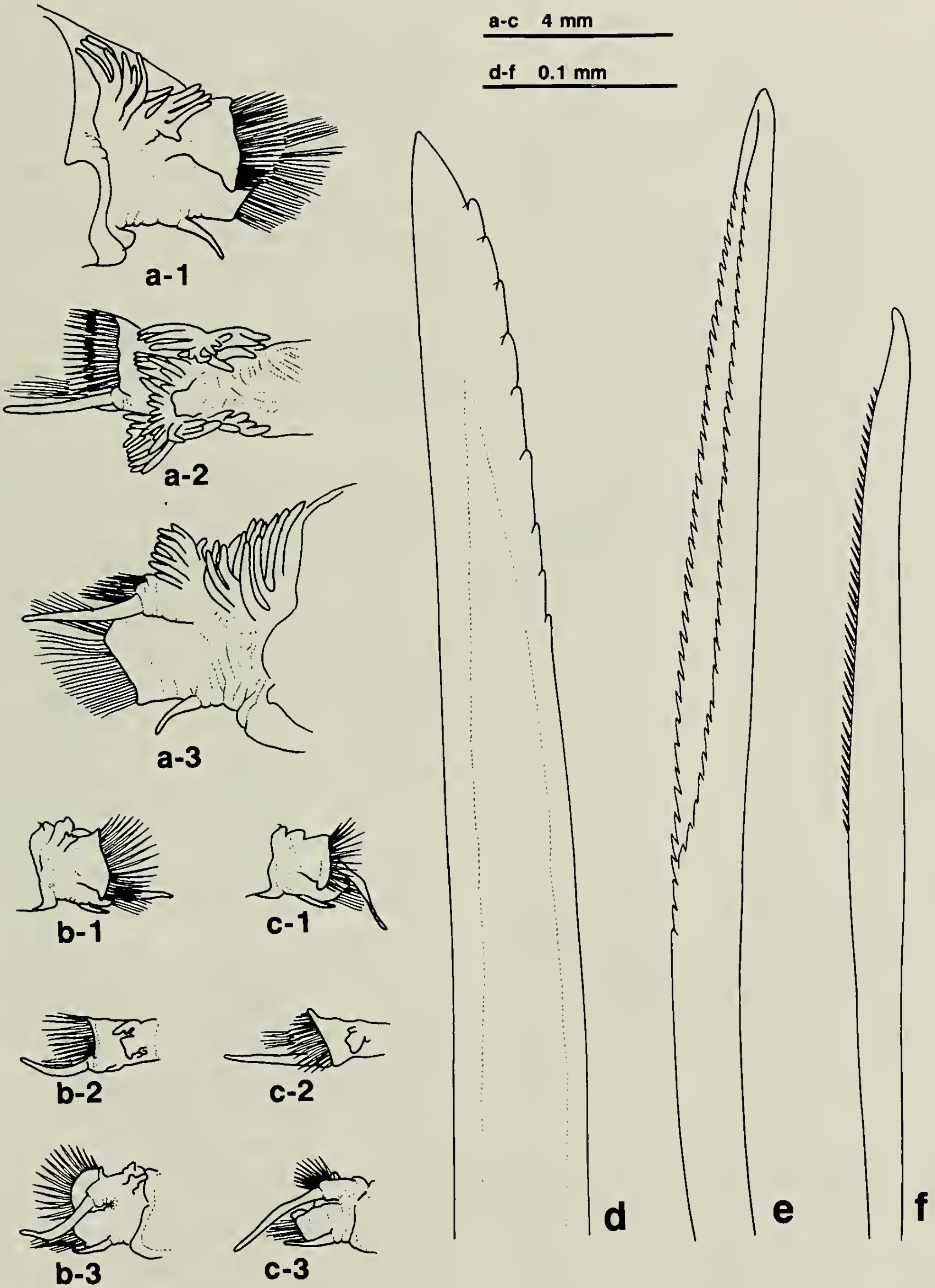

Fig. 4. *Thermopolynoe branchiata,* new species. Paratype (MNHN UD 265): a-1, Left cirrigerous parapodium from segment 10, anterior view; a-2, Same, dorsal view; a-3, Same, posterior view; b-1, Left cirrigerous parapodium from segment 26, anterior view; b-2, Same, dorsal view; b-3, Same, posterior view; c-1, Left cirrigerous parapodium from segment 27, anterior view; c-2, Same, dorsal view; c-3, Same, posterior view; d, Notoseta from segment 9; e, Supraacicular neuroseta from same; f, Subacicular neuroseta from same.

cirri, similar to posterior dorsal cirri (Fig. 3c, d).

Variation in paratypes.—Among the paratypes, two small (young) specimens had less than 27 segments. They were 8.1 and 13 mm long by 4.4 and 6.1 mm wide with 24 and 25 segments, respectively. The specimens with 27 segments varied from 12 mm to 53 mm in length and from 6.5 to 20 mm in width. Of the 22 specimens examined, 12 had three pairs of elongate ventral papillae on segments 12–14, a single specimen had two pairs on segments 12–13, and nine lacked ventral papillae.

Etymology.—The name was derived from the arborescent branchiae of the species.

Remarks.—The structure of prostomium, tentacular segment, and pharynx of the new species recalls the subfamilies Macellicephalinae and Lepidonotopodinae (Pettibone 1976, 1983, 1984b, 1985b, 1988, 1989, 1990). Of the genera of these two subfamilies, *Thermopolynoe* is the closest to *Lepidonotopodium* in having well-developed notopodial bracts, 11 pairs of elytra, long segmental papillae, seven pairs of pharyngeal papillae, and fimbriated neuropodia. However, *Thermopolynoe branchiata* clearly differs from the species of *Lepidonotopodium* in having well-developed arborescent branchiae instead of lacking them.

In the family Polynoidae, the species of three subfamilies, Branchipolynoinae, Branchinotogluminae and Branchiplicatinae, have well-developed branchiae. The first two families have arborescent type of branchiae and the Branchiplicatinae, folded type (Pettibone 1985a). *Peinaleopolynoe sillardi* Desbruyères & Laubier, whose affiliation on the subfamily was not assigned by the authors, also has arborescent branchiae (Desbruyères & Laubier 1988). The species was recently examined and referred to the Branchinotogluminae by Pettibone (1993), along with a new species of *Peinaleopolynoe*: *P. santacatalina.* The presence of these well-developed arborescent branchiae is an unusual feature in the family Polynoidae as mentioned by Pettibone (1984a). *Thermopolynoe branchiata* is, however, unique among these branchiate polynoids in having well-developed bracts encircling the notopodia. The new species differs from them also in the position of branchiae: branchiae are separated in anterior and posterior groups or forming single continued branchial areas in *T. branchiata,* but divided in upper and lower groups in others.

Subfamily Iphioninae Baird, 1865
Thermiphione Hartmann-Schröder, 1992
Thermiphione fijiensis, new species
Figs. 5–7

Material.—White Lady, North Fiji Basin, DSRV *Nautile* Dive 16, 11 Jul 1989, STARMER II Station 4, 16°59.5′S, 173°55.5′W, 2000 m, Holotype (MNHN UD 266) & 8 paratypes (USNM 168326, MNHN UD 263, KU); Dive 20, 15 Jul 1989, 1 paratype (JAMSTEC); Dive 21, 16 Jul 1989, 1 paratype (JAMSTEC).

Description.—Holotype 14 mm long, 7 mm wide including setae, with 31 segments including first setigerous tentacular segment. Largest paratype 20 mm long, 10 mm wide, with 30 segments. Body short, ovate, flattened ventrally and slightly arched dorsally (Fig. 5a, b). Pygidium without appendages (Fig. 5e).

Elytra 14 pairs, large, strongly imbricated, light yellow, stiff, rough with numerous papillae (Figs. 5a, 6a–e), present on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 26, and 27. Eltyra on segment 2 oval, with fringes of short papillae, covered with filamentous bacteria (Fig. 6a, g, h). Other elytra elongate subreniform, narrower medially, wider laterally; lateral borders with fringes of short papillae (Fig. 6b–e). Elytral surfaces covered with hexagonal or polygonal areas with secondary areolae (Fig. 6f). Elytrophores bulbous, transversely elongated; places of attachment with latero-posterior extensions (Fig. 5c, e). Dorsal tubercles on cirrigerous segments bulbous, prominent, transversely elongated, continuous with enlarged cirrophores of dorsal cirri

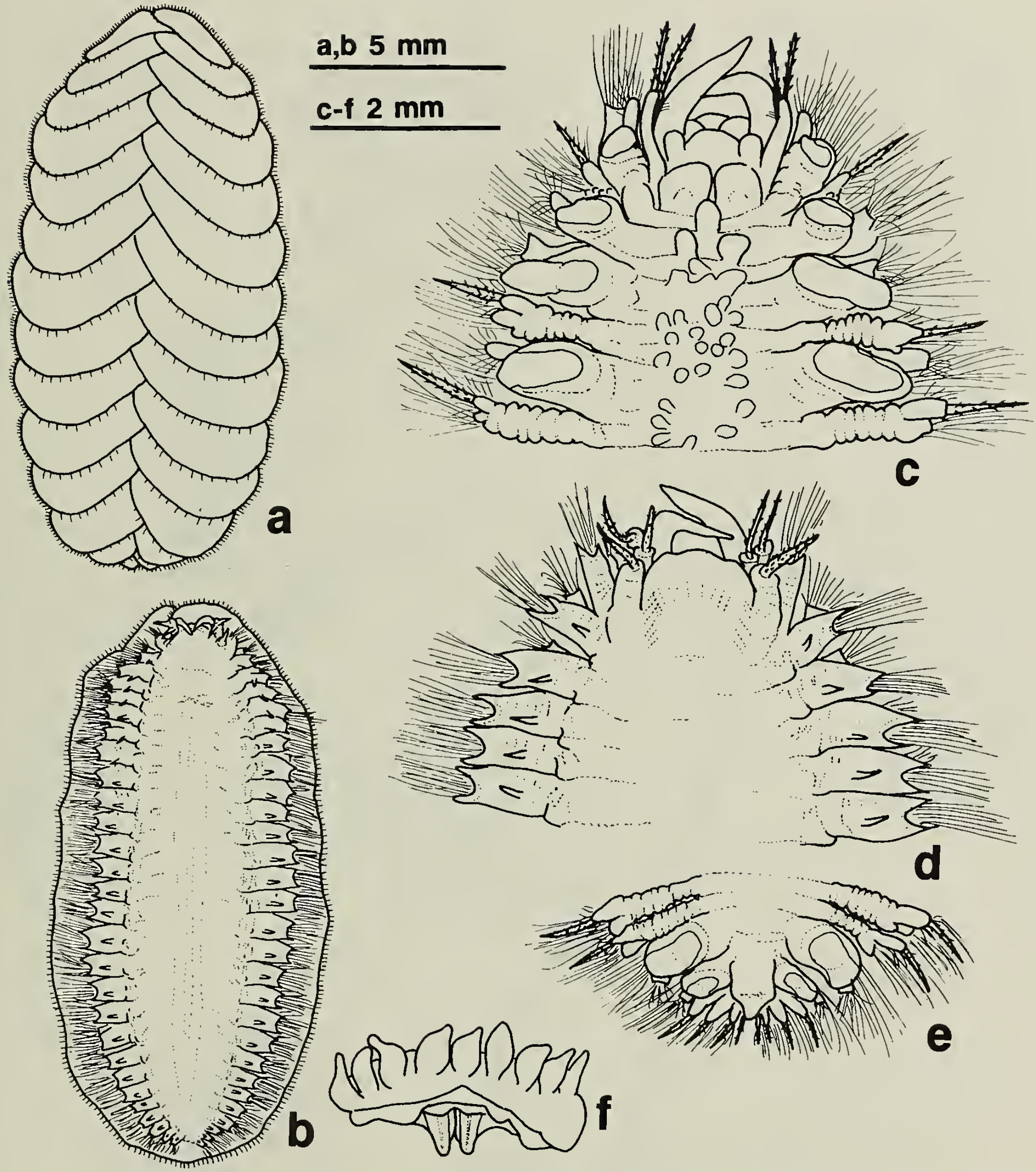

Fig. 5. *Thermiphione fijiensis,* new species. Holotype (MNHN UD 266): a, Dorsal view; b, Ventral view; c, Anterior end, dorsal view; d, Same, ventral view; d, Posterior end, dorsal view; Paratype (JAMSTEC): f, Distal end of pharynx showing jaws and border papillae.

(Figs. 5c, 7e). Dorsal cirri on non-elytrigerous segments with long cylindrical cirrophores and short styles, extending to tips of neurosetae (Figs. 5c, 7c, e). Dorsal and ventral cirri with short clavate papillae (Fig. 7f).

Prostomium partially fused to tentacular segment, and withdrawn in anterior segments (Fig. 5c, d). Prostomium bilobed, forming separate rounded lobes, with anterolateral extensions; without antennae; palps thick, smooth, ventral to lateral prostomial extensions (Fig. 5c). Tentacular segment with long cylindrical tentaculophores lateral to prostomium; each with single aci-

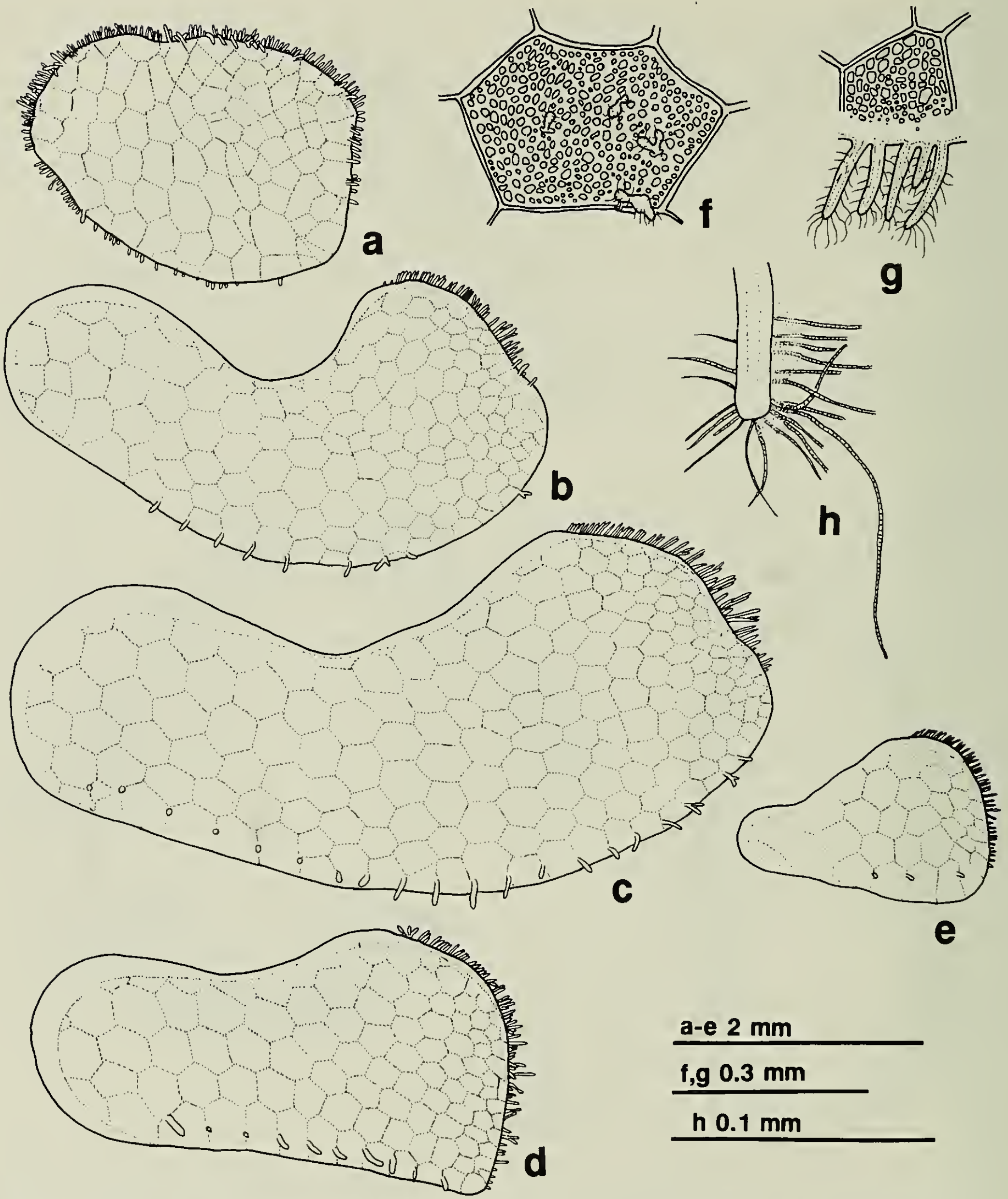

Fig. 6. *Thermiphione fijiensis,* new species. Holotype (MNHN UD 266): a, Right first elytron from segment 2; b, Right elytron from segment 5; c, Right elytron from segment 17; d, Right elytron from segment 26; e, Right elytron from segment 27; f, Enlarged hexagonal area enclosing small areolae of right elytron from segment 2; g, Enlarged margin of right elytron from same; h, Enlarged marginal papilla of same, with filamentous bacteria.

culum, few capillary setae, and dorsal and ventral tentacular cirri, shorter than palps (Figs. 5c, d, 7a, g). Nodular papillae arising from dorsum of anterior segments; more than 20 papillae on anterior 7 segment; arranged in two or more rows before segment 14, thereafter in single row, absent posterior to segment 20 (Fig. 5c).

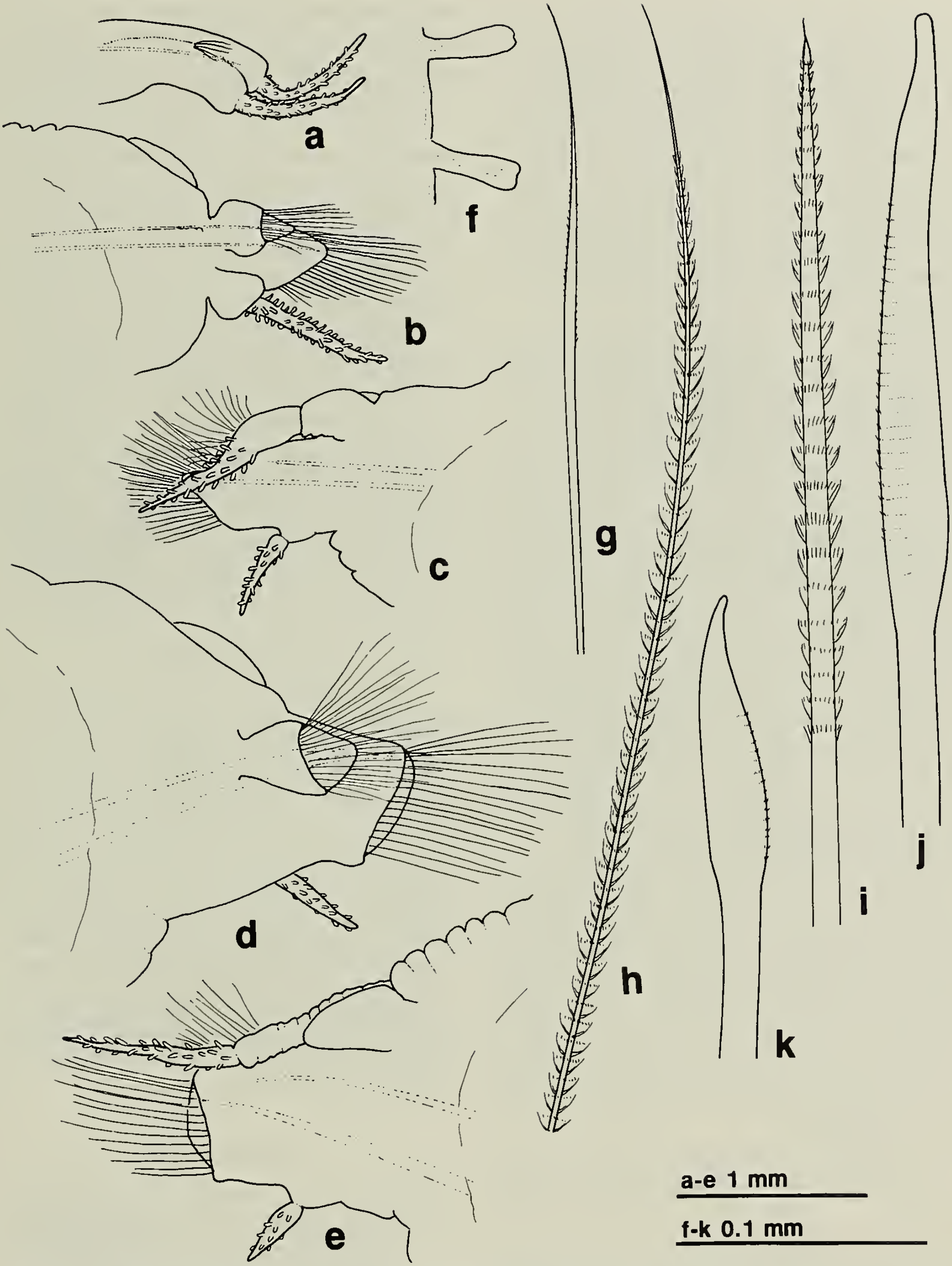

Fig. 7. *Thermiphione fijiensis,* new species. Holotype (MNHN UD 266): a, Left tentaculophore, inner ventral view, single aciculum dotted; b, Left elytrigerous parapodium from segment 2, anterior view, noto- and neuroaciculum dotted; c, Left cirrigerous parapodium from segment 3, posterior view; d, Left elytrigerous parapodium from segment 13, anterior view; e, Left cirrigerous parapodium from segment 14, posterior view; f, Enlarged papillae on ventral buccal cirrus of segment 2; g, Capillary seta from tentaculophore; h, Notoseta; i, Upper feathered neuroseta; j, Middle slightly hooked neuroseta; k, Lower hooked neuroseta.

Segment 2 with single rounded nuchal lobe, elongated elytrophores, first pair of elytra, biramous parapodia, and ventral buccal cirri attached basally on prominent cirrophores lateral to mouth, with styles similar to tentacular cirri, longer than following ventral cirri (Figs. 5c, d, 7b). Muscular pharynx encircled by nine pairs of bulbous papillae subequal in size; dorsal and ventral pairs of jaws fused medially, without teeth (Fig. 5f).

Segment 3 not visible dorsally, with dorsal cirri, and parapodia wedged between elytrophores of segments 2 and 4 (Figs. 5c, 7c). Biramous parapodia with short notopodia on anterodorsal sides of large truncate neuropodia (Fig. 7d, e). Notopodia subconical, with projecting acicular lobes hidden by numerous notosetae (Fig. 7d). Notosetae forming radiating bundles of dense tufts, shorter than neurosetae, feathered, with slender axes and long capillary tips (Fig. 7h). Upper neurosetae feathered, stouter than notoseta, with short capillary tips (Fig. 7i); middle neurosetae stout, hooked, with long, faint spinous areas (Fig. 7j); lower neurosetae similar but shorter, hooked, with short, faint spinous areas (Fig. 7k). Hooked neurosetae first present on segment 3.

Variation in paratypes.—Among the type specimens, three small (young) specimens had less than 30 segments, with 10–12 pairs of elytra. The other specimens had 30 segments and 14 pairs of elytra, except for the holotype with 31 segments. These larger specimens varied from 10.0 to 19.6 mm in length and from 5.5 to 10.0 mm in width. In all specimens, hooked neurosetae started from segment 3.

Etymology.—The species name is derived from the type locality, the North Fiji Basin.

Remarks.—The presence of only a remnant or the complete absence of a median prostomial antenna is characteristic for the subfamily Iphioninae. The Iphioninae differ from other polynoids also by the unique reticulated elytra with hexagonal or polygonal honey-comb-like areas, the tentaculophore of the first segment with a few capillary setae, and styles of the dorsal and ventral parapodial cirri. In four previously known genera of the subfamily, *Iphionides* differs from others in having secondary lattice structure in each polygonal area of elytron, small dorsal tubercles, up to 39 segments, and up to 20 pairs of elytra (Pettibone 1986). Both *Iphione* and *Iphionella* have 29 segments and 13 pairs of elytra. *Thermiphione* differs from the above three genera in having 30–31 segments and 14 pairs of elytra. The last two elytra occur on segments 23 and 27 in *Iphione,* on 23 and 26 in *Iphionella,* and on segments 26 and 27 in *Thermiphione. Thermiphione fijiensis* differs from the other congeneric species *T. tungari* by the first occurrence of hooked neurosetae: segment 3 instead of segment 4 of the latter (Hartmann-Schröder, 1992).

Acknowledgments

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ELECTRA VENTURAENSIS, A NEW SPECIES (BRYOZOA: CHEILOSTOMATA: MEMBRANIPORIDAE) FROM SOUTHERN CALIFORNIA

William C. Banta and Mae M. Crosby

Abstract.—*Electra venturaensis* is described from shallow subtidal water near Ventura, California. It is distinguished from *E. monostachys* (Busk) by lacking typical lateral spines and possessing a calcified operculum, and from *E. crustulenta* (Pallas) by possessing numerous frontal heterozoids and occupying a non-estuarine habitat. Adventitious buds derived from reparative buds or kenozoids derived from spines may form pseudoancestrulae and subcolonies in later astogenetic stages.

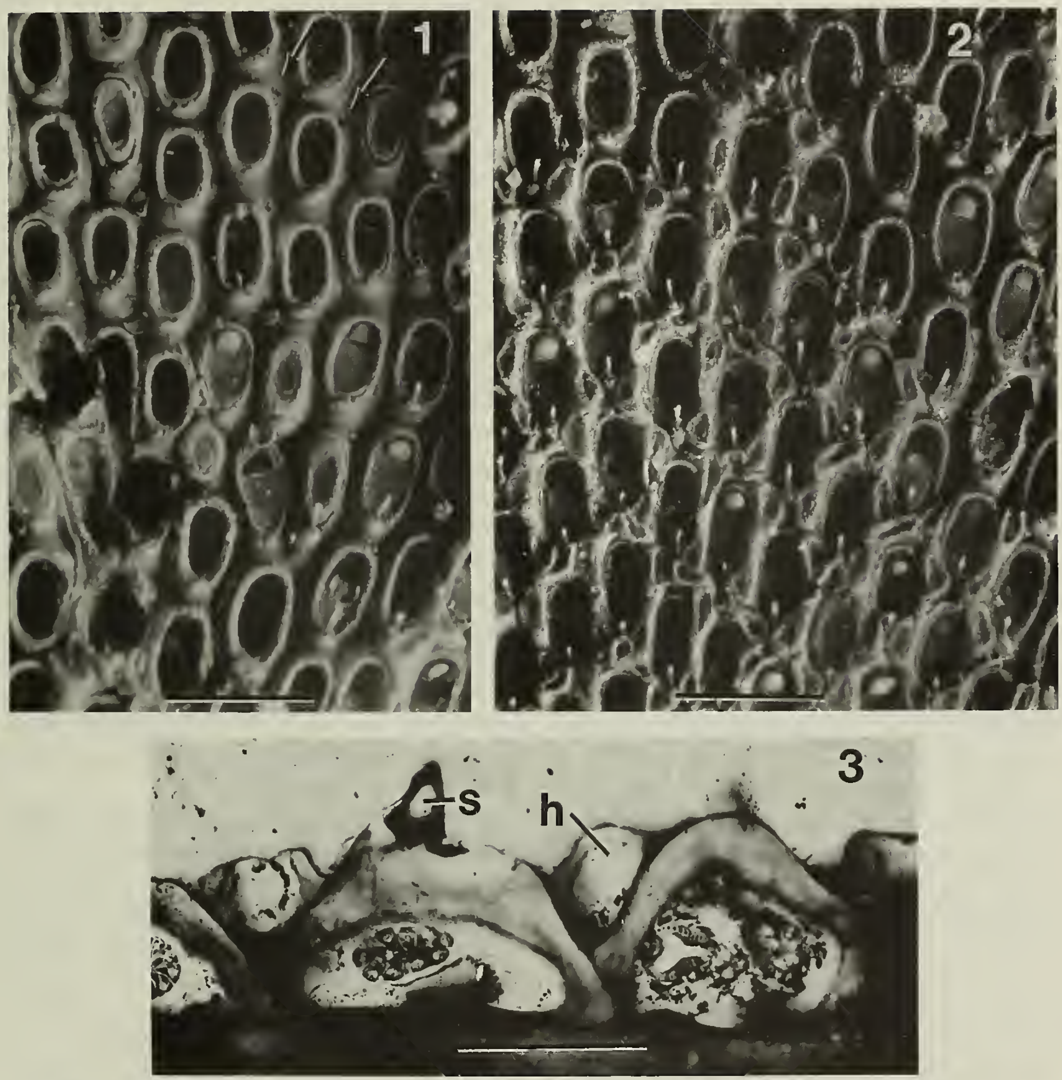
Methods and Materials

Pelecypod shells and other substrates were collected by snorkel in shallow subtidal waters off Rincon Beach, about 5 miles north of Ventura, California on 24 March 1968. Fragments of about 15 colonies were preserved in 70% ethyl alcohol. Some colony fragments were dried and treated varying times in 5% NaOCl or cleaned with dilute detergent in an ultrasonic cleaner. Dry specimens were dyed with 1% aqueous congo red and coated with sublimed ammonium chloride for light photomacrography (Kier et al. 1976). Some material was dehydrated in ethanol to propylene glycol and vacuum-imbedded in Epotuf resin for thin-ground sections containing calcareous tissues in place next to soft tissues (Nye et al. 1972). Additional topotype material: material encrusting sandstone collected 29 Jan 1965, one dry colony and one preserved in 70% alcohol; one dried colony on sandstone collected Dec 1963.

Family Electrinidae Stach, 1937
Genus *Electra* Lamouroux, 1816
Electra venturaensis, new species

Type material.—Holotype: National Museum of Natural History bryozoan Type USNM 477681, slide of dried material (Figs. 1, 2). Paratype: USNM 15005 and 15006, slides of dried material. Topotype material originally identified and labelled *Electra crustulenta arctica* (Borg) was collected at the same site in Dec 1963, and 29 Jan 1965 and preserved dry.

Diagnosis.—Colony pale tan, encrusting shells, unilaminar to multilaminar (1–3 layers). Autozoids arranged in quincunx, completely covering the substrate, without uniserial rows. Ten tentacles. Early astogenetic stages: unilaminar, with proximal, smooth, mostly imperforate gymnocyst occupying about one third of the frontal surface; cryptocyst a narrow, minutely tuberculated rim completely surrounding the opesium. A median proximal, pointed, cuticular spine, a quarter to a third the length of the opesium, projects obliquely forward over the opesium. The base of the spine becomes increasingly calcified with age, forming a centrally perforate hemispherical boss on the gymnocyst. Minute gymnocystal windows, from which frontal-marginal kenozoids will form, are present at the distolateral zoid corners (Fig. 1, arrows). No ovicells, avicularia or other spines. Operculum shaped like a thumbnail, with a straight transverse proximal border; always evenly calcified, white, translucent. Basal wall complete, thinly cal-



Figs. 1–3. 1: *Electra venturaensis,* new species, holotype. Distolateral gymnocystal windows, from which heterozoids develop, are indicated by arrows. Scale, 0.50 mm; 2: Another part of the holotype colony, showing heterozoids. Scale, 0.50 mm; 3: Transverse Epotuf thin section of paratype encrusting a pelecypod shell, showing heterozoids (h) and a spine (s). Scale, 0.10 mm.

cified. Later astogenetic stages: ectocystal buds, calcified basally and laterally, are produced frontolaterally from windows at the distolateral zoidal corners. These buds fill zoidal margins by a rim of frontal kenozoids, which may become partly to completely occluded by annularly calcifying gymnocyst and cryptocyst. Parts of the colony at this stage resemble species of *Conopeum* or *Antropora.* Finally, some kenozoids may enlarge into pseudoancestrular autozoids, which grow out over older colony layers to form subcolonies: superficial layers of autozoids and kenozoids which smother out older layers. Reparative buds, growing from septulae of damaged zoids, may also form new pseudocolonies.

Additional description of the holotype.—

Table 1.—Measurements of the holotype, of *Electra venturaensis* $n = 30$, measurements in mm.

Metric	Autozoid Length	Autozoid Width	Opesium Length	Opesium Width	Operculum Length	Operculum Width
Mean	0.457	0.236	0.335	0.157	0.111	0.095
SD	0.034	0.021	0.028	0.017	0.014	0.011
Min	0.380	0.190	0.270	0.120	0.080	0.080
Max	0.500	0.290	0.380	0.190	0.140	0.120
Range	0.120	0.100	0.110	0.070	0.060	0.040

The holotype comprises several NaOCl-treated fragments of a single colony which encrusted a pelecypod shell. Measurements are given in Table 1. All the features described in the diagnosis are represented except parts lost in cleaning, notably opercula and distal parts of the spines. Distal and lateral septulae are multiporous pore plates, which become surrounded by thick vertical and oblique calcareous buttresses. The gymnocyst is usually imperforate, but minute cuticular windows may occur on its distal-frontolateral face. These windows are the source of kenozoid buds, which appear in later astogeny. The asynchronous development of buds and autozoids is reflected in the structure of the interzoidal walls viewed in section (Fig. 3). Cuticle is present between autozoids and heterozoids in all planes of section except those passing through the relatively small pore plates. Kenozoids contain cells and sometimes parietal muscles, but no polypide. They communicate basally with the parent zoid; this arrangement, together with their location suggests that they represent highly modified, flattened spines.

The first signs of frontal kenozoids occur in distal regions after at least 10 zoidal generations of simple *Electra* morphology. Frontal budding in this species, therefore, may represent either programmed astogenetic change or a response to some microenvironmental cue (Boardman et al. 1969).

Generic placement.—The most widely accepted generic concept of *Electra* is that of Ryland & Hayward (1977:64) who studied European type material. It includes simple malacostegans with relatively large gymnocysts, small cryptocysts, and a median proximal spine, often with additional spines near the opesium. A consistently calcified operculum is rare among cheilostomes, but found in some species of *Electra,* notably *E. crustulenta* Pallas, 1766:39. The generic diagnosis is herein revised to include *E. venturaensis,* which possesses frontal kenozoids.

Etymology.—The species name refers to the city of Ventura, California, derived from archaic Spanish, meaning 'good luck,' 'happiness,' and 'fair destiny.'

Related species.—Horowitz (1992) lists 38 species and subspecies referred to *Electra.* Most closely related is *E. crustulenta typica* (Borg 1931:27), a European stenohaline marine species (Prenant & Bobin 1966:153). A proximal median spine is usually the only spination and there is a calcified operculum with a straight or concave proximal border. It differs from *E. venturaensis* in lacking regular frontal budding, in having more elongated autozoids with a greater average length, 0.72 mm long according to Borg 1931:30, compared to 0.46 for *E. venturaensis*). *Electra crustulenta baltica* (Borg 1931:27) is similar to *E. crustulenta typica,* an exclusively estuarine species frequently lacking median proximal spines. *Electra monostachys* (Busk 1854:61), a British estuarine species, forms uniserial to oligoserial (2–3 rows) stellate or dendritic patches. The median proximal spine may be lacking and numerous spines frequently occur around the opesium; a pair of spines is usually present lateral to the operculum and the operculum is uncalcified (Ryland & Hayward 1977:70). *Electra artica* (Borg 1931:27), is circumpolar, stenohaline (Powell 1968:2282), sometimes pluriserial, the operculum is calcified and the gymnocyst is extensive and imperforate; frontal heterozoids are absent (see Powell & Crowell 1967: 339). Specimens from Alaska identified by Osburn as *Electra crustulenta arctica* (Borg) in the reference collections of the National Museum of Natural History are largely oligoserial and lack frontal heterozoids.

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THE MORPHOLOGY AND GENERIC RELATIONSHIPS OF SOME FISSIPAROUS HETERONEMERTINES

Nathan W. Riser

Abstract.—No morphological difference could be found between a fissiparous heteronemertine from New Zealand and other fissiparous species with similar external appearances. All constitute a single species. Significant anatomical characters are shared with *Lineus lacteus* (Rathke, 1843) and *L. pseudolacteus* Gontcharoff, 1951. The genus *Myoisophagos* is erected to contain the three species with *M. sanguineus* (Rathke, 1799) designated as type species. Significant morphological characters separate the new genus from the genus *Lineus.*

Clumps of slender nemertines were encountered beneath rocks on the reef just seaward of the rubble beach along the outer face of the Kaikoura Peninsula, New Zealand during the early months of 1983 and 1986. The clusters were reminiscent of *Lineus socialis* (Leidy, 1855) from New England midtidal rocky shores as was the pigmentation and rather regularly spaced annuli behind the head region of the body to that of the New England species. Five specimens of comparable size were bisected, one at the first annulus and the others successively one annulus further back to determine if the animals could regenerate. The heads were retained in a single jar, and each of the posterior pieces was placed in a separate jar of sea water maintained on a sea water table. Two days later, the posterior pieces had fragmented; with most of the fragments bearing one or two annuli, rarely three. Fourteen days after fission, the fragments had developed white heads with two red eyes. Existing descriptions of fissiparous lineid species contain no anatomical data by which species can be identified. Living specimens of "species" to which names had been assigned were obtained and a morphological comparison was undertaken.

Materials and Methods

In addition to the specimens from Kaikoura, New Zealand, living specimens of *Lineus lacteus* (Rathke, 1843), *L. pseudolacteus* Gontcharoff, 1951, *L. sanguineus* (Rathke, 1799), and *L. nigricans* Bürger, 1892 were obtained from the colonies maintained by Prof. J. Bierne. Living specimens of *L. vegetus* Coe, 1931 were furnished by Prof. P. Roe from central California rocky beaches, and *L. socialis* (Leidy, 1855) was collected from a number of rocky shoreline outcroppings between Nahant, Massachusetts and Georgetown, Maine. Anesthetization, fixation, sectioning, and staining were as described in Riser (1988).

Systematic Account

Lineidae *sensu* Gibson, 1982
Myoisophagos, new genus

Type species.—*Myoisophagos sanguineus* (Rathke, 1799), new combination.

Diagnosis.—With three apical sensory organs; frontal glands absent; rhynchodaeum attached ventrally and thus with a single cephalic blood lacuna arched over the rhynchodaeum; rhynchocoel muscle layers not interwoven nor interwoven with muscles of body wall; proboscis with two muscle layers, inner longitudinal and outer circular; vascular plexus in foregut region; neurochord cells and caudal cirrus absent; subepidermal gland cells penetrate OLM, some contact medullary nerve plexus; with subepithelial esophageal gland cells and longitudinal muscles; longitudinal muscle plate between rhynchocoel and foregut absent; radial muscles to either side of the rhynchocoel pass beneath the rhynchocoel crossing to the opposite side and continue around the foregut.

Etymology.—*myos* Gr. muscular, *oisophagos* Gr. esophagus.

Radial muscles from the body wall arboresce through the subepithelial esophageal gland layer (Figs. 8, 11). They, with the subepithelial esophageal longitudinal muscles control expansion and contraction of the foregut. The dorsal radial muscles form a sling around the rhynchocoel (Fig. 11) crossing beneath that organ and continuing around the foregut as circular bands. These bands lie amidst the bases of the esophageal glands of the empty foregut (Fig. 8), but are pressed closer to the subepithelial longitudinal muscles of the inflated organ. Friedrich (1935) referred to these radial fibers in the foregut region as dorsoventral muscles.

Bürger (1897–1907; table 3, fig. 18) illustrated the penetration of the sub-epidermal glands to the ICM, as later described by Coe (1931).

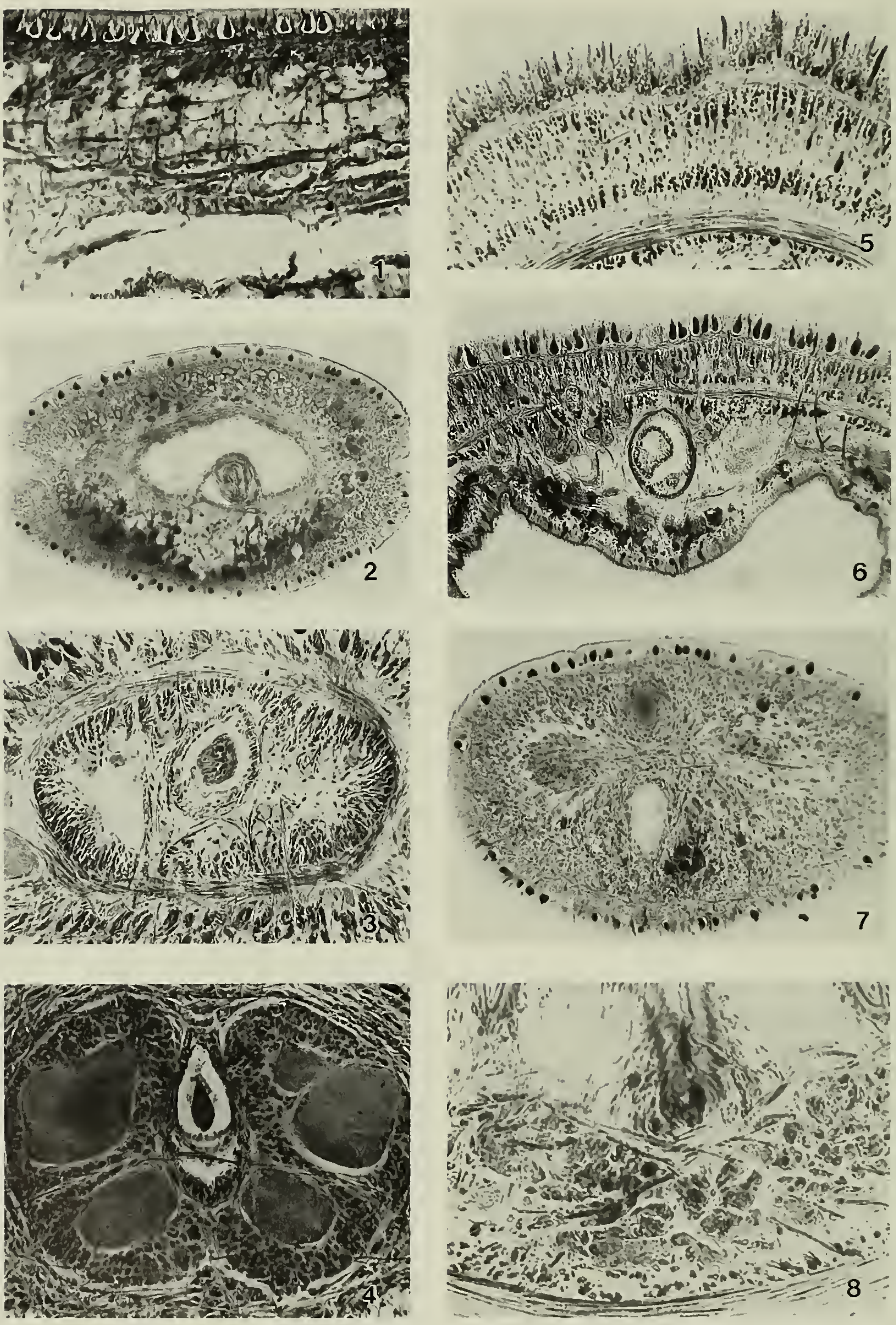
Myoisophagos sanguineus (Rathke, 1799), new combination
Figs. 5, 8–11

Planaria sanguinea Rathke, 1799:83.
Lineus sanguineus McIntosh, 1873–1874: 188–190. auctt.
Lineus nigricans Bürger, 1892:159. auctt. not *L. nigricans* Isler 1901, 1902.
Nemertes socialis Leidy, 1855:143; Verrill, 1873:324, 392, 628.
Lineus socialis Verrill 1892:424–425. auctt.
Lineus ruber, forme β Oxner 1909, 1910; Nusbaum & Oxner, 1910a, 1910b. not *Lineus ruber* (Müller, 1771).
Lineus vegetus Coe, 1931:54–60. auctt.

Species diagnosis.—Gliding individuals may attain 20 cm in length and 1.2 mm diameter. Brain region red, body of small individuals (less than 15 mm long) transparent white or cream color, larger specimens vary from greyish green to brownish black or red. Three to seven ocelli in dorsal wall of cephalic fissures on each side, occasionally the same number on both sides. Anterior end of buccal cavity close to posterior ends of cerebral organs. Subepidermal glands do not penetrate the inner circular muscles. Subepidermal longitudinal muscle bundles are almost as large (Fig. 11) as the bundles of the OLM. Ganglion layer of brain enclosed with connective tissue (Fig. 4). Excretory system usually with a short segment in dorsal wall of right preoral blood lacuna. Sexual reproduction abortive, oocytes aberrant, fissiparous. Contract by spiral coiling.

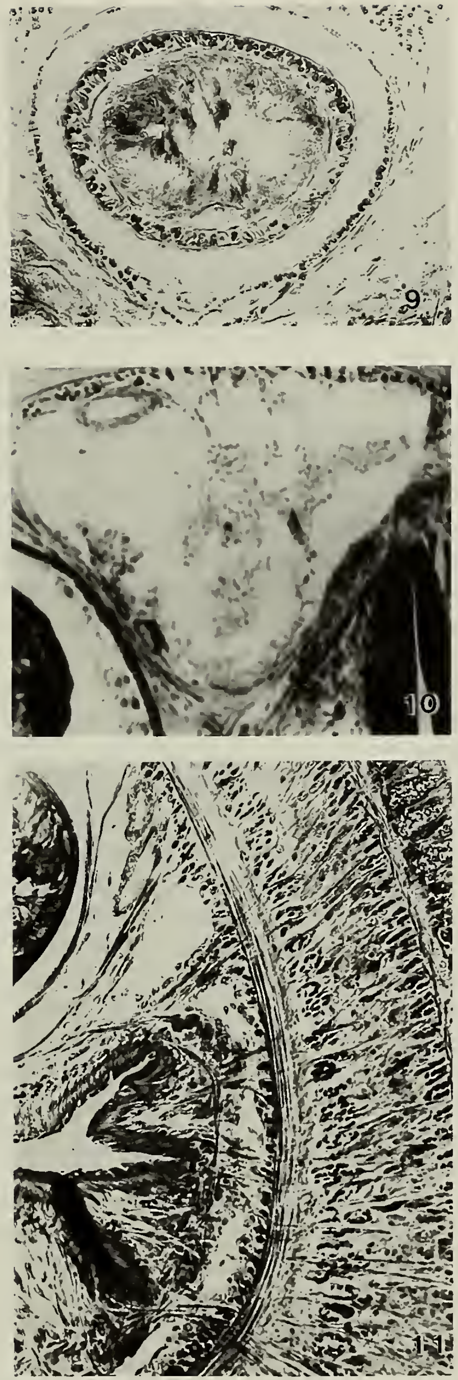
Dr. Janet Moore generously recorded length versus color and ocelli number of living specimens at Kaikoura. She noted that individuals under 20 mm, "slightly extended," were white with three ocelli on each side; specimens from 25–35 mm were red with 3–6 ocelli per side, and beyond that were "very dark" with 5–7 eyes on each side. This corresponds with personal observations of individuals in the Gulf of Maine and with regenerating fragments of the other "species." Specimens collected from mussel beds on exposed cliff faces at Nahant are frequently bright red while those beneath rocks on the nearby reef vary much like the New Zealand individuals. Riser (1993) noted that in culture all of these "species" were indistinguishable by color when fed a diet of *Mytillus/Buccinum* gonad/digestive gland. The uroporphyrin pigment (Vernet & Bierne 1983, Vernet 1983) diminishes in regenerating fragments, and the very small and widely scattered pigment granules are not readily evident in histological preparations of regenerates that have not begun feeding. Regenerating individuals usually pass through a color phase similar to figure 12 in the description of *Lineus flammeus* Monastero, 1930. The closeness of the buccal cavity to the cerebral organs is obvious in living animals.

Preoral contraction may alter the shape of the mouth from elongate to round; draw



Figs. 1–8. 1–4, 7, *Myoisophagos lacteus*; 1, longitudinal section in preoral region packed with parenchymatous connective tissue; 2, cross section near anterior end with ventral parenchymatous tissue, serous glands, and pale (grey) mucus glands; 3, pre-oral, postcerebral cross section through rhynchocoel, and paired cerebral lacunae; 4, cross section through brain with ganglion cells enclosed by connective tissue; 5, *M. sanguineus*, cross section through dorsal body wall; 6, *M. pseudolacteus*, cross section near posterior end of mouth; 7, cross section near rhynchodaeal pore, three apical sensory organs not cut in common plane; 8, *M. sanguineus*, cross section through ventral body wall of foregut region.

the cerebral organs posteriorly to proximate the buccal cavity; and alter the location of post cerebral as well as periforegut organs. Coe (1951b) noted the unique presence of the preoral segment of the excretory system and that it was not connected to the postoral portion, however he mistook the anterior end of the system on the left side to be the posterior end of a preoral segment. Figures 19 and 20 of Corrêa (1956) clearly show the two systems with the efferent duct at the anterior end of the left side exiting in the midoral region. The efferent duct is at the posterior end of the preoral segment and exits on the dorsolateral surface of the body near the anterior end of the mouth. It is not connected with the remainder of the system which begins near the middle of the mouth. In the present study, three or more efferent ducts were routinely encountered on each side in addition to the duct from the preoral system of the one side. Oudemans (1885) noted that the excretory system of his "greatly contracted" specimens did not "reach the mouth" anteriorly, and that the number of efferent ducts appeared to be related to the "growth and age" of the individual. Coe (1931) reported the presence of "several pairs" of "efferent ducts" in *L. vegetus* and one specimen, with five on one side and six on the other. (The type specimens of *L. vegetus* have disappeared and the only slides that he deposited with the Peabody Museum at Yale University are labeled "for anatomical study." The sections are shrunken and folded so that very little information can be obtained from them.) Of the twenty seven anterior ends of specimens sectioned in the present study, one (*socialis*) lacked the preoral segment of the system. Moretto et al. (1976) did not mention a preoral segment in their account and figured three efferent ducts on each side. Cyrtocytes occur in clumps at the anterior ends of both excretory segments, most obviously projecting from the rhynchocoel wall (Fig. 10) but also in scattered clumps along the dorsal and lateral walls of the blood lacunae.



Figs. 9–11. *Myoisophagos sanguineus*; 9, cross section through anterior proboscis; 10, cross section through anterior oral region with cyrtocytes on rhynchocoel wall; 11, cross section through posterior oral region with radial muscles forming sling and circular bands.

Differential contraction of the muscles can be seen in cross sections in which the subepidermal longitudinal muscle bundles appear to be duplicated with a spiral fiber from the subepidermal circular muscles dividing the bundles (Fig. 5).

Coe (1899) stated that the eggs of *L. socialis* matured in "mid-winter" and sometimes were "deposited in captivity in masses of mucus" where they developed "readily at least to the stage of swimming gastrulae." In 1943, he listed *L. socialis* as an abundant species which furnished "excellent material for the study of normal and experimental embryology" and, without elaboration, stated that "some individuals reproduce sexually during the autumn and early spring." McIntosh (1873–1874) reported that the eggs of *L. sanguineus* matured in October but did not mention spawning. Gontcharoff (1951) noted the presence of gonopores in the males of *M. sanguineus* and a single observation of the shedding of sperm. She noted that female gonoducts rarely could be found penetrating the epidermis; oocytes were few in number; spawning did not occur in culture, nor when freshly collected specimens were paired in vitro. She tentatively concluded that oogenesis was abortive, and that propagation of the species was by asexual reproduction. She noted absorption of oocytes, and their occasional occurrence in the intestine. The ovaries of some females collected at Nahant in April and May contained oocytes which had undergone autolysis, with only the nucleolus, nuclear membrane and much wrinkled cell membrane distinguishable. Degeneration of the nearby wall of the intestine as reported by Gontcharoff, sometimes was apparent, although oocytes were not encountered in the lumen of the gut. "Normal oocyte development" was reported for *L. sanguineus* from Uruguay by Bierne (1983), [recorded as *L. socialis* in Bierne et al. (1993)]. Oocyte production and sexual reproduction are not synonymous and references to the latter event are questionable, but, genetic evidence (Alex Rogers, pers. comm.) suggests that some sexual reproduction occurs in this species.

Coe (1951) noted that the fauna of southern Florida was tropical and that boreal species such as *L. socialis* were restricted to the northern Gulf of Mexico and northern coast of Florida on the Atlantic side. J. Norenburg (pers. comm.) observed "*L. socialis*" with "mature ova" along the Indian River near Fort Pierce, Florida in January. The identification by Corrêa (1961) of *L. socialis* from the Virgin Islands based upon the appearance of the head of a "preserved fragment" is suspect. Isler (1901, 1902) recorded *L. nigricans* from Punta Arenas, Chile among the preserved specimens collected by Plate, but furnished no data to support the identification. His slides are of an unknown species which does not conform to *Lineus* nor to *Myoisophagos. M. sanguineus* is a temperate-water intertidal species that is tolerant of gradual salinity and thermal changes. Under adverse conditions, individuals undergo fragmentation and some of the fragments may encyst. Verrill (1873) listed *Nemertes socialis* among "species commonly found on piles and timbers of wharves and bridges on buoys, bottoms of vessels, and other submerged wood-work." The biology of *M. sanguineus* would allow for transport in the fouling community on ships and account for the wide distribution of the species in temperate waters.

Myoisophagos pseudolacteus (Gontcharoff, 1951), new combination

Fig. 6

Lineus pseudolacteus Gontcharoff, 1951:157 auctt.

Lineus sanguineus pseudolacteus Bierne, Tarpin, & Vernet, 1993:165.

Species diagnosis.—Gliding individuals may attain 20 cm in length and near 1.2 mm in diameter. Brain region red, body pink anteriorly and yellowish white posteriorly, sometimes with a slight greyish tinge or blotching. Approximately seven small ocelli in roof of each cephalic fissure. Posterior end of cerebral organs some distance in front of buccal cavity. Some subepidermal glands penetrate into lateral rhynchocoelic blood lacunae (Fig. 6) and into lacunae dorsal and lateral to buccal cavity and initial esophagus. Ganglion layer of brain scattered into surrounding tissues, not enclosed in connective tissue. Sexual reproduction abortive, fissiparous. Contract by coiling.

No preoral excretory tissue was evident in any of the five specimens that were sectioned but a short segment was present to either side of the mouth (Fig. 6) with the efferent ducts exiting dorsally anterior to the esophagus. The nephric tubules of the rest of the system were of very small diameter and were often encased in subepidermal packet glands. They were not connected to the oral segments, and were first encountered some distance posteriorly but exited anterior to the esophageal/intestinal junction. Two lots of specimens were obtained about a year apart in an effort to resolve the peculiarities of this system. It was difficult to trace efferent ducts beyond the ICM, in part because of the large necks (Fig. 6) of the packet glands. All of the specimens may have belonged to a single clone and the peculiarities of the excretory system might be an abnormality. In some of the specimens there was a proliferation of mesenchyme cells obliterating the blood lacunae around parts of the foregut.

Gontcharoff (1951) considered the relationship of the posterior ends of the cerebral organs to the buccal cavity to warrant the separation of the species from *L. sanguineus.* Bierne (1993) utilized the color pattern of the adult antecerebral end as a character state distinguishing the subspecies *pseudolacteus* from *sanguineus.* They also noted that female *pseudolacteus* had never been collected.

Myoisophagos lacteus (Rathke, 1843),
new combination
Figs. 1–4, 7

Ramphogordius lacteus Rathke, 1843:237.
Nemertes lactea Grube, 1855:151; Diesing, 1862:303; Czerniavsky, 1881:255.
Borlasia lactea Parfitt, 1867:215; McIntosh 1868, 1869.
Lineus lacteus McIntosh, 1873–1874:190. auctt.

Species diagnosis.—Gliding individuals may attain lengths in excess of 20 cm and 2 mm in diameter. Brain region red, body white to cream color. Ocelli may exceed seven in number on each side. Buccal cavity some distance behind posterior ends of cerebral organs. Some subepidermal glands penetrate into the two rhynchocoelic blood vessels and into the two dorsal blood lacunae above the buccal cavity, many abut the nerve plexus outside the inner circular muscles behind the mouth. Ganglion layer of brain enclosed with connective tissue. Excretory system with preoral segment on both sides. Gonochoric with pilidium larva. Contract by spiral coiling.

The distance between the buccal cavity and the cerebral organs, which is obvious in living animals, may be shortened by poor fixation procedures. The presence of excretory tubules in both lateral rhynchocoelic blood vessels and the penetration of the cell bodies of subepidermal glands (Fig. 3) into those vessels should alleviate any problems in identifying the species from serial sections.

Bierne et al. (1993) stated that "the five fissiparous *Lineus* species" shed eggs "directly in the sea water to develop into pilidium larvae." This has only been observed for *M. lacteus,* females being unknown in *M. pseudolacteus,* and the questionable comment by Coe (1889) re "*L. socialis*" is in total disagreement.

Remarks.—There is extensive literature dealing with this group of species, but most of it is involved with fissioning, grafting, and regeneration. The heterograft studies of Bierne & Langlet (1974) clearly indicated genetic affinities of the species included in *Myoisophagos* in contrast to the disparate genetic implications of results with other *Lineus* species. Isozyme analyses by Alex Rogers (pers. comm.) support the separation of *Myoisophagos* from *Lineus* as well as the necessity for generic reassignment of *L. ruber* and *L. viridis.* The phylogenetic analysis by Bierne et al. (1993) utilized many of these characters but did not include morphological features. Their data lumped all of the fissiparous species including *L. pseudolacteus,* into a single species, *L. sanguineus,* and they erected three subspecies. Riser (1993) had concluded that all except the latter form constituted the species *L. sanguineus.*

The genus *Lineus* is characterized by the dorsal and ventral attachment of the rhynchodaeum dividing the cephalic blood lacuna into two lacunae which unite anterior to the rhynchodaeal pore, the presence of a thick layer of connective tissue separating the subepidermal gland layer from the OLM, the radial muscles forming a sling around the rhynchocoel but not continuing as a loop around the foregut, and the presence of a longitudinal muscle plate between the foregut and rhynchocoel. (The longitudinal muscle plate is initially interwoven with the bottom of the muscle sling that suspends the rhynchocoel from the dorsal wall of the body. These longitudinal muscles spread across the foregut postorally and extend between the bases of the subepithelial glands and the walls of the blood lacunae around the lateral esophageal wall almost to the level of the lateral nerve cords. They frequently occur among the bases of the glands in sections of contracted specimens.) These morphological features are not present in *Myoisophagos.* The subepithelial longitudinal esophageal muscles of *Myoisophagos* (Figs. 6, 11) continue beneath the intestinal cells for a short distance. Foregut rugae are rarely encountered dorsally in heteronemertines but usually are present laterally and ventrally where radial muscles insert among the epithelial cells of this portion of the gut (Fig. 11), facilitating dilation of the organ for ingestion of food, and producing sulci and rugae in the empty organ. Species of *Myoisophagos* are capable of ingesting food items more than twice the diameter of their bodies. *Tenuilineus* species are similar in dimensions to *Myoisophagos* but lack subepithelial esophageal longitudinal muscles and have a weakly developed radial musculature with very shallow sulci between small rugae and thus, the foregut is not capable of much expansion, nor of independent peristaltic waves to pass large particles into the hindgut. [The circular bands around the foregut of *Parborlasia corrugatus* (McIntosh, 1867), a species which can ingest very large food items, receive many fibers from the lateral and ventral radial muscles, producing a very thick layer which presses against the subepithelial glands but does not penetrate amongst them, however the dorsal radial muscles cross beneath the rhynchocoel as in *Myoisophagos.* The type specimens of *Mixolineus tauricus* Müller & Scripcariu, 1971 were retained by the authors and their present disposition is unknown. Their description differs from *Myoisophagos* in the absence of "splanchnic" muscles and the presence of an internal circular muscle layer in the proboscis. The role of radial fibers around the foregut is discussed and the reference to the absence of "splanchnische Muskulatur" appears to refer to the derivation of circular fibers from radial fibers. The figure of the cross section of the anterior proboscis Of *Mixolineus tauricus* is similar to that routinely encountered in *Myoisophagos* (Fig. 9) in which the thick endothelium can be mistaken for muscles especially where individual cells have been lifted off the longitudinal muscles.] Subepidermal mucus glands do not discharge at the apex of the head, and thus, frontal glands are absent. A few subepidermal mucus glands discharge laterally and ventrally around the proboscis pore (Fig. 7). The concentrated parenchymatous tissue of the precerebral region (Figs. 1, 2) sometimes included with the subepidermal glands as cephalic glands in heteronemertines extends ventrally almost to the brain but does not extend quite that far dorsally. Prenant (1922 Pl.V, fig. 2) referred to this tissue as supportive tissue consisting of "cellules vésiculeuse à mucus."

Moretto et al. (1976) noted the absence of a longitudinal muscle plate between the rhynchocoel and foregut, and the presence of the subepithelial longitudinal esophageal muscles, as characters that distinguish *M. sanguineus* and *M. lacteus* from *Lineus ruber* and *L. viridis.* The latter two species have an undivided blood lacuna arched over the rhynchodaeum, and lack a connective tissue layer separating the subepidermal glands from the OLM as noted by Riser (1993), and thus cannot be retained in the genus *Lineus.* Friedrich (1935) established the genus *Heterolineus* and against the rules of nomenclature, designated *Lineus longissimus,* the type species of the genus *Lineus,* as the type species of his new genus. Cantell (1976) noted without comment that the basic morphology of *Heterolineus longissimus* Friedrich, 1935 differed radically from that of *Lineus longissimus* (Gunnerus, 1770). *Heterolineus* may be a valid genus but the type species must be rediscovered and adequately described. Neither species assigned to it can be placed in *Myoisophagos.*

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COLOLOBUS, PSEUDOPIPTOCARPHA, AND *TREPADONIA,* THREE NEW GENERA FROM SOUTH AMERICA (VERNONIEAE: ASTERACEAE)

Harold Robinson

Abstract.—Three genera of Vernonieae subtribe Vernoniinae are described as new from South America. *Cololobus* includes three species from the Espirito Santo area of Brazil. The type species, *C. hatschbachii* H. Robinson, is described as new, and combinations are made for *Vernonia rupestris* Gardner and *V. longiangustatus.* The genus is unique in the Vernonieae and most of the Cichorioideae in the short lobes of the disk corollas. *Pseudopiptocarpha* is described from Colombia, and combinations are made for the type, *Vernonia elaeagnoides* H.B.K., and a second species *V. schultzii* Karsten, which have small axillary heads, appressed and short-stalked T-shaped hairs, quadrate raphids in the achene wall, and *Aynia*-type pollen. *Trepadonia* is named from the Andes of northern Peru for the single species *V. mexiae* H. Rob. The genus is similar to *Vernonanthura* H. Robinson but differs in the pyramidally thrysoid inflorescences with long racemiform branches and is unusual in the scandent habit.

Studies of the neotropical Vernonieae have resulted in removal from *Vernonia* Schreb. of most species of that area that were once placed in the genus (Robinson 1980, 1987a, 1987b, 1987c, 1988a, 1988b, 1988c, 1989a, 1989b, 1990, 1992a, 1992b, 1993a, 1993b; Robinson & Funk 1987; Robinson & King 1979). Of the few species of *Vernonia* from South America not transferred, two of the Brazilian species, *V. echioides* Less. and *V. incana* Less., have the decumbent stem bases and wholly cymiform inflorescences of true *Vernonia* and are considered a peripheral element of that genus. There are other isolated species that have been studied and that are awaiting transfer to existing segregate genera. The remaining unplaced species of *Vernonia* in Brazil, Colombia, and Peru that are treated here form three genera here described as new. The Brazilian species are placed here in the new genus *Cololobus.* The genus *Trepadonia* is established for *Vernonia mexiae* H. Robinson (1981) from Peru. *Pseudopiptocarpha* is established for two species from Colombia that have been treated at different times as part of *Vernonia* or, in the case of one species, as part of *Piptocarpha* R.Br.

The pollen grains are measured in Hoyer's solution.

Cololobus H. Robinson, gen. nov.

Type: *Cololobus hatschbachii* H. Robinson
Figs. 1–9

Plantae suffruticosae vel subarborescentes ad 2.5 m altae pauce ramosae. Caules brunnescentes teretes vix striati non fistulosi tomentelli vel in parte glabri in ramis juvenitatis lanati, pilis biformibus interdum uniseriatis base 1–5-septatis in cellulis apicalibus elongatis interdum sessilis T-formibus longe ramosis. Folia alterna, petiolis ad 3 cm longis interdum alatis; laminae subcoriaceae oblongae vel obovatae base acuminatae margine crenulatae vel serrulatae apice obtusae supra puberulae subtus tomentellae et dense glandulo-punctatae, nervis secundariis crebro pinnatis utrinque 12 vel ultra late patentibus. Inflorescentiae thyrsoideo-paniculatae in ramis thyrsoideae in ramulis corymbiformes; bracteis inflorescentiis anguste ellipticis vel linearibus, pedunculis brevibus puberulis. Capitula homogama; involucra late campanulata 4–5 mm alta et 6–8 mm late; bracteae involucri gradatim auctae leniter induratae ovatae vel lanceolatae, exteriores fusco-virides puberulae vel tomentellae ca. 4-seriatae, interiores persistentes pallides plerumque glabrae ca. 2-seriatae in sicco leniter contortae; receptacula epaleacea. Flores 20–30 in capitulo; corollae roseae regulares anguste infundibulares 4.0–6.5 mm longae extus non piliferae, in tubis et faucibus canalibus resiniferis brevibus obsoletis dispositis, tubis superne sensim infundibularibus, faucibus ca. 1.5 mm longis, lobis brevioribus erectis non contortis 0.5–1.3 mm longis extus minute glanduliferis non ductiferis, nervis distaliter vix incrassatis; thecae antherarum 1.0–1.3 mm longae base rotundatae non caudatae; appendices antherarum apicales ovatae 0.3–0.4 mm longae glabrae in parietibus cellularum non incrassatae non ornatae; basi stylorum annuliformiter nodati; rami stylorum 1–2 mm longi non glanduliferi hispiduli; pili stylorum apice rotundati. Achenia matura non visa; achenia immatura ad 1 mm longa glandulifera setulifera et interdum T-formiter pilifera, raphidibus subquadratis; carpopodia breviter obturaculiformia; setae pappi ca. 20 albidae subpersistentes 2.5–5.0 mm longae apice distincte vel non latiores plerumque margine scabridae; squamae exteriores oblongae 0.5–1.0 mm longae extus sublaeves. Grana pollinis in diametro ca. 42 μm tricolporata echinata in areolis omnino in tectis perforatis obsita.

Three Brasilian species from the State of Espirito Santo and nearby areas of Minas Gerais and the Serra dos Orgãos of Ets. Rio de Janeiro are placed here in the new genus *Cololobus.* They are members of the subtribe Vernoniinae, having an enlarged basal style node and the persistent involucral bracts typical of that subtribe. This is in spite of the fact that the style hairs are blunt as in many members of the Piptocarphinae. The position within the Vernoniinae is with *Vernonia* and *Vernonanthura* H. Robinson rather than with the *Lepidaploa* complex as indicated in *Cololobus* by the type A pollen, the lack of hairs on the corollas, and the subquadrate raphids of the achene wall. *Cololobus* has erect, branching stems and thyrsoid inflorescences as in *Vernonanthura,* a genus containing more than 60 species and found throughout the neotropics (Robinson 1992b), but it differs in the form of its corollas.

The corolla of *Cololobus* is its most distinctive feature. The disk corollas are unique in the Vernonieae and among the few in the Cichorioideae with short lobes. Corolla lobes of disk corollas in the Cichorioideae are usually lanceolate or linear. It is the subfamily Asteroideae that usually has shorter lobes in the disk corollas. The lobes in *Cololobus* are 1–2 times as long as wide. There is no evidence of resin ducts in the lobes. Resin ducts in the corollas have not been surveyed extensively in the Vernonieae, but ducts are evident in the lobes of many species of all parts of the genus *Vernonanthura.* Such resin ducts have not been seen elsewhere in Vernonieae, except in the close *Vernonanthura* relative *Trepadonia* H. Robinson. *Cololobus* has only some series of cells in the tube and throat of the corolla that may be rudimentary resin ducts.

The new genus is named *Cololobus* in reference to the abbreviated nature of its corolla lobes.

The three species of *Cololobus* are keyed as follows:

1. Petioles winged to base; stems tomentellous; achenes sometimes with many T-formed hairs having short lower arm and long upper arm; style branches ca. 2 mm long . . *C. rupestris*

Figs. 1–9. *Cololobus.* 1–8. *C. hatschbachii* H. Robinson: 1. Habit; 2. Head; 3. Corolla with anther and style tips; 4. ½ of corolla with included stamens; 5. Style with small basal node; 6. Achene with pappus; 7. Raphids of achene wall; 8. Setula of achene. 9. *C. rupestris* (Gardner) H. Robinson; T-shaped hair from achene from Brade 19780 (US).

1. Petioles not or scarcely winged; stems partly glabrous to tomentellous; achenes with only glands, biseriate setulae, and a few short uniseriate hairs; style branches ca. 1 mm long.
2. Involucral bracts all with erect tips; corolla lobes scarcely longer than wide; tips of pappus bristles broadened, with crowded cells .... *C. longiangustatus*
2. Outer involucral bracts with recurved tips; corolla lobes half again as long as wide; pappus bristles not broadened at tips, without more crowded apical cells ... *C. hatschbachii*

Cololobus hatschbachii
H. Robinson, sp. nov.
Figs. 1–8

Plantae fruticosae 1.5 m altae; caules glabrescentes, internodis 5–10 mm longis. Folia alterna, petiolis 1.0–1.5 cm longis distaliter indistincte delimitatis vix alatis; laminae obovatae 5–9 cm longae 1.5–3.5 cm latae basi anguste cuneatae margine dense serrulatae apice obtusae supra dense pilosulis subtus cinereo-tomentellis et dense fuscate glandulo-punctatae. Inflorescentia anguste thyrsoidea ca. 28 cm altae, ramis thyrsoideis 1.5–5.0 cm longis in ramulis corymbiformibus, superficiis sparse subtomentellis, bracteis primariis anguste ellipticis vel linearibus 0.5–3.0 cm longis, bracteis ramulorum minutis 2–3 mm longis scariosis, pedunculis 1–5 mm longis tomentellis. Capitula late campanulata 7–9 mm alta et lata; bracteae involucri 5- vel 6-seriatae; bracteae exteriores ca. 35 ca. 4-seriatae fuscae ovatae 1.5–2.5 mm longae ca. 0.8 mm latae dense tomentellae apice reflexae; bracteae interiores ca. 22 ca. 2-seriatae flavae lanceolatae ca. 5 mm longae et 0.8 mm latae subglabrae apice non vel leniter reflexae. Flores in capitulo 20–30; corollae lilacinae ca. 5 mm longae, tubis ca. 2.5 mm longis, faucibus ca. 1.5 mm longis, lobis ca. 1 mm longis extus minute glanduliferis; thecae antherarum ca. 1 mm longae; appendices apicales antherarum ca. 0.42 mm longae; rami stylorum ca. 1 mm longi. Achenia immatura ca. 1 mm longa ca. 8-costata inter costam dense setulifera solum basi et apice pauce glandulifera, idioblastae nullae; setae pappi ca. 3.5 mm longae, cellulis apicalibus non densiores non patentiores; squamae exteriores 0.5–0.7 mm longae. Grana pollinis in diametro ca. 42 μm.

Type: Brazil; Espirito Santo: Rod. BR-101, 5–10 km S de João Neiva, paredoes rochosos, arbusto 1.50 m, capitulos lilas, 13 Oct 1992, Hatschbach, Cervi & Silva 58012 (holotype MBM, isotype US).

The species is most easily distinguished by the reflexed tips of the involucral bracts. The stems also are partly glabrous or glabrescent in the type specimen, but the full range of the latter character is not known. The new species lacks the tomentellous stems, winged petioles, longer style branches, or long uniseriate hairs and more uniformly distributed glands on the achene seen in *C. rupestre*. At the same time it lacks the short equilaterally triangular corolla lobes, obvious idioblasts on the achene, and denser more spreading apical cells of the pappus seen in *C. longiangustatus*.

Cololobus longiangustatus
(G. M. Barroso)
H. Robinson, comb. nov.

Vernonia longi-angustata G. M. Barroso, Arq. Jard. Bot. Rio de Janeiro 13:12. 1954. Espirito Santo, Minas Gerais.

Cololobus rupestris (Gardner)
H. Robinson, comb. nov.

Vernonia rupestris Gardner, London J. Bot. 4:114. 1845. Rio de Janeiro, Espirito Santo.

One specimen observed from southwestern Espirito Santo (Brade 19780, US) shows unusual T-shaped hairs (Fig. 9) in addition to the setulae and glands on the achene. The hairs have a long arm pointing upward and a shorter arm pointing downward. Such hairs have not been seen in a specimen from the State of Rio de Janeiro (Sucre 2488/Braga 330, single sheet, NY).

Pseudopiptocarpha H. Robinson, gen. nov.

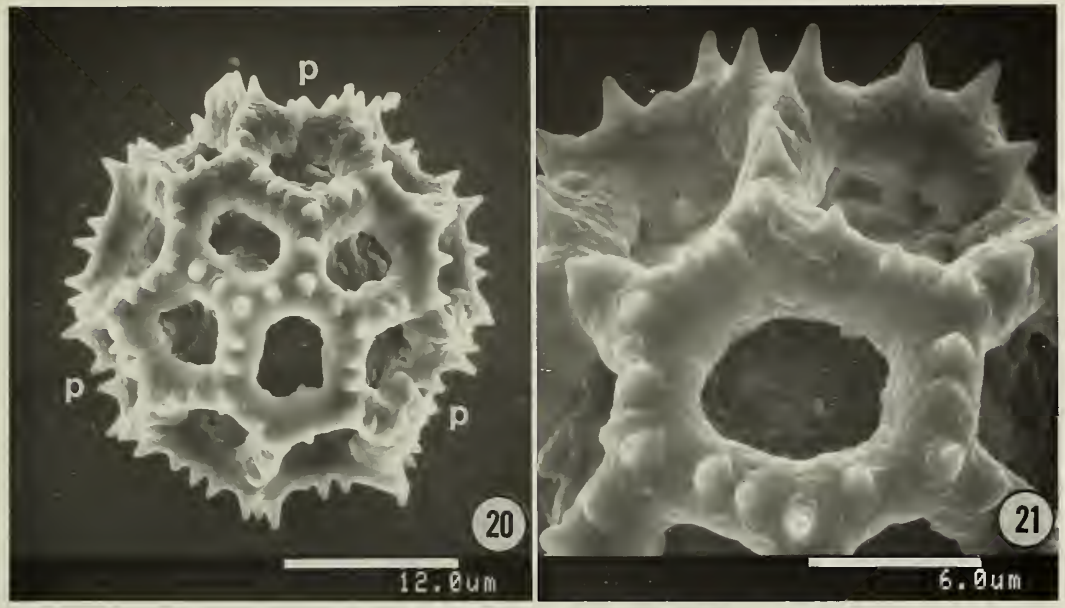
Type: *Vernonia elaeagnoides* H.B.K.
Figs. 10–21

Plantae suffruticosae vel fruticosae ad 0.6–2.5 m altae pauce ramosae in caulibus in superficiis inferioribus foliorum et in inflorescentibus in pilis appresse T-formibus obsitae. Caules teretes vel vix angulati non fistulosi. Folia alterna, petiolis 0.3–1.5 cm longis; laminae subcoriaceae anguste lanceolatae vel late ellipticae base et apice anguste vel late acutae vel leniter acuminatae margine integrae supra parce pilosulae et impresse fuscescentiter glandulo-punctatae subtus dense pallide appresse piliferae, nervis secundariis pinnatis utrinque ca. 7–15 patentiter vel ascendentiter divergentes. Inflorescentiae axillares; capitula sessilia vel subsessilia 1–6 aggregata anguste campanulata 8–9 mm alta ca. 5 mm lata; bracteae involucri 25–30 persistentes gradatim auctae leniter induratae apice erectae appressae rotundatae extus parce vel dense pilosae; receptacula epaleacea. Flores 8–10 in capitulo; corollae pallide lavandulae vel roseae regulares anguste infundibulares ca. 6.5 mm longae extus plerumque glabrae, tubis ca. 3 mm longis, faucibus ca. 1 mm longis, lobis anguste oblongis ca. 3 mm longis distaliter paucie pilosulis, pilis subsessiliter T-formibus, nervis apice incrassatis; thecae antherarum 1.7–1.9 mm longae; appendices basilares truncatae subquadratae margine leniter dentatae in parietibus cellularibus firmae non incrassatae; appendices apicales antherarum ovatae ca. 0.7 mm longae glabrae in parietibus cellularum in partibus incrassatae; basi stylorum annuliformiter nodati; rami stylorum 1.5–2.0 mm longi antrorse pilosuli, pilis argute acutis. Achenia 1.5–2.0 mm longa 10-costata inter costas sinuate setulifera pauce glandulo-punctata et idioblastifera raphidibus subquadratis; carpopodia breviter obturaculiformia; setae pappi 30–35 albidae vel rubescentes facile deciduae ca. 4 mm longae apice latiores margine et extus scabridae; squamae exteriores oblongae 0.2–0.6 mm longae ca. 0.1 mm latae extus parce scabridae. Grana pollinis in diametro 40–45 μm tricolporata lophata Ayniaforma.

Pseudopiptocarpha is established for two species from Colombia that have been treated at different times as part of *Vernonia* Schreb. or, in the case of one species, as part of *Piptocarpha* R.Br. In annotations dated 1984, Gerald L. Smith, monographer of *Piptocarpha* (unpublished), rejected the one species from *Piptocarpha* and returned it to *Vernonia.* Smith's rejection is confirmed by the non-deciduous bracts of the involucre, the lophate form of the pollen, and the non-sclerified basal appendages or tails on the anther thecae.

Vernonia elaeagnoides H.B.K. and *V. schultzii* Karsten of Colombia differ from *Vernonia* by their lophate pollen and hairs on the corolla, both characteristics of the *Lepidaploa* relationship within the subtribe Vernoniinae. A few characters of phyletic value such as the subquadrate raphids of the achene wall indicate closest relation to *Aynia* H. Robinson (1988c) and *Lessingianthus* H. Robinson (1988a) of the *Lepidaploa* complex, and the firmness of attachment of the crests of the lophate pollen indicates baculate, non-rhizomatous pollen like that of the latter two genera, a feature confirmed by SEM observation (Fig. 21). The glands on the achenes are unlike most of *Lessingianthus,* which is concentrated in Brazil, and might indicate closest relationship to *Aynia* of Peru, which has the same type of lophate pattern on the pollen. The two Colombian species differ from both *Aynia* and *Lessingianthus* by having only 8–10 florets in their heads and the T-shaped

Figs. 10–19. *Pseudopiptocarpha eleagnoides* (H.B.K.) H. Robinson. 10. Habit; 11. Enlargement showing spreading involucre with persistent bracts; 12. Head; 13. Corolla showing tips of style; 14. ½ of corolla with included stamens; 15. T-shaped hair from involucre; 16. Style showing small basal node; 17. Achene with pappus; 18. Setula of achene; 19. Raphids of achene wall.



Figs. 20, 21. *Pseudopiptocarpha eleagnoides* (H.B.K.) H. Robinson, pollen. 20. Polar view with position of each of each of three pores indicated by a letter "p"; 21. Enlargement of crests showing subtending baculae.

hairs on their stems, leaves, and corollas. The T-shaped hairs occur in some species of the more distantly related genus *Lepidaploa* (Cass.) Cass. (Robinson 1990) in the group of genera with elongate raphids in the walls its achenes and rhizomatous crests in its pollen.

The two Colombian species are distinct from all other genera in the *Lepidaploa* complex by the often numerous small heads in the axils of large leaves and the partially sclerified cell walls of the apical anther appendages. The 10 or fewer florets in the heads distinguishes the pair of species from all genera of the complex except *Stenocephalum* Sch.Bip. (Robinson 1987a). The other genera rarely have as few as 10 florets in the heads. The heads of *Pseudopiptocarpha* often appear to be single or in pairs in the leaf axils, but closer examination shows many small buds that develop over a longer period of time. Apparently the axillary inflorescences are reduced branch systems. The number of heads is usually actually five or six, a higher number than is seen in other members of the *Lepidaploa* complex.

The type of echinolophate pollen pattern shared by the Colombian species and the genus *Aynia* has now been seen in five genera. Other isolated occurrences are in *Lepidaploa tovarensis* (Gleason) H. Robinson of Venezuela, some *Stilpnopappus* Mart. ex DC. and the monospecific *Harleya* Blake of Central America (Robinson 1990). The pattern superficially resembles the more common type D pollen with three supra-colpar areoles reaching the poles, but the three polar areoles in *Aynia* are aligned with the intercolpi rather than the colpi. The occurrence of the *Aynia* type areole pattern in *Lepidaploa tovarensis* differs in detail by having a rhizomate rather than purely baculate substructure of the crests.

The clusters of small axillary heads and the more sclerified apical anther appendages cause the two Colombian species of this study to resemble the genus *Piptocarpha,* and the former characteristic was evidently a factor in the transfer of *Vernonia elaeagnoides* to that genus by Baker (1873). The resemblance of the Colombian species to *Piptocarpha* is phyletically misleading, but provides a basis for the new generic name, *Pseudopiptocarpha.*

The species of *Pseudopiptocarpha* are known only from Colombia at elevations between 400–1700 m. Specimens have been seen from the Departments of Cundinamarca, Huila, Santander, and Tolima.

Key to the species of *Pseudopiptocarpha*

1. Leaf blades linear to narrowly lanceolate, 0.6–2.0 cm wide; secondary veins short, spreading at only 35–45°, arched from near midvein; basal involucral bracts often obscured by pubescence; pappus usually reddish .... *P. elaeagnoides*
1. Leaf blades elliptical to obovate, 2.3–9.3 cm wide; secondary veins elongate, spreading at 45–55°, straight near midvein; involucral bracts not totally obscured by pubescence; pappus bristles whitish or slightly sordid .... *P. schultzii*

The two species of *Pseudopiptocarpha* are as follows:

Pseudopiptocarpha elaeagnoides (H.B.K.)
H. Robinson, comb. nov.

Vernonia elaeagnoides H.B.K., Nov. Gen. Sp., ed. fol. 4:33. 1818. *Piptocarpha elaeagnoides* (H.B.K.) Baker in Mart., Fl. brasiliensis 6(2):126. 1873.

Vernonia micans Benth., Pl. Hartw. 196. 1845.

Distribution.—Colombia: Cundinamarca, Huila, Tolima.

The species was illustrated by one of the artists working for Mutis about the year 1800, and the illustration was first published in 1985 under the name *Vernonia rubricaulis* Humb. & Bonpl. (≡*Lessingianthus rubricaulis* (H. & B.) H. Rob.) (Díaz Piedrahita 1985:67, pl. 86, 87).

Pseudopiptocarpha schultzii (Karsten)
H. Robinson, comb. nov.

Vernonia (*Vanillosma*) *schultzii* Karsten ex Sch.Bip., Linnaea 30:168. 1859.

Distribution.—Colombia: Cundinamarca, Huila, Santander.

Trepadonia H. Robinson, gen. nov.
Type: *Vernonia mexiae* H. Robinson.
Figs. 22–29

Plantae fruticosae scandentes ad 10 m longae. Caules brunnescentes teretes vix striati non fistulosi dense minute appresse puberuli, pilis uniseriatis base 1–5-septatis in cellulis apicalibus elongatis. Folia alterna, petiolis ca. 1 cm longis; laminae subcoriaceae oblongo-ovatae vel oblongae base rotundatae vel obtusae margine integrae apice acuminatae supra glabrae subtus appresse puberulae non glandulo-punctatae, nervis secundariis pinnatis leniter arcuate patentibus utrinque ca. 7, pilis brevibus. Inflorescentiae longe pyramidaliter thyrsoideo-paniculatae in ramis subracemosae, ramulis unicapitulis vel glomerulate paucicapitatis; bracteis inflorescentiis minute foliiformibus vel subulatis, pedicellis 0.3–6.0 mm longis minute puberulis. Capitula homogama; involucra late campanulata 4–5 mm alta et 3–4 mm lata; squamae involucri ca. 25 persistentes erecto-appressae oblongae vel suborbiculares 1–4 mm longae et 0.7–1.0 mm latae apice rotundatae vel vix apiculatae extus glabrae vel subglabrae; receptacula epaleacea. Flores 8–10 in capitulo; corollae purpureo-rosae regulares anguste infundibulares ca. 5 mm longae extus praeter apicem loborum glabrae; tubis 1.5–2.0 mm longis, faucibus ca. 1.6–2.0 mm longis, lobis erectis non contortis lanceolatis ca. 1.3–1.5 mm longis et base ca. 0.4 mm latis apice pauce minute glanduliferis in

Figs. 22–28. *Trepadonia mexiae* (H. Robinson) H. Robinson. 22. Branch with inflorescence; 23. Head; 24. Corolla with included style; 25. Style with enlarged base; 26. ½ of corolla with included stamens, lines in lobes representing ducts; 27. Achene with pappus; 28. Raphids of achene wall.

laminis in canalibus resiniferis longitudinaliter multo striatis, nervis distaliter vix incrassatis; thecae antherarum ca. 1.5 mm longae base calcaratae rotundatae non appendiculatae; appendices antherarum apicales lanceolatae ca. 0.6 mm longae et 0.17 mm latae glabrae in parietibus cellularum non incrassatae; basi stylorum annuliformiter nodati; rami stylorum ca. 2 mm longi non glanduliferi hispiduli, pilis argute acutis. Achenia ad 2 mm longa 10-costata hispidule setulifera, setulis plerumque in partibus uniseriatis; raphidibus subquadratis; carpopodia doliformia ca. 0.15 mm longa et 0.3 mm lata; setae pappi ca. 35 albidae vel flavescentes subpersistentes plerumque 3.5–4.0 mm longae apice vix vel non latiores margine et extus dense scabridulae; squamae exteriores anguste oblongae 0.5–0.7 mm longae extus scabridulae. Grana pollinis in diametro ca. 35 μm tricolporata echinata in areolis omnino in tectis perforatis obsita.

Vernonia mexiae H. Robinson (1981) from Peru, has a scandent habit and a pyramidally thyrsoid inflorescence unlike most members of the tribe Vernonieae. The following analysis attempts to determine the proper relationship of the new genus in the tribe. Two of the neotropical subtribes of the Vernonieae have been considered in the present attempt, the Piptocarphinae and Vernoniinae.

The habit of *Vernonia mexiae* resembles some members of the subtribe Piptocarphinae, especially members of the genera *Piptocarpha* R.Br. and *Critoniopsis* Sch.Bip. (Robinson 1980, 1993a). However, the Peruvian species lacks the distinguishing characters of the Piptocarphinae, the deciduous inner bracts of the involucre, the thickened cell walls of the anther appendage, the usually extensively glanduliferous outer surfaces of the corolla lobes, and the often blunt-tipped sweeping-hairs of the style. The corymbose or axillary forms of inflorescence in the Piptocarphinae are unlike the pyramidal form with widely spreading racemiform branches in the Peruvian *Trepadonia.*

The subtribe Vernoniinae has recently been resolved mostly into two groups (Robinson 1992b). Of the two groups, the *Lepidaploa* complex differs from *Vernonia mexiae* by the usually lophate pollen with perforated tectum restricted to the crests, the hairy corolla lobes, and the elongate raphids in the wall of the achenes in most genera. *Vernonia mexiae* belongs to the other group of genera, including *Vernonia* Schreb. and *Vernonanthura* H. Robinson, having echinate pollen with perforated tectum continuous in the intercolpus, essentially glabrous corolla lobes, and subquadrate raphids in the achene walls. *Vernonia mexiae* is particularly linked to *Vernonanthura* by the presence of a series of longitudinal resin ducts in the central parts of the corolla lobes (Robinson 1992b). These ducts have been seen only in *Vernonia mexiae* (Fig. 29) and *Vernonanthura* (Figs. 30–32). The former species is strikingly distinct from *Vernonanthura* in its pyramidally thyrsoid inflorescences.

The form of the inflorescence is unusual for the whole tribe, with the elongate main axis and the racemiform branches bearing short corymbiform branchlets. The corymbose-cymose pattern of lateral branching seen in *Vernonanthura* is completely lacking. Also, in *Vernonanthura* the scandent habit has been noted only in *V. cocleana* (Keeley) H. Rob. of Panama. Many species of *Vernonanthura* differ by having distinct sterile appendages at the bases of the calcarate anther thecae.

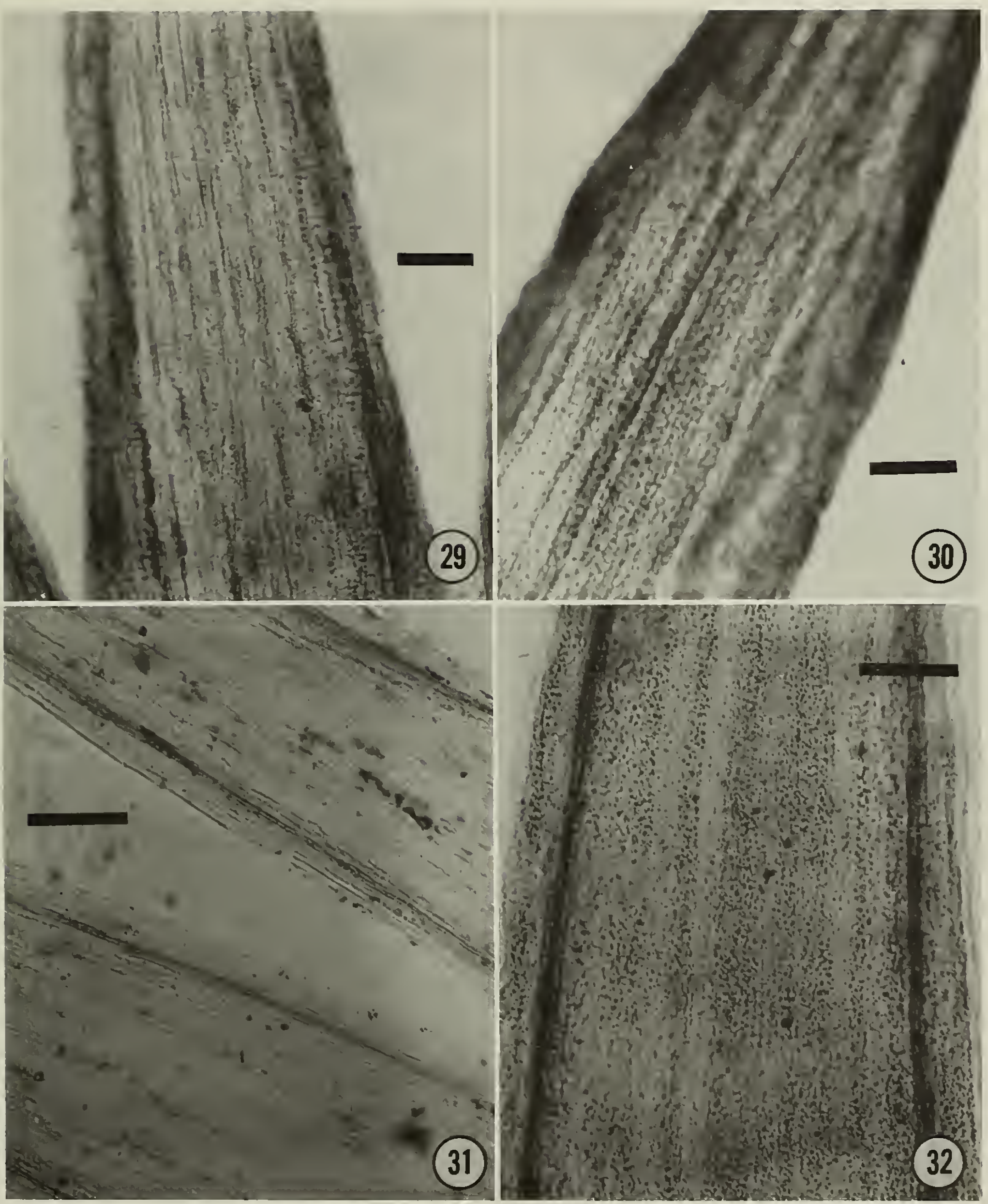
The new generic name is drawn from the Spanish word for climber, *trepadora,* with the ending from *Vernonia.*

The single species of the genus is as follows:

Trepadonia mexiae (H. Robinson)
H. Robinson, comb. nov.

Vernonia mexiae H. Robinson, Phytologia 49:265. 1981.

Distribution.—Peru: Huánuco, San Martín.



Figs. 29–32. Corolla lobes of *Trepadonia* and *Vernonanthura* showing longitudinal resin ducts. 29. *Trepadonia mexiae* (H. Robinson) H. Robinson, Peru, Ferreyra 17483 (US); 30. *Vernonanthura brasiliana* (L.) H. Robinson, Brazil, Irwin et al. 17793 (US); 31. *V. laxa* (Gardner) H. Robinson, Brazil, Dusén 16708 (US); 32. *V. cymosa* (Vell. Conc.) H. Robinson, Brazil, Eiten & Eiten 2564 (US); scale bars = 100 μm.

The species shows some variation. The holotype from Huánuco has less elongate inflorescences with shorter branches, obtuse to rounded tips of the outer involucral bracts, obtuse and slightly crenulate tips on the apical anther appendages, and short, only partially biseriate setulae of the achene. Material from San Martín has more attenuate pyramidal inflorescences with long racemiform branches, more apiculate tips of the outer involucral bracts, acute and subentire tips on the anther appendages, and longer, more strongly biseriate setulae on the achene.

Acknowledgments

The ink drawings of *Cololobus, Pseudopiptocarpha,* and *Trepadonia* were prepared by Alice Tangerini, of the Department of Botany, National Museum of Natural History, Smithsonian Institution. The SEM photos of *Pseudopiptocarpha* were taken by Peter Viola of the Smithsonian Museum of Natural History SEM Laboratory using a Hitachi 570 scanning electron microscope. The microphotographs of the corolla lobes and SEM prints were prepared by Victor E. Krantz, Staff Photographer, National Museum of Natural History.

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Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

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107(3), 1994, p. 569

BIOLOGICAL SOCIETY OF WASHINGTON
121st Annual Meeting, 11 May 1994

The meeting was called to order at 11:15 a.m. in the Waldo Schmitt Room, National Museum of Natural History, by Janet Reid, President-Elect, who assumed the responsibilities of the office of President in Storrs Olson's absence.

Janet announced that two new committees have been established by the Council: (1) a Financial Planning Committee, to assist the treasurer in managing the finances of the Society; and (2) a Membership Committee. Janet noted that Oliver Flint and Frank Ferrari will chair the committees, respectively. In discussion following the announcement of the establishment of a Membership Committee, Chad Walter reported that the Society had 57 new members and 25 new institutional subscriptions in 1993. However, total mailings of the *Proceedings* increased by only 33 for the year, indicating attrition of 49 members or institutions.

Janet also noted that the Council had voted to donate a nearly complete set of back-issues of the *Proceedings* to the Museo Nacional de Historia Natural in Havana, Cuba. Additionally, the Council authorized the purchase of a replacement printer for use by the Treasurer.

Brian Robbins, Editor, then presented a report from the Editorial Committee. Four issues comprising 80 papers and 788 pages were published in volume 106 in 1993. There were 87 submissions (vs. 93 in 1992). As of 1 May 1994, there were 34 submissions, slightly fewer than in 1993 (40). Brian noted that there were no editorial staff changes in 1993.

Chad Walter, Treasurer, summarized the financial operations of the Society for 1993. Total income for the period of 1 January 1993 to 31 December 1993 was $73,716.90, and total expenditures were $76,042.66, resulting in a net operating loss of $2,325.76. Chad noted that the FY92–93 values do not reflect all of the income and expenditures associated with issue 106-4 and thus may not indicate a real loss for the production of volume 106. Nevertheless, upon comparing the costs associated with the production of volumes 104–106 of the *Proceedings,* Chad found that expenditures exceeded income for issues 106-1 and 106-4 more than for the other 10 issues because the society received no remuneration for over 50% of the pages in issues 106-1 and 106-4. In other issues of volumes 104–106, 5.9–35.2% of the pages were published at no cost to the authors. In the preceding Council session, the Council decided that the Society's policy regarding the waiving of page charges should be further scrutinized.

The meeting was adjourned at 11:30 a.m.

Respectfully submitted,
Carole C. Baldwin
Secretary

PROC. BIOL. SOC. WASH.
107(3), 1994, pp. 570–571

Applications published in the *Bulletin of Zoological Nomenclature*

The following Applications were published on 30 June 1994 in Vol. 51, Part 2 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.

2809 *Fursenkoina* Loeblich & Tappan, 1961 (Foraminiferida): proposed conservation.

2848 *Chromadora* Bastian, 1865 and *Euchromadora* de Man, 1886 (Nematoda): proposed conservation of usage by the designation of *C. nudicapitata* Bastian, 1865 as the type species of *Chromadora.*

2870 *Xerophila geyeri* Soós, 1926 (currently *Trochoidea geyeri*; Mollusca, Gastropoda): proposed conservation of the specific name.

2862 A. A. H. Lichtenstein's (1796, 1797) Catalogus musei zoologici . . . Sectio tertia. Continens Insecta and D. H. Schneider's (1800) Verzeichniss einer Parthei Insekten . . .: proposed suppression, with conservation of some Lichenstein (1796) names (Insecta and Arachnida).

2890 *Rhopalosiphum monardae* Davis, 1911 (currently *Hyalomyzus monardae*; Insecta, Homoptera): proposed conservation of the specific name.

2929 *Bhatia* Distant, 1908 (Insecta, Homoptera): proposed confirmation of *Eutettix*? *olivaceus* Melichar, 1903 as the type species.

2878 *Scarabaeus rufus* Moll, 1782 (currently *Aphodius rufus*), *Scarabaeus rufus* Fabricius, 1792 (currently *Aegialia rufa*) and *Scarabaeus foetidus* Herbst, 1783 (currently *Aphodius foetidus*) (Insecta, Coleoptera): proposed conservation of usage of the specific names.

2885 *Ischyrus* Lacordaire, 1842, *Lybas* Lacordaire, 1842, *Mycotretus* Lacordaire, 1842 and *Megischyrus* Crotch, 1873 (Insecta, Coleoptera): proposed conservation.

2919 *Lithobius piceus* L. Koch, 1862 (Chilopoda): proposed conservation of the specific name.

2928 Regnum Animale . . ., Ed. 2 (M. J. Brisson, 1762): proposed rejection, with the conservation of the mammalian generic names *Philander* (Marsupialia), *Pteropus* (Chiroptera), *Glis, Cuniculus* and *Hydrochoerus* (Rodentia), *Meles, Lutra* and *Hyaena* (Carnivora), *Tapirus* (Perissodactyla), *Tragulus* and *Giraffa* (Artiodactyla).

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 30 June 1994 in Vol. 51, 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.

1765 *Fusus* Helbling, 1779 (Mollusca, Gastropoda): suppressed, and *Fusinus* Rafinesque, 1815 and *Colubraria* Schumacher, 1817: conserved.

1766 *Tortaxis* Pilsbry, 1906 and *Allopeas* Baker, 1935 (Mollusca, Gastropoda): conserved by the designation of a neotype for *Achatina erecta* Benson, 1842.

1767 *Pleurobranchus forskalii* Rüppell & Leuckart, [1828] and *P. testudinarius* Cantraine, 1835 (Mollusca, Gastropoda): specific names conserved.

1768 *Taningia danae* Joubin, 1931 (Mollusca, Cephalopoda): given precedence over *Octopodoteuthis persica* Naef, 1923.

1769 *Styloptocuma* Băcescu & Muradian, 1974 (Crustacea, Cumacea): conserved with *S. antipai* Băcescu & Muradian, 1974 designated as the type species.

1770 *Pachyrhynchus* Germar, 1824, *Somatodes* Schönherr, 1840 and the specific name of *Pachyrhynchus moniliferus* Germar, 1824 (Insecta, Coleoptera): conserved.

1771 *Cryptophagus advena* Waltl, 1834 (currently *Ahasverus advena*; Insecta, Coleoptera): specific name conserved.

1772 METOPIINI Raffray, 1904 (Insecta, Coleoptera): spelling emended to METOPIASINI, and METOPIINI Townsend, 1908 (Insecta, Diptera): spelling emended to METOPIAINI, so removing the homonymy with METOPIINAE Foerster, [1869] (Insecta, Hymenoptera).

1773 *Nacaduba* Moore, [1881] (Insecta, Lepidoptera): given precedence over *Pepliphorus* Hüber, [1819].

1774 *Catocala connubialis* Guenée, 1852 (Insecta, Lepidoptera): specific name conserved.

1775 *Banksinella luteolateralis* var. *albothorax* Theobald, 1907 (currently *Aedes* (*Neomelaniconion*) *albothorax*), *B. luteolateralis* var. *circumluteola* Theobald, 1908 (currently *A.* (*N.*) *circumluteolus*) and *A.* (*N.*) *mcintoshi* Huang, 1985 (Insecta, Diptera): specific names conserved, and *A.* (*N.*) *albothorax*: neotype designated.

1776 *Rana megapoda* Taylor, 1942 (Amphibia, Anura): specific name conserved.

1777 *Anisolepis grilli* Boulenger, 1891 (Reptilia, Squamata): specific name conserved.

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.

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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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CHESAPEAKE BAY PHYTOPLANKTON: I. COMPOSITION

Harold G. Marshall

Abstract.—A list of 708 phytoplankton taxa from 10 algal divisions has been compiled for the Chesapeake Bay and is based on the analysis of 2384 water samples over three decades of study. The flora represents a diverse assemblage of algae, dominated annually by a variety of diatoms and phytoflagellates.

Chesapeake Bay is the largest estuary in the United States. It is a temperate estuary, located within Virginia and Maryland, with a drainage basin of 165,760 km^2 (Wright & Phillips 1988). Schubel & Pritchard (1987) characterize the Bay as having a mean depth of 8.42 m, a surface area of 6.5 × 10^3 km^2, and a north–south orientation of about 320 km. Pritchard (1952) stated that the Bay has a net surface flow seaward and a net bottom flow of higher saline waters landward. The turbidity maximum is located north of the Patapsco River, in the upper portion of the Bay (Wright & Phillips 1988). The stratification and vertical homogeneity in the Bay are influenced by monthly flow rates, temperatures, tides, storms and the Coreolis effect (Haas 1977, Wright & Phillips 1988, Schubel & Pritchard 1987, Pritchard 1952). Highest freshwater influx follows the spring rains and occurs in March and April, with the lowest rates from August to October. Schubel & Pritchard (1987) classify Chesapeake Bay as a partially mixed estuary. It has at different times seasonally, and in different segments of the Bay, either different degrees of vertical homogeneity, or stratification, and is dissimilar to the characteristic salt wedge estuary. The presence of the pycnocline will vary seasonally, being most developed during the summer months. Subpycnocline transport is a mechanism in which phytoplankton species may be distributed up the Bay (Tyler & Seliger 1978).

The earliest study of phytoplankton composition and abundance in Chesapeake Bay was by Wolfe et al. (1926), reporting on several seasonal collections taken along the length of the Bay between 1916 and 1922. They collected whole water samples, followed by a centrifugation procedure to obtain a concentrate from which a sub-sample was analyzed. Their taxon list for Chesapeake Bay included 83 diatoms, 12 dinoflagellates and 4 chrysophytes (total = 99), with late spring and fall maxima, dominated by *Skeletonema costatum* and *Prorocentrum micans* respectively. Cowles (1930) discussed this data set in more detail and made geographic groupings of species, noting that temperate neritic forms were most abundant, with the phytoplankton having frequently higher cell concentrations along the western side of the Bay. Three decades later, Griffith (1961) prepared an illustrated guide of phytoplankton genera in Chesapeake Bay and its tributaries. These were listed under 4 taxonomic categories that included 217 diatoms, 80 dinoflagellates, 33 cyanobacteria (cyanophytes), and 16 chlorophytes.

The first comprehensive study of phytoplankton composition and abundance in the lower Chesapeake Bay was by Patten et al. (1963) Using both whole water and net collections, they compared 24 data sets taken at 5 station locations over a 12 month period. Their net collections contained representative taxa from only the diatoms (123) and dinoflagellates (12). Greater species representation, over a broader size range of cells, was obtained from their set of whole water samples. In these, they noted 107 taxa, composed of 57 diatoms, 33 dinoflagellates, 2 euglenoids, 7 chrysophytes (which included 2 cryptomonad taxa), and 8 chlorophytes, with highest cell counts along the western Bay in the vicinity of the tributaries. Their results also indicated multiple seasonal maxima during the year. Earlier reports on phytoplankton data from these same cruises were made by Mulford (1962, 1963). Other Bay surveys were conducted by Marshall (1966), using data from a single cruise, and Whaley & Taylor (1968), who conducted a one year survey in the Bay using net collections. They recorded 63 diatoms, 19 dinoflagellates, 10 chlorophytes, and one cyanobacterium, with 28 of these as generic listings only.

Mulford (1972) commented on the status of phytoplankton studies in Chesapeake Bay and described 36 dominant phytoplankters. These included 1 silicoflagellate, 28 diatoms, and 7 dinoflagellates. In a later study and using concentrates from whole water samples, Marshall (1980) reported 219 taxa in the lower Chesapeake Bay during a 14 month study. These included 129 diatoms, 42 dinoflagellates, 8 chrysophytes, 7 euglenoids, 7 prasinophytes, 2 xanthophytes, 8 cyanophytes, 6 haptophytes, 3 chlorophytes, and 7 cryptomonads. Additional papers on the composition and abundance of Chesapeake Bay phytoplankton include those by Marshall (1982, 1989, 1991, 1992), Marshall & Lacouture (1986), and Marshall & Alden (1990a, 1993).

The importance of the Bay's nano-picoplankton components has been emphasized by McCarthy et al. (1974), Van Valkenburg & Flemer (1974), Marshall (1980) and Affronti & Marshall (1993). Specific phytoplankton relationships to ecological variables in the Bay have been addressed by Fisher et al. (1988, 1992), Harding et al. (1986), Loftus et al. (1972), Magnien et al. (1992), Marshall (1992), Marshall & Alden (1991), among others. Productivity reports for the Bay region have included those by McCarthy et al. (1974), Sellner (1987), Marshall (1992) and Marshall & Nesius (1993).

The Chesapeake Bay flora is presently dominated by diatoms that are responsible for high periods of growth during late winter-spring, summer, and fall (Marshall 1992). Dinoflagellates, cryptomonads, and autotrophic picoplankters (e.g., cyanobacteria) are dominant categories during the summer and early fall. Although the shelf waters entering the Bay provide for an intrusion of neritic species, these are mainly concentrated at the Bay entrance, along the southeastern side of the Bay, and in sub-pycnocline waters throughout the lower Bay (Marshall & Alden 1990a). In this lower strata, they may be transported not only up the Bay, but may also be introduced into adjacent tributaries (Marshall & Alden 1990b). Different degrees of turbulence are found in this system, which allow these species to be mixed with waters above the pycnocline. Thus, these waters contain a general mixture of riverine, estuarine, and neritic species. The degree to which this mixture changes in composition throughout the year is influenced by the spring rains and subsequent flow rates in the rivers and Bay. In addition, climatic and/or local conditions may influence turbulence and mixing of the water column. Within this system there is a seasonal succession of species within the Bay, as well as spatial distribution patterns that occur annually (Marshall & Alden 1990a).

The purpose of this paper is to provide a comprehensive list of phytoplankton taxa that have been observed by the author in Chesapeake Bay. This information has been derived from the analysis of 2384 water samples collected between 1963 and 1993 and analyzed in the author's phytoplankton laboratory at Old Dominion University. Samples collected prior to 1985 came mainly from seasonal studies or single cruise collections by the author. Since 1985, water samples were obtained consistently every month above and below the pycnocline at stations in the lower Bay as part of the Chesapeake Bay Plankton Monitoring Program (Marshall 1992). This list is intended to provide the reader with an overall representation of the phytoplankton that currently characterize the Chesapeake Bay flora. It is expected that other species will subsequently be added to this list.

Methods

All collections that were made and analyzed in this study were whole water samples taken by either hydrocasts with collection bottles, or by using a pump to obtain water from various depths, to subsequently obtain 0.5–1.0 liters of water for analysis. Over the years of collections, the samples were preserved in either acidic or neutral solutions of Lugol's (Throndsen 1978), or buffered formalin. These samples were processed through a settling and siphoning procedure to obtain a final concentrate that was examined with an inverted plankton microscope using a modified Utermöhl technique (Marshall & Alden 1990a). Cell identifications and counts were made at either 125×, 350×, or 500×. In addition, a scanning electron microscope (SEM) was used when needed to identify species that were not clearly defined with light microscopy. Autotrophic picoplankters were also enumerated using epifluorescence microscopy (Affronti & Marshall 1993). This report is based on the examination of 610 samples prior to 1985 and 1774 samples taken during the following 8 years.

The classification system used here is patterned after Van Landingham (1967–1979), Parke & Dixon (1976), and Hartley (1986). Taxonomic references include Lebour (1925), Hustedt (1927–1966, 1955), Gemeinhardt (1930), Schiller (1930, 1933–1937), Geitler (1932), Cupp (1943), Prescott (1951), Butcher (1959), Hendey (1964), Hulburt (1965), McIntyre & Bè (1967), Fott (1968), Campbell (1973), and Dodge (1982). Also used were the various volumes of Süsswasserflora von Mitteleuropa, Das Phytoplankton des Süsswassers, and the series in Rabenhorst's *Kryptogamen-Flora.* There were also numerous journal publications (e.g., Journal of Phycology, Phycologia, Diatom Research, etc.), on specific taxa that are too numerous to list here, but represent essential reading to the systematist and may be obtained through routine searches of the literature. The reader must also contend with the changing systematics that is associated with several of the phytoplankton taxa and realize many present listings are destined to be changed. A major revision of the cyanobacteria (Cyanophyceae) is given in the series by Anagnostidis & Komárek (1985, 1988, 1990) and Komárek & Anagnostidis (1986, 1989). The classification of the cryptophyceae is also under revision; suggested references within this group include those by Butcher (1967), Anton & Duthie (1981), Santore (1984, 1985), Hill & Wetherbee (1989), and Hill (1991). Other categories in need of more taxonomic work are the various groups often included under the collective term naked microflagellates. There are also several genera that are traditionally included among the phytoplankton (e.g., *Calycomonas, Dictyocha, Distephanus*) whose status with the algal flora is questionable. Other references on classification of marine phytoplankton include Chrétiennot-Dinet et al. (1993) and Tomas (1993).

Results

A total of 708 phytoplankton taxa have been identified from water samples taken from Chesapeake Bay. These include 360 Bacillariophyceae, 125 Dinophyceae, 87 Chlorophyceae, 38 Cyanophyceae (cyanobacteria), 24 Haptophyceae, 22 Euglenophyceae, 22 Chrysophyceae, 17 Cryptophyceae, 9 Prasinophyceae and 4 Xanthophyceae. Within the Phytoplankton Monitoring data set from 1985 through 1992, 21

Table 1.—Phytoplankton that occurred in more than 50% of the water samples taken above and below the pycnocline from Chesapeake Bay, 1985–1992.

I. Diatoms	
Asterionella glacialis	51.0%
Cerataulina pelagica	65.5
Chaetoceros pendulus	51.8
Cyclotella spp.	86.3
Cylindrotheca closterium	76.6
Ditylum brightwellii	60.5
Leptocylindrus minimus	62.6
Pseudonitzschia pungens	61.3
Pleurosigma angulatum	53.5
Rhizosolenia calcar-avis	66.4
Rhizosolenia delicatula	54.3
Rhizosolenia setigera	50.0
Skeletonema costatum	84.0
Thalassionema nitzschioides	89.4
II. Dinoflagellates	
Ceratium lineatum	52.5%
Gymnodinium spp.	83.1
Gyrodinium spp.	63.4
Katodinium rotundatum	60.6
Prorocentrum micans	84.0
Prorocentrum minimum	68.9
Protoperidinium spp.	59.9

taxa were found in greater than 50% of the 1774 samples, and are considered ubiquitous (Table 1). These consist of 14 diatom and 7 dinoflagellate taxa that represent many of the most common phytoplankters in the Bay. Not included in this list are other ubiquitous forms, often collectively counted in routine sample analysis under broad categories, or size groups, e.g., autotrophic picoplankton, cryptomonads, and unidentified microflagellates. Among the most common species throughout the study were the diatoms *Thalassionema nitzschioides, Skeletonema costatum,* and *Cyclotella* spp., plus the dinoflagellates *Prorocentrum micans, P. minimum,* and *Katodinium rotundatum.* A total of 38 taxa were recorded in 25% of the samples, and 128 species (18.1%) had only one record of occurrence in the Bay. These results indicate that the plankton flora in the Bay is dominated by a small number of species that occur annually and that these are accompanied by a large variety of background species that change seasonally. Occasionally, several of these background species produce pulses of rapid growth and abundance. Generally, these expressions are of short duration, and are not consistently produced in following years. The list also includes numerous benthic species (pennate diatoms), whose presence in the water column is not common. These periodically may appear in water samples and are often associated with areas of turbulence, or with active current flow. Over the period of these collections, the number of taxa recorded per sample (0.5 l) ranged from 20 to 92, with a mean of 43.

Several common producers of sporadic blooms in the Bay, which are usually of limited scope and duration, are *Ceratium furca, Cochlodinium heterolobatum, Gymnodinium nelsoni, Noctiluca scintillans,* and *Prorocentrum minimum.* Flora associated with longer lasting seasonal expressions of abundance include *Asterionella glacialis, Cyclotella* spp., *Heterocapsa triquetra, Katodinium rotundatum, Leptocylindrus minimus,* and *Skeletonema costatum.* Although 6 or 7 seasonal assemblages may occur annually within the Bay (Marshall & Alden 1990a), there tends to be an overlying composition of "cold" and "warm" water species categories when these forms are most abundant. For instance, assemblages common in winter-spring may include *Asterionella glacialis, Cerataulina pelagica, Heterocapsa triquetra, Leptocylindrus danicus, L. minimus, Paralia sulcata, Rhizosolenia fragilissima, R. setigera, Skeletonema costatum,* and *Pseudonitzschia pungens.* A summer-early fall assemblage may consist of *Chaetoceros affinis, C. compressus, C. constrictum, C. neogracillis, Cyclotella* spp., *Eucampia zodiacus, Lauderia borealis, Lithodesmium undulatum, Rhizosolenia alata,* and *R. stolterfothii.*

One of the most common diatom assemblages in the Bay is a *Cyclotella* complex that is present in high concentrations (10^6 cells/l) throughout most of the year. This group is dominated by a small (<10 μm diam) species of *Cyclotella* that was previously identified as *C. caspia* in the Chesapeake Bay (Marshall 1980, Marshall & Alden 1990b) and in European waters (Hasle 1962, Kiss et al. 1988). Hakansson et al. (1993) have compared several of the smaller *Cyclotella* species to the original type material for *C. caspia* Grunow. They concluded that the species which is common in the Bay is distinct from *C. caspia* and that it should be classified as *C. choctawhatcheeana* Prasad, with *C. hakanssoniae* Wendker as a synonym (see Prasad et al. 1990, for a description of *C. choctawhatcheeana*). It is *C. choctawhatcheeana* that dominates the higher (>18 ppt) saline waters of the lower Bay; with this species, plus *C. striata* and *C. meneghiniana,* forming an abundant *Cyclotella* complex in the lower saline regions of the Bay and in its tidal tributaries. There is considerable morphological variability among many of these small *Cyclotella* species, so that SEM usage is necessary for accurate identification. Further studies of this assemblage may reveal that additional varieties or species are present in the Bay.

Several phytoplankton species that have been reported as potential toxin producers are included in this Bay list: 1) the dinoflagellates *Cochlodinium heterolobatum, Dinophysis acuminata, D. acuta, D. fortii, Gyrodinium aureolum, Noctiluca scintillans, Prorocentrum micans, P. minimum,* and 2) the diatoms *Amphora coffeaeformis* and *Pseudonitzschia pseudodelicatissima.* Although not observed in the current collections of the lower Chesapeake Bay, two other toxin-producing species have been reported from this system: the diatom *Pseudonitzschia pungens* f. *multiseries* (Hasle) Hasle was noted years ago in a sample from the Bay (Hasle 1965), and the dinoflagellate *Pfiesteria piscimorte* was identified recently from Jenkins Creek off the Choptank River (Blankenship 1993).

The increased number of species reported here, in comparison to past studies in Chesapeake Bay, is attributed to several factors. The long term monitoring of this flora has provided a larger number of samples for analysis. These have been collected over a broader areal coverage of the Bay, and spatially throughout the water column. The repeated monthly collections, under a variety of changing environmental conditions, provided species in the samples that frequently have more limited periods of growth and abundance and which easily could be missed in a less concentrated sampling program. For example, many of the earlier studies were made along limited cruise tracts, with fewer representative stations and more limited temporal coverage. The use of nets in several of these earlier studies would have biased their results by omitting many of the smaller species. Throndsen (1978) has also indicated that the use of different fixatives will effect the preservation of different algal categories, which in turn may influence their identification. In this study, 577 of the 705 species (81.8%) were recorded more than once, with a mean count of 43 species found in each sample. This level of species representation is attributed to using whole water samples and to following an Utermöhl methodology in the analysis. Additional SEM usage provided for the identification of species whose traits could not be adequately discernable with light microscopy.

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Phytoplankton Recorded from the Chesapeake Bay

CHRYSOPHYTA

I. Bacillariophyceae

Centrales:

Actinocyclus normanii (Gregory) Hustedt.

Actinoptychus sp., *A. senarius* (Ehrenberg) Ehrenberg, *A. undulatus* (J. W. Bailey) Ralfs.

Asteromphalus heptactis (Brébisson) Ralfs.

Aulacoseira distans (Ehrenberg) Simonsen, *A. granulata* (Ehrenberg) Simonsen, *A. granulata* var. *angustissima* (O. Müller) Simonsen, *A. islandica* (O. Müller) Simonsen, *A. islandica* var. *helvetica* (O. Müller) Simonsen.

Auliscus sculptus (W. Smith) Ralfs.

Bacteriastrum sp., *B. delicatulum* Cleve.

Biddulphia sp., *B. alternans* (J. W. Bailey) Van Heurck, *B. biddulphiana* J. E. Smith, *B. reticulum* (Ehrenberg) Boyer.

Campylosira sp., *C. cymbelliformis* (A. Schmidt) Grunow.

Cerataulina pelagica (Cleve) Hendey.

Cerataulus radiatus (Roper) R. Ross.

Chaetoceros sp., *C. affinis* Lauder, *C. atlanticus* Cleve, *C. atlanticus* var. *neapolitana* (Schröder) Hustedt, *C. brevis* Schütt, *C. coarctatus* Lauder, *C. compressus* Lauder, *C. constrictus* Gran, *C. convolutus* Castracane, *C. costatus* Pavillard, *C. crinitus* Schütt, *C. danicus* Cleve, *C. debilis* Cleve, *C. decipiens* Cleve, *C. densus* (Cleve) Cleve, *C. didymus* Ehrenberg, *C. didymus* var. *protuberans* (Lauder) Gran & Yendo, *C. difficilis* Cleve, *C. laciniosus* Schütt, *C. neogracilis* Van Laningham, *C. pelagicus* Cleve, *C. pendulum* Karsten, *C. peruvianus* Brightwell, *C. pseudocurvisetus* Mangin, *C. rostratus* Lauder, *C. socialis* Lauder, *C. subtilis* Cleve.

Climacodium frauenfeldianum Grunow.

Corethron sp., *C. criophilum* Castracane.

Coscinodiscus sp., *C. asteromphalus* Ehrenberg, *C. centralis* Ehrenberg, *C. concinnus* Wm. Smith, *C. granii* Gough, *C. kuetzingii* A. Schmidt, *C. marginatus* Ehrenberg, *C. nodulifer* A. Schmidt, *C. oculus-iridis* Ehrenberg, *C. perforatus* var. *cellulosus* Grunow, *C. radiatus* Ehrenberg, *C. subbulliens* Jörgensen, *C. wailesii* Gran & Angst.

Coscinosira sp., *C. polychorda* (Gran) Gran.

Cyclostephanos sp., *C. dubius* (Fricke) Round.

Cyclotella sp., *C. atomus* Hustedt, *C. caspia* Grunow, *C. cryptica* Reimann, Lawin & Guillard, *C. glomerata* Bachmann, *C. choctawhatcheeana* Prasad, *C. meneghiniana* Kützing, *C. striata* (Kützing) Grunow.

Dactyliosolen mediterraneus (H. Peragallo) H. Peragallo.

Detonula confervacea (Cleve) Gran.

Ditylum brightwellii (T. West) Grunow.

Ellerbeckia arenaria (Moore) Crawford.

Eucampia cornuta (Cleve) Grunow, *E. zodiacus* Ehrenberg.

Guinardia flaccida (Castracane) H. Peragallo.

Hemiaulus sp., *H. hauckii* Grunow, *H. membranaceus* Cleve, *H. sinensis* Greville.

Lauderia borealis Gran.

Leptocylindrus danicus Cleve, *L. minimus* Gran.

Lithodesmium sp., *L. undulatum* Ehrenberg.

Melosira dickiei (Thwaites) Kützing, *M. moniliformis* (O. F. Müller) C. Agardh, *M. nummuloides* Agardh, *M. varians* C. Agardh.

Neodelpheneis pelagica Takano.

Odontella sp., *O. aurita* (Lyngbye) Agardh, *O. mobiliensis* (J. W. Bailey) Grunow, *O. obtusa* Kützing, *O. rhombus* (Ehrenberg) Kützing, *O. rhombus* f. *trigona* (Cleve) R. Ross, *O. sinensis* (Greville) Grunow.

Paralia sulcata (Ehrenberg) Cleve.

Rhizosolenia sp., *R. acuminata* (H. Peragallo) H. & M. Peragallo, *R. alata* Brightwell, *R. alata* f. *gracillima* (Cleve) Grunow, *R. alata* f. *indica* (H. Peragallo) Gran, *R. bergonii* H. Peragallo, *R. calcar-avis* Schultze, *R. castracanei* H. Peragallo, *R. delicatula* Cleve, *R. fragilissima* Bergon, *R. hebetata* f. *hiemalis* Gran, *R. hebetata* f. *semispina* (Hensen) Gran, *R. imbricata* Brightwell, *R. rhombus* Karsten, *R. robusta* Norman, *R. setigera* Brightwell, *R. stolterfothii* H. Peragallo, *R. styliformis* Brightwell, *R. styliformis* var. *latissima* Brightwell, *R. styliformis* var. *longispina* Hustedt.

Schroederella delicatula (H. Peragallo) Pavillard.

Skeletonema sp., *S. costatum* (Greville) Cleve, *S. potamos* (Weber) Hasle.

Stephanodiscus sp., *S. hantzschii* Grunow.

Stephanopyxis sp., *S. palmeriana* (Greville) Grunow, *S. turris* (Greville & Arnott) Ralfs.

Streptotheca tamesis Shrubsole.

Thalassiosira sp., *T. aestivalis* Gran & Angst, *T. baltica* (Grunow) Ostenfeld, *T. decipiens* (Grunow) Jörgensen, *T. delicatula* Ostenfeld, *T. eccentrica* (Ehrenberg) Cleve, *T. gravida* Cleve, *T. lacustris* (Grunow) Hasle & Fryxell *T. nordenskioeldii* Cleve, *T. oestrupii* var. *venrickae* Fryxell & Hasle, *T. pseudonana* (Hustedt) Hasle & Heimdal, *T. rotula* Meunier, *T. leptopus* (Grunow) Fryxell & Hasle, *T. subtilis* (Ostenfeld) Gran, *T. tenera* Proschkina-Laurenko *T. visurgis* Hustedt.

Triceratium sp., *T. acutum* Ehrenberg, *T. favus* Ehrenberg.

Pennales:

Achnanthes sp., *A. danica* (Flögel) Grunow, *A. delicatula* (Kützing) Grunow, *A. lemmermannii* Hustedt.

Amphiprora sp., *A. alata* (Ehrenberg) Kützing.

Amphora sp., *A. angusta* Gregory, *A. coffeaeformis* (C. Agardh) Kützing, *A. costata* W. Smith, *A. crassa* Gregory, *A. lineolata* Ehrenberg, *A. luciae* Cholnoky, *A. obtusa* Gregory, *A. ovalis* (Kützing) Kützing, *A. proteus* Gregory, *A. rhombica* Kitton, *A. sabyii* Salah.

Asterionella sp., *A. formosa* Hassall, *A. glacialis* Castracane, *A. gracillima* (Hantzsch) Heiberg.

Bacillaria paxillifer (Müller) Hendey.

Berkeleya rutilans (Trentepohl) Grunow.

Caloneis sp., *C. lepidula* (Grunow) Cleve.

Campylodiscus echeneis Ehrenberg, *C. limbatus* Brébisson.

Catenula adhaerens (Mereschkowsky) Mereschkowsky.

Cocconeis sp., *C. costata* Gregory, *C. disculus* (Schumann) Cleve, *C. placentula* Ehrenberg, *C. scutellum* Ehrenberg, *C. scutellum* var. *ornata* Grunow.

Cylindrotheca closterium (Ehrenberg) Reiman & Lewin.

Cymbella sp., *C. excisa* Kützing, *C. tumida* (Brébisson) Grunow.

Delphineis surirella (Ehrenberg) G. Andrews.

Denticula subtilis Grunow.

Diatoma sp., *D. hyemale* (Roth) Heiberg, *D. tenue* C. Agardh.

Dimeregramma minor (Gregory) Ralfs.

Diploneis sp., *D. bombus* (Ehrenberg) Ehrenberg, *D. crabro* (Ehrenberg) Ehrenberg, *D. elliptica* (Kützing) Cleve, *D. litoralis* (Donkin) Cleve, *D. subcincta* (A. Schmidt) Cleve.

Eunotia sp.

Fragilaria sp., *F. crotonensis* Kitton, *F. oceanica* Cleve, *F. pinnata* Ehrenberg, *F. virescens* Ralfs.

Gomphonema sp., *G. acuminatum* Ehrenberg, *G. exiguum* Kützing, *G. sphaerophorum* Ehrenberg.

Grammatophora sp., *G. marina* (Lyngbye) Kützing.

Gyrosigma sp., *G. balticum* (Ehrenberg) Rabenhorst, *G. balticum* var. *similis* (Grunow) Cleve, *G. fasciola* (Ehrenberg) Griffith & Henfrey, *G. hippocampus* (Ehrenberg) Hassall, *G. macrum* (W. Smith) Griffith & Henfrey, *G. spenceri* (Quekett) Griffith & Henfrey, *G. wansbeckii* (Donkin) Cleve.

Hantzschia sp., *H. amphioxys* (Ehrenberg) Grunow, *H. marina* (Donkin) Grunow.

Licmophora sp., *L. abbreviata* C. Agardh, *L. flabellata* (Greville) C. Agardh, *L. paradoxa* (Lyngbye) C. Agardh, *L. paradoxa* var. *tincta* (C. Agardh) Hustedt.

Mastogloia sp., *M. exigua* Lewis.

Meridion circulare (Greville) C. Agardh.

Navicula sp., *N. amphipleuroides* Hustedt, *N. apiculata* Brébisson, *N. arenaria* Donkin, *N. cancellata* Donkin, *N. caterva* Hohn & Hellerman, *N. crucicula* (W. Smith) Donkin, *N. cruciculoides* Brockmann, *N. delawarensis* Grunow, *N. digitoradiata* (Gregory) Ralfs, *N. directa* (W. Smith) Ralfs, *N. distans* (W. Smith) Ralfs, *N. escorialis* Simonsen, *N. forcipata* Greville, *N. gastrum* (Ehrenberg) Kützing, *N. gracilis* var. *neglecta* (Thwaites) Grunow, *N. granulata* J. W. Bailey, *N. gregaria* Donkin, *N. hanseni* Möller, *N. humerosa* Brébisson, *N. laevissima* Kützing, *N. longa* (Gregory) Ralfs, *N. lundstroemii* Cleve, *N. maculosa* Donkin, *N. marina* Ralfs, *N. peregrina* (Ehrenberg) Kützing, *N. phyllepa* Kützing, *N. placenta* Ehrenberg, *N. pusilla* W. Smith, *N. rhynchocephala* Kützing, *N. salinarum* Grunow, *N. sovereignae* Hustedt, *N. tripunctata* (O. F. Müller) Bory.

Nitzschia sp., *N. acicularis* (Kützing) W. Smith, *N. bergii* A. Cleve-Euler, *N. bilobata* var. *minor* Grunow, *N. calida* Grunow, *N. clausii* Hantzsch, *N. compressa* (J. W. Bailey) Boyer, *N. constricta* (Kützing) Ralfs, *N. dissipata* (Kützing) Grunow, *N. frustulum* (Kützing) Grunow, *N. gracillima* Heiden & Kolbe, *N. gracilis* Hantzsch, *N. granulata* Grunow, *N. hybrida* Grunow, *N. lanceolata* W. Smith, *N. liebethruthii* Rabenhorst, *N. linearis* (C. Agardh) W. Smith, *N. longissima* (Brébisson) Grunow, *N. microcephala* Grunow, *N. obtusa* var. *scalpelliformis* Grunow, *N. ovalis* Arnott, *N. palea* (Kützing) W. Smith, *N. pellucida* Grunow, *N. pusilla* Grunow, *N. sigma* (Kützing) W. Smith, *N. spathulata* Brébisson, *N. sociabilis* Hustedt, *N. valida* Grunow, *N. vermicularis* (Kützing) Hantzsch.

Operhora martyi Héribaud, *O. olsenii* Müller, *O. schulzii* (Brockmann) Simonsen.

Pinnularia sp., *P. major* (Kützing) Rabenhorst.

Plagiogramma sp., *Plagiogramma van-heurckii* Grunow.

Pleurosigma sp., *P. anculatum* (Quekett) W. Smith, *P. aestuarii* (Brébisson) W. Smith, *P. delicatulum* W. Smith, *P. elongatum* W. Smith, *P. obscurum* W. Smith, *P. rigidum* W. Smith, *P. salinarum* (Grunow) Grunow, *P. strigosum* W. Smith.

Pseudonitzschia fraudulenta (Cleve) Hasle, *P. pseudodelicatissima* (Hasle) Hasle, *P. pungens* f. *pungens* Grunow, *P. salinarum* (Grunow) Grunow, *P. seriata* (Cleve) H. Peragallo, *P. subpacifica* Hasle.

Rhabdonema minutum Kützing.

Rhaphoneis sp., *R. amphiceros* (Ehrenberg) Ehrenberg, *R. nitida* (Gregory) Grunow.

Rhoicosphenia abbreviata (C. Agardh) Lange-Bertalot.

Rhopalodia gibberula (Ehrenberg) O. Müller, *R. operculata* (C. Agardh) Hakansson.

Scoliotropis latestriata (Brébisson) Cleve.

Stauroneis sp., *S. membranacea* (Cleve) F. W. Mills, *S. phoenicenteron* (Nitzsch) Ehrenberg, *S. salina* W. Smith.

Striatella sp., *S. unipunctata* (Lyngbye) C. Agardh.

Surirella sp., *S. fastuosa* Ehrenberg, *S. gemma* Ehrenberg, *S. ovalis* Brébisson, *S. robusta* Ehrenberg, *S. striatula* Turpin.

Synedra sp., *S. acus* Kützing, *S. closterioides* Grunow, *S. crystallina* (Agardh) Kützing, *S. fasciculata* (Agardh) Kützing, *S. fulgens* (Greville) W. Smith, *S. ulna* (Nitzsch) Ehrenberg, *S. undulata* (J. W. Bailey) W. Smith.
Tabellaria sp., *T. fenestrata* (Lyngbye) Kützing, *T. flocculosa* var. *asterionelloides* Grunow.
Tetracyclus sp.
Thalassionema sp., *T. nitzschioides* (Grunow) Grunow.
Thalassiothrix sp., *T. delicatula* Cupp, *T. frauenfeldii* (Grunow) Grunow, *T. mediterranea* Pavillard.
Tropidoneis sp., *T. lepidoptera* (Gregory) Cleve.

II. Chrysophyceae

Ochromonadales:

Dinobryon sp., *D. cylindricum* Imhof.
Mallomonas sp.
Ochromonas sp., *O. caroliniana* Campbell, *O. variabilis* Meyer.
Olisthodiscus carterae Hulburt, *O. luteus* N. Carter, *O. magnus* Hulburt.
Synura sp., *S. uvella* Ehrenberg.

Chromulinales:

Apedinella spinifera (Throndsen) Throndsen.
Calycomonas ovalis Wulff, *C. wulffii* Conrad & Kufferath.
Chromulina sp.

Chloromonales:

Vacuolaria virescens Cienkowski.

Dictyochales:

Dictyocha fibula Ehrenberg.
Distephanus speculum (Ehrenberg) Haekel.

III. Xanthophyceae

Mischococcales:

Monodus guttula Butcher.

Tribonematales:

Tribonema sp., *T. affine* West, *T. minus* (Wille) Hazen.

DINOPHYTA

Dinophyceae

Prorocentrales:

Prorocentrum sp., *P. aporum* (J. Schiller) Dodge, *P. balticum* (Lohmann) Loeblich III, *P. compressum* (Bailey) Abé, *P. dentatum* Stein, *P. gracile* Schütt, *P. lima* (Ehrenberg) Dodge, *P. micans* Ehrenberg, *P. minimum* (Pavillard) Schiller, *P. triestinum* Schiller.

Dinophysiales:

Ceratocorys horrida Stein
Dinophysis sp., *D. acuminata* Claparede & Lachmann, *D. acuta* Ehrenberg, *D. caudata* Kent, *D. fortii* Pavillard, *D. norvegica* Claparede & Lachmann, *D. ovum* Schütt, *D. pulchella* (Lebour) Balech, *D. punctata* Jörgensen, *D. rotundata* Claparade & Lachmann, *D. schuettii* Murray & Whitting.
Ornithocercus sp., *O. magnificus* Stein.
Phalacroma sp.

Gymnodiniales:

Amphidinium sp., *A. bipes* Herdman, *A. crassum* Lohmann, *A. lacustre* Stein, *A. longum* Lohmann, *A. operculatum* Caparède & Lachmann, *A. ovoideum* (Lemmermann) Lemmermann, *A. sphenoides* Wulff, *A. steinii* (Lemmermann) Kofoid & Swezy.
Cochlodinium sp., *C. brandtii* Wulff, *C. helicoides* Lebour, *C. heterolobatum* Sousa Silva.
Gymnodinium sp., *G. arcticum* Wulff, *G. danicans* Campbell, *G. galesianum* Campbell, *G. marinum* Kent, *G. nelsoni* Martin, *G. roseostigma* Campbell, *G. simplex* (Lohmann) Kofoid & Swezy, *G. splendens* Lebour.
Gyrodinium sp., *G. aureolum* Hulburt, *G. dominans* Campbell, *G. estuariale* Hulburt, *G. fusiforme* Kofoid & Swezy, *G. spirale* (Bergh) Kofoid & Swezy, *G. uncatenatum* Campbell.
Katodinium asymmetricum (Massart) Loeblich III, *K. rotundatum* (Lohmann) Loeblich III.
Oxyrrhis marina Dujardin.
Polykrikos kofoidii Chatton.

Noctilucales:

Noctiluca scintillans (Macartney) Ehrenberg.

Pyrocystales:

Dissodium asymmetricum (Mangin) Loeblich III.

Peridiniales:

Amphidoma sp.
Ceratium sp., *C. arietinum* Cleve, *C. extensum* (Gourret) Cleve, *C. furca* (Ehrenberg) Claparede & Lachmann, *C. fusus* (Ehrenberg) Dujardin, *C. hirundinella* (O. F. Müler) Dujardin, *C. horridum* (Cleve) Gran, *C. inflatum* (Kofoid) Jörgensen, *C. lineatum* (Ehrenberg) Cleve, *C. longipes* (Bailey) Gran, *C. macroceros* (Ehrenberg) Vanhöffen, *C. massiliense* (Gourret) Jörgensen, *C. minutum* Jörgensen, *C. setaceum* Jörgensen, *C. teres* Kofoid, *C. tripos* (O. F. Müller) Nitzsch.
Corythodinium reticulatum (Stein) Taylor.
Diplopsalis lenticula Bergh.
Glenodinium gymnodinium Penard.
Gonyaulax sp., *G. verior* Sournia, *G. digitale* (Pouchet) Kofoid, *G. polyedra* Stein, *G. polygramma* Stein, *G. spinifera* (Claparede & Lachmann) Diesing, *G. triacantha* Jörgensen.
Heterocapsa triquetra (Ehrenberg) Stein.

Micracanthodinium claytonii (R. W. Holmes) Balech.
Oblea rotunda (Lebour) Balech.
Oxytoxum sp., *O. milneri* Murray & Whitting, *O. sceptrum* (Stein) Schröder, *O. scolopax* Stein.
Peridinium aciculiferum Lemmermann.
Podolampas sp.
Protoperidinium sp., *P. bipes* (Paulsen) Balech, *P. breve* (Paulsen) Balech, *P. brevipes* (Paulsen) Balech, *P. cerasus* (Paulson) Balech, *P. claudicans* (Paulsen) Balech, *P. conicoides* (Paulsen) Balech, *P. conicum* (Gran) Balech, *P. depressum* (Bailey) Balech, *P. diabolum* (Cleve) Balech, *P. divergens* (Ehrenberg) Balech, *P. excavatum* (Martin) Balech, *P. globulum* (Stein) Balech, *P. granii* (Ostenfeld) Balech, *P. minutum* (Kofoid) Loeblich III, *P. oblongum* (Aurivillius) Parke & Dodge, *P. oceanicum* (Vanhöffen) Balech, *P. ovatum* Pouchet, *P. pallidum* (Ostenfeld) Balech, *P. pellucidum* Bergh, *P. pentagonum* (Gran) Balech, *P. subinerme* (Paulsen) Loeblich III, *P. steinii* (Jörgensen) Balech, *P. thorianum* (Paulsen) Balech.
Pyrodinium bahamense Plate.
Pyrophacus horologium Stein.
Scrippsiella trochoidea (Stein) Loeblich III.
Triadinium polyedricum (Pouchet) Dodge.
Zygabikodinium lenticulatum (Paulsen) Loeblich & Loeblich III.

HAPTOPHYTA

Haptophyceae

Isochrysidales:

Emiliania huxleyi (Lohmann) Hay & Mohler.
Genhyrocapsa oceanica Kamptner.
Hymenomonas roseola Stein.
Pleurochrysis carterae (Braarud & Fagerland) Christensen.

Coccosphaerales:

Acanthoica quattrospina Lohmann.
Algirosphaera robusta (Lohmann) Norris.
Calciosolenia sp., *C. granii* Schiller, *C. murrayi* Gran.
Discosphaera tubifera (Murray & Blackman) Ostenfeld.
Michaelsarsia elegans Gran.
Ophiaster hydroideus (Lohmann) Lohmann.
Pontosphaera sp., *P. syracusana* Lohmann.
Rhabdosphaera sp., *R. claviger* Murray & Blackman, *R. hispida* Lohmann.
Scyphosphaera apsteinii Lohmann.
Syracosphaera histrica Kamptner, *S. pulchra* Lohmann.

Prymnesiales:

Chrysochromulina sp., *C. minor* Parke & Manton.
Prymnesium parvum N. Carter.

Pavlovales:

Pavlova salina (N. Carter) Green.

CRYPTOPHYTA

Cryptophyceae

Cryptomonadales:

Campylomonas reflexa (Skuja) Hill.
Chilomonas sp.
Chroomonas sp., *C. amphioxeia* (Conrad) Butcher, *C. caroliniana* Campbell, *C. pusilla* (Backman) Happey-Wood, *C. vectensis* N. Carter.
Cryptomonas sp., *C. erosa* Ehrenberg, *C. ovata* Ehrenberg, *C. stigmatica* Wislouch.
Hemiselmis sp. *H. virescens* Droop.
Hillea sp.
Rhodomonas baltica Karsten, *R. salina* (Wislouch) Hill & Wetherbee.
Teleaulax acuta (Butcher) Hill.

CYANOPHYTA (CYANOBACTERIA)

Cyanophyceae

Chroococcales:

Anacystis sp.
Aphanothece sp.
Aphanocapsa sp.
Chroococcus dispersus (Keissler) Lemmermann, *C. limneticus* Lemmermann, *C. limneticus* var. *elegans* G. M. Smith.
Gomphosphaeria sp., *G. aponina* Kützing.
Marssoniella elegans Lemmermann.
Merismopedia sp., *M. elegans* A. Braun, *M. glauca* (Ehrenberg) Nägeli, *M. punctata* Meyen, *M. tenuissima* Lemmermann.
Microcystis sp., *M. aeruginosa* Kützing, *M. incerta* Lemmermann.
Rhabdoderma sp.
Rhabdogloea sp., *R. fascicularis* Lemmermann.
Synechococcus sp.

Nostocales:

Anabaena sp., *A. spiroides* Klebahn.
Calothrix sp.
Nostoc sp., *N. commune* Voucher.
Richelia intracellularis Schmidt.
Trichodesmium erythraeum (Ehrenberg) Gomont.

Oscillatoriales:

Lyngbya sp.
Oscillatoria sp., *O. limnetica* Lemmermann, *O. lutea* C. Agardh, *O. tenuis* C. Agardh, *O. submembranacea* Ardiss & Strafford.
Phormidium sp.
Planktolyngbya contorta (Lemmermann) Anagnostidis & Komárek.
Spirulina sp., *S. subsalsa* Oersted.

EUGLENOPHYYA

Euglenophyceae

Euglenales:

Euglena sp., *E. acus* Ehrenberg, *E. agiles* Carter, *E. ehrenbergii* Klebs, *E. deses* Ehrenberg, *E. mutabilis* Schmitz, *E. proxima* Dangeard, *E. spirogyra* Ehrenberg.
Eutreptia sp., *E. lanowii* Steuer, *E. viridis* Perty.
Eutreptiella sp., *E. marina* Cunha.
Phacus sp., *P. lemmermannii* (Swirenko) Skvortzow, *P. longicauda* (Ehrenberg) Dujardin, *P. suecicus* Lemmermann.
Trachelomonas sp., *T. hispida* (Perty) Stein, *T. hispida* var. *punctata* Lemmermann, *T. intermedia* Dangeard, *T. volvocina* Ehrenberg.

CHLOROPHYTA

I. Chlorophyceae

Volvocales:

Chlamydomonas sp., *C. vectensis* Butcher.
Dunaliella sp.
Eudorina sp.
Gonium sp.
Volvox tertius A. Meyer.

Zygnematales:

Closterium sp., *C. gracile* Brébisson.
Coelastrum sp., *C. cambricum* Archer.
Cosmarium sp., *C. turpinii* Brébisson.
Desmidium sp.
Euastrum sp., *E. abrurtum* West & West.
Staurastrum sp., *S. americanum* (West & West) G. M. Smith, *S. paradoxum* Meyen.
Zygnema sp.

Oedogoniales:

Oedogonium sp.

Chlorococcales:

Actinastrum sp., *A. hantzschii* Lagerheim, *A. hantzschii* var. *fluviatile* Schröder.
Ankistrodesmus sp., *A. convolutus* Corda, *A. falcatus* (Corda) Ralfs, *A. falcatus* var. *acicularis* (A. Braun) West, *A. spiralis* (Turner) Lemmermann.
Arthrodesmus sp.
Chlorella sp., *C. vulgaris* Beijerinck.
Closteriopsis longissima Lemmermann.
Crucigenia sp., *C. apiculata* (Lemmermann) Schmidle, *C. crucifera* (Wolle) Collins, *C. fenestrata* Schmidle, *C. irregularis* Wille, *C. lauterbornii* Schmidle, *C. quadrata* Morren, *C. tetrapedia* (Kirchner) West & West.
Dictyosphaerium sp., *D. planctonicum* Tiffany & Ahlstrom, *D. pulchellum* Wood.
Elakatothrix gelatinosa Wille.
Errerella bornhemiensis Conrad.
Franceia ovalis (Francé) Lemmermann.
Kirchneriella sp., *K. contorta* (Schmidle) Bohlin, *K. lunaris* (Kirchner) Möbius.
Micractinium sp., *M. pusillum* Fresenius.
Microspora sp.
Mougetia sp.
Nannochloris atomus Butcher.
Oocystis sp.
Pediastrum biradiatum Meyen, *P. duplex* Meyen, *P. duplex* var. *reticulatum* Lagerheim, *P. simplex* (Meyen) Lemmermann, *P. simplex* var. *duodenarium* (Bailey) Rabenhorst, *P. tetras* (Ehrenberg) Ralfs.
Polyedriopsis spinulosa Schmidle.
Quadrigula sp., *Q. lacustris* (Chodat) G. M. Smith.
Scenedesmus sp., *S. arcuatus* Lemmermann, *S. acuminatus* (Lagerheim) Chodat, *S. armatus* (Chodat) G. M. Smith, *S. bijuga* (Turpin) Lagerheim, *S. bijuga* var. *alternans* (Reinsch) Hansgirg, *S. denticulatus* Lagerheim, *S. dimorphus* (Turpin) Kützing, *S. hystrix* Lagerheim, *S. perforatus* Lemmerman, *S. quadricauda* (Turpin) Brébisson.
Selenastrum sp.
Schroederia setigera (Schröder) Lemmermann.
Tetraëdron sp., *T. gracile* (Reinsch) Hansgirg, *T. minimum* (A. Braun) Hansgirg, *T. pentaedricum* West & West, *T. regulare* Kützing, *T. regulare* var. *incus* Teiling, *T. trigonium* (Nägeli) Hansgirg.
Tetradesmus smithii Prescott.
Tetrastrum glabrum (Roll) Ahlstrom & Tiffany, *T. staurogeniaeforme* (Schröder) Lemmermann.

II. Prasinophyceae

Pyramimonadales:

Pyramimonas sp., *P. amylifera* Conrad, *P. grossii* Parke, *P. micron* Conrad & Kufferath, *P. obovata* N. Carter, *P. plurioculata* Butcher.

Prasinocladales:

Tetraselmis sp., *T. gracilis* (Kylin) Butcher, *T. maculata* Butcher.

OTHER CATEGORIES

Unidentified microflagellates (<10 microns)

Unidentified picoplankters (<2 microns)

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LETEPSAMMIA FRANKI, A NEW SPECIES OF DEEP-SEA CORAL (COELENTERATA: SCLERACTINIA: MICRABACIIDAE)

Joan Murrell Owens

Abstract.–Letepsammia franki, a new species of deep-sea, solitary corals belonging to the family Micrabaciidae, is described and figured. This new species resembles the type species, *L. formosissima* (Moseley, 1876), in having highly perforated septa and wall, and well-developed deltas. It differs in the distinctly beaded appearance of its septa, deltas, and columella; its slightly biconvex corallum with prominent basal apex; its projection of costae beyond septa at the distal edge, forming a narrow marginal shelf; and its more open basal wall. It is Recent in origin and is found in the Indian Ocean off the southeast coast of Africa at depths varying from approximately 50 to 650 meters. It thus falls within both the geologic and bathymetric ranges of the type species, *L. formosissima.*

Letepsammia was erected by Yabe & Eguchi in 1932, as a subgenus of *Stephanophyllia.* They based this subgenus by monotypy on the well-developed, spongy columella, and highly perforated septa and wall of the subgenotype, *S. formosissima* Moseley. More recent authors, such as Squires (1965, 1967), Keller (1977), Cairns (1982), and Owens (1984a, 1984b, 1986a), however, deemed these differences, along with its larger size, thinner base, and more prominent marginal shelf, sufficient to denote generic differences, and informally acknowledged the subgenus as a genus in itself. Eventually, Owens (1986b) formally described and officially elevated *Letepsammia* to generic rank.

At present, *Letepsammia* consists of only two species, *L. formosissima* and the new species described herein, *L. franki.*

Order Scleractinia
Suborder Fungiida
Superfamily Fungioidea Vaughan & Wells, 1943
Family Micrabaciidae Vaughan, 1905
Genus *Letepsammia* Yabe & Eguchi, 1932
Letepsammia franki, new species
Figs. 1, 2

Description. —Corallum large, loose, slightly biconvex, with narrow but prominent shelf. Wall thin, highly perforate. Calicular depression deep, narrow, elongate. Fusion of proximal margins of tertiary septa with inner edges of secondary septa form broad, porous, coarsely dentate deltoid structures. Diameter of specimens 10.5–31 mm, height 3–11 mm, average H:D ratio 0.39.

Costae long, thin, nearly smooth, thickening slightly distally. Intercostal loculi wider than costae, but interrupted by closely spaced synapticulae that connect adjacent costae with base of intervening septum. Outer margins of costae finely serrated. Costae begin as six (first cycle) at apex of convex base and bifurcate immediately (second cycle); outer costae of each system bifurcate about one-eighth the distance from center, with inner pairs dividing soon after (third cycle); fourth and fifth cycles overlap, with outermost costae of each system undergoing

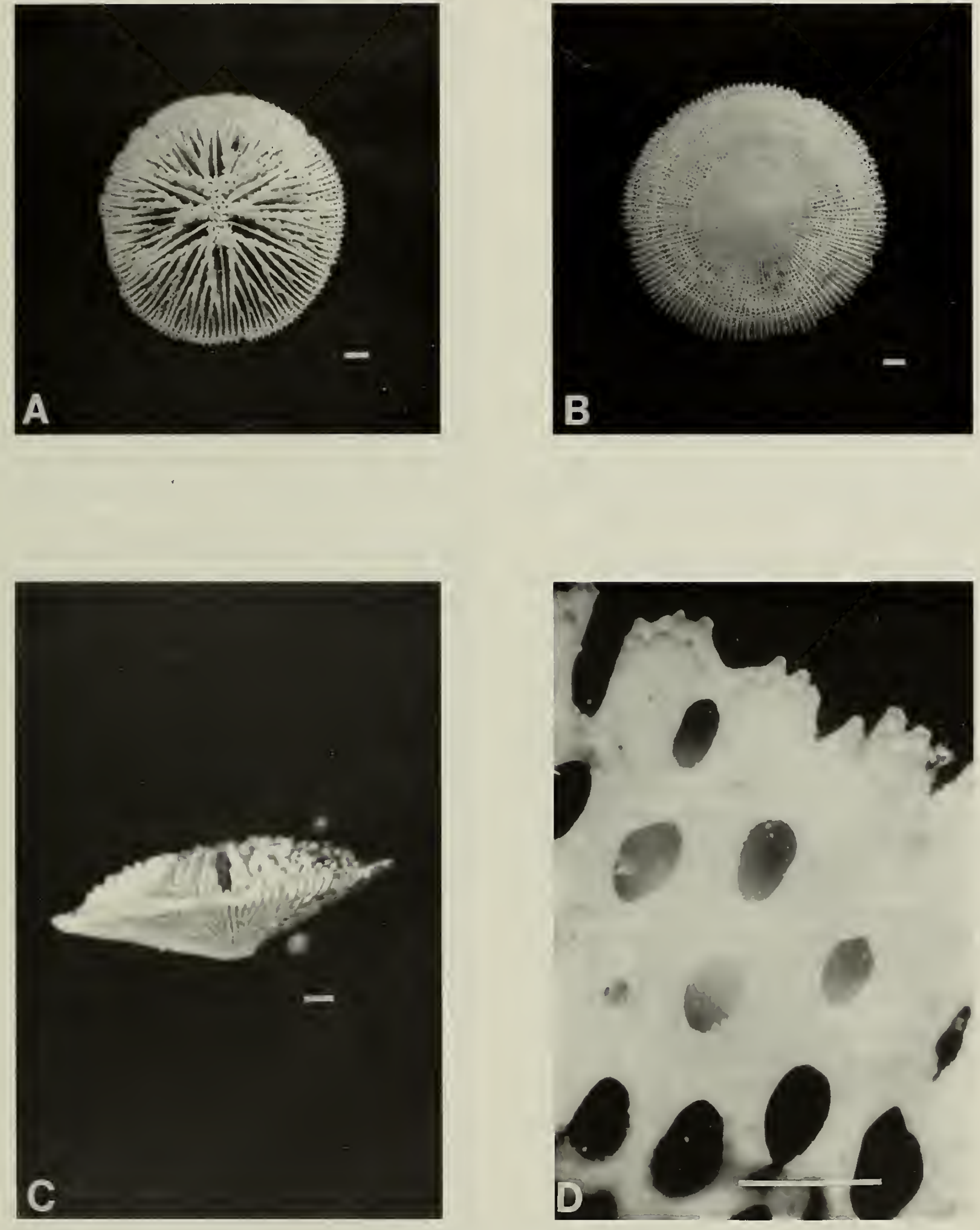

Fig. 1. *Letepsammia franki*: A, Oral view of holotype (USNM 75638), Anton Bruun 390-S; B, Aboral view of holotype; C, Side view of a paratype (USNM 75639), Anton Bruun 390-S; D, Thin section of a paratype (USNM 75640), under reflected light, showing thin, widely spaced trabeculae, radial perforations, and coarse dentation of distal margin of septum, Anton Bruun 390-S. Scale bars = 2 mm.

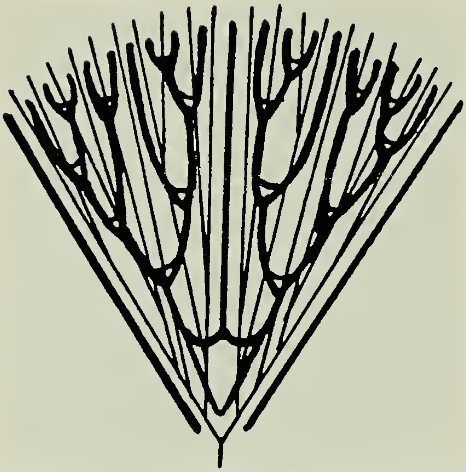

Fig. 2. Diagrammatic representation of one system of *Letepsammia franki*. Heavy lines represent septa; thin lines, costae. 5×.

two bifurcations before innermost again divide; sixth cycle incomplete, with only one outer pair and one inner pair of each system bifurcating (Fig. 2).

Septa thin, highly perforate, and, except for primaries, irregularly lined with vepreculae. Vepreculae closely and evenly spaced on primaries. Interspaces much broader than septa. Synapticulae scarce except along distal base of septa. Primaries free, straight, lower than adjacent septa; finely serrated proximally but coarsely dentate with short, clubby spines near distal margin. Secondaries straight, as tall as neighboring septa, and dentate with short, broad spines along full length of margin. Adjacent septa in tertiary position unite proximally with secondaries in conspicuous, triangular, trabecular masses that form broad, porous deltas. Tertiary septa do not extend to distal margin, but instead give rise to a series of bifurcations immediately beyond deltas to produce higher cycle septa, for a total of 120 septa.

Columella spongy, elongate, narrow, with single row of stubby spines running full length.

Trabeculae simple, wavy, grouped in three's in loose fan system; interareas arcuate between groupings, undifferentiated within; perforations of various sizes roughly aligned horizontally and radially.

Types. — Holotype: USNM 75638, Anton Bruun 390-S (29°35′S, 31°42′E; 138 m). Paratypes: USNM 75639 (1), 75640 (36), Anton Bruun 390-S (same as holotype); 75641 (1), Anton Bruun 370-H (24°41′S, 35°28′E; 311–320 m); 75642 (16), Anton Bruun 370-G (24°40′S, 35°28′E; 635 m); 75643 (2), Anton Bruun 372-G (24°53′S, 34°56′E; 55 m); 75644 (6), Vema Cruise 14, Sat 6 (29°48′S, 31°16′E; 232 m).

Occurrence. — Recent, Indian Ocean off southeast coast of Africa; 50–650 meters.

Discussion. — *Letepsammia franki* resembles both *Rhombopsammia niphada* and *L. formosissima, R niphada* because of its slightly biconvex corallum, its deep, long, narrow calicular depression, and its narrow but prominent shelf; and *L. formosissima* because of its highly perforate septa and wall, its well-developed deltas, and the reduced, restricted trabecular pattern of its septa—similarities of generic significance. *Letepsammia franki* is unique in having a papillose columella and coarse septal dentation that give its corallum a distinctly beaded appearance. Owens (1986a), in noting the similarities between *L. formosissima* and *R. niphada,* suggested that *R. niphada* may be a morphologic intermediate between *Letepsammia* and *Rhombopsammia.* The similarities between *L. franki* and *R. niphada* strongly reinforce this suggestion.

Cairns (1989), who had seen the specimens of *L. franki* deposited at the National Museum of Natural History, believed that specimens of *L. formosissima* from the western Indian Ocean referred to by Van der Horst (1927) and Boshoff (1981), and those from the Red Sea mentioned by Gardiner & Waugh (1939) are probably *L. franki,* the then undescribed species of *Letepsammia* alluded to by both Squires (1967) and Owens (1986b). Cairns & Keller (1993) also remarked on the same undescribed species, which Cairns in a later personal communication considered to be this new species. Similarly, the "button coral" figured by Williams (1986), which he referred to as "genus *Stephanophyllia,*" is most likely *L. franki.*

When Yabe & Eguchi (1932, 1934) erected the subgenus *Letepsammia,* they included in their subgenus a fossil form from the Plio-Pleistocene boundary, *Stephanophyllia* (*L.*) *japonica* nov. This species was subsequently determined by Squires (ca. 1967) to be synonymous with *S. superstes* Ortman, which he further reassigned as *L. superstes.* Thus, when Owens (1986b) formally described *Letepsammia,* she accepted Squires' redesignation and included in the genus two species: *L. formosissima* and *L. superstes.*

More recently, however, Cairns (1989) recounted a personal communication with H. Zibrowius, in which Zibrowius stated that he had examined the holotype of *S. superstes* and believed it to be a juvenile form of *L. formosissima.* If these synonymies are correct, then the geologic range of *L. formosissima* must be extended to the Plio-Pleistocene boundary, and thus exceeds the geologic range of the new species, *L. franki.*

Consequently, the genus *Letepsammia* presently includes only *L. formosissima* and *L. franki.*

Etymology.—The species name is in honor of Frank A. Owens, my husband, whose photographs of specimens are an integral part of my published works.

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I wish to thank S. D. Cairns of the Smithsonian Institution for making available to me the specimens used in this study; D. A. Dean of the Smithsonian Institution for his assistance in thin-sectioning some of the specimens; and F. A. Owens and E. H. Hughes for photographing the specimens used in this paper. I also wish to make special acknowledgment of D. F. Squires whose unfinished work on micrabaciid corals inspired me to undertake my own study of this group.

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SIDERASTREA GLYNNI, A NEW SPECIES OF SCLERACTINIAN CORAL (CNIDARIA: ANTHOZOA) FROM THE EASTERN PACIFIC

Ann F. Budd and Hector M. Guzmán

Abstract.—A new species of *Siderastrea* (*S. glynni*) has been found in shallow (7–8.5 m deep) reef rubble north of Isla Uraba, Bay of Panama, in the eastern Pacific region. The species is extremely rare. Its colonies are unattached, spheroidal in shape, and approximately 7–10 cm in diameter. *Siderastrea glynni* is distinguished by relatively small corallites (2.5–3.5 mm); numerous thin septa (40–48 per corallite); a porous columella; and a distinctive synapticular meshwork. The discovery of the new species is unusual because the genus *Siderastrea* typically occurs today in the Atlantic and Indian Oceans and is known in the Pacific only from a rare occurrence in the Philippine Islands.

A total of 19 species and seven genera of modern hermatypic scleractinian corals have been reported from the eastern Pacific coast of Panama (Holst & Guzmán 1993). The 19 species consist of: two "*Cycloseris,*" one *Gardineroseris,* five *Pavona,* five *Pocillopora,* two *Porites,* three *Psammocora,* and one *Siderastrea.* Six or more of the species are restricted to the extreme eastern Pacific (Wells 1983); however, the distributions of all seven genera except *Siderastrea* are widespread across the Indo-Pacific (Veron 1993). Here we describe an unusual new species of *Siderastrea.* It was recently discovered by one of us (HMG) while diving at depth of 7–8.5 m along an upper reef slope north of Isla Uraba in the Bay of Panama near the Pacific entrance to the Panama Canal (Fig. 1). Despite extensive search, only one population of the species has been found. It originally consisted of five unattached colonies, all of which were spheroidal in shape and approximately 7–10 cm in diameter (Fig. 2). The five colonies were found in a small patch (<8 m^2) over coral rubble within a 1 m distance from one another. One of the five colonies was collected and is described below. Since field observations suggested that the species may be close to extinction, the other four colonies were left alive at the original discovery site in an effort to preserve the species. The rarity of this species is similar to *Millepora boschmai* Weerdt & Glynn, 1991, a recently discovered eastern Pacific species of Hydrozoa.

The discovery of the *Siderastrea glynni* is particularly noteworthy because the genus occurs today mainly in the Atlantic and Indian Oceans (Veron 1986). Although Veron (1986) alludes to possible Indo-Pacific occurrences of *S. radians,* only one species, *S. savignyana,* is well-documented in the central Indo-Pacific, represented by one specimen from the Philippine Islands (Veron 1993). Another species of the genus (*Siderastrea mendenhalli*), however, was extremely abundant in south-central California at the northernmost end of the Gulf of California during early Pliocene time (Foster 1979, 1980a; Budd 1989).

Comparisons among *Siderastrea glynni,* the two Pacific species noted above, and three modern and two fossil Atlantic species (Table 1) indicate that the new species, *S. glynni,* is morphologically unique. *S. glynni* differs from the modern and the fossil Pacific species primarily in its small, well-rounded, unattached colony shape and in

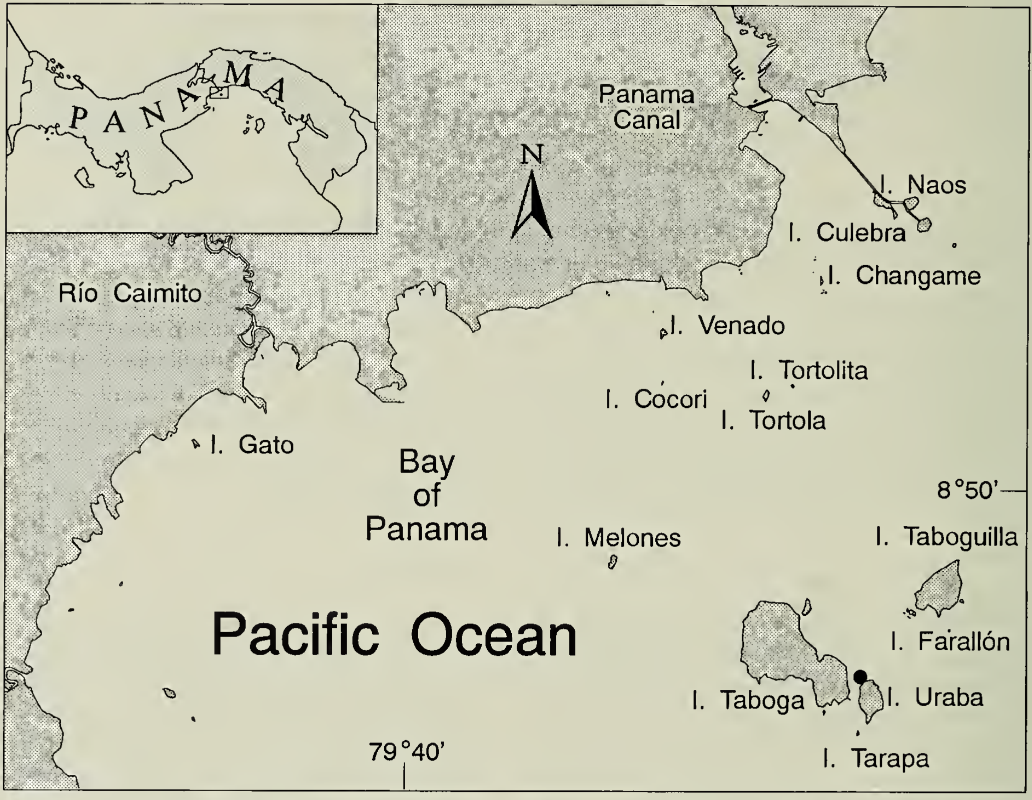

Fig. 1. Type locality (black dot) of *Siderastrea glynni.* Five colonies were found in a small patch at a depth of 7–8.5 m on the upper reef slope north of Isla Uraba, Bay of Panama.

its small corallite size and numerous septa (Fig. 3). It also has a relatively thinner wall and a shallower columellar fossa than modern Indo-Pacific *S. savignyana. Siderastrea glynni* differs similarly from the two common modern Caribbean species of *Siderastrea* (*S. radians, S. siderea*) by having small, shallow calices and numerous thin septa (Fig. 4). Of the two modern Caribbean species, *S. glynni* is most similar to *S. radians,* but differs in septal number and thickness, and in the development of the columella and synapticulae. Of the three Neogene Caribbean species in Table 1, *Siderastrea glynni* is most similar to *S. mendenhalli,* the species noted above whose distribution extended to the eastern Pacific. However, *S. glynni* has smaller corallites and fewer septa than *S. mendenhalli.*

On the basis of these distributional and morphologic comparisons, we recognize *S. glynni* as sufficiently distinct to describe it below as a new species.

Abbreviations of Repository Institutions.—USNM: U.S. National Museum of Natural History, Department of Invertebrate Zoology, Smithsonian Institution, Washington, D.C. 20560. SUI: University of Iowa, Department of Geology, Iowa City, IA 52242.

Order Scleractinia Bourne, 1900
Suborder Fungiina Verrill, 1865
Family Siderastreidae Vaughan & Wells, 1943
Genus *Siderastrea* de Blainville, 1830

Type species.—*Madrepora radians* Pallas, 1766:322–323. The holotype is figured in

Seba, 1756, pl. 122, figs. 12, 14, 18; and is currently lost.

Diagnosis.—Massive, branching or encrusting colonies. Cerioid corallites formed by extratentacular budding. Well-defined, synapticulothecate wall structure. Septa straight, generally not fusing.

Distribution.—Cretaceous to Recent; Caribbean, eastern and western Atlantic, Mediterranean, Red Sea, Indian Ocean (Wells 1956, Chevalier 1961, Veron 1993). One specimen is reported in the Pacific from the Philippine Islands (Veron 1993). The new occurrence in the present report adds the eastern Pacific to the known distribution of the genus.

Siderastrea glynni, new species
Figs. 2, 3, 5, 6

Etymology.—Named after Peter W. Glynn for his pioneering work on eastern Pacific coral reefs.

Diagnosis.—Small corallites. Well-developed outer synapticular rings forming a distinctive regular meshwork. Low. straight, moderately thick corallite wall. Numerous equally thin, dentate septa in four cycles, the last sometimes incomplete. Columella porous with a shallow fossa.

Fig. 2. *Siderastrea glynni.* Holotype, USNM 93956. Recent, 7–8.5 m depth, Isla Uraba, Bay of Panama. (a) Whole colony with soft tissue soon after collection, × ½. (b) A 5 mm thick slab cut through the growth axis of the colony, × 1.

Description.—Colonies massive, unattached, spheroidal; 7–10 cm in diameter; with a well-rounded, smooth outer surface. Calices hexagonal or pentagonal; relatively small in diameter (2.5–3.5 mm). Outermost synapticular rings regular and well-developed, forming a distinctive meshwork on the upper calical surface. Corallite wall low, solid, straight, continuous, intermediate in thickness (~0.15 mm). Synapticulae arranged in 3 or 4 rings, intermediate in thickness (~0.15 mm). Septa relatively thin, equal in thickness, usually continuous between adjacent corallites. Septal margins strongly dentate, with 8–10 dentations per primary septum. Septal surfaces weakly ornamented. Four septal cycles, with the fourth cycle sometimes incomplete; 40–48 septa per corallite. First and second cycles free; third cycle fuses with second near columella. Fourth cycle free, intermediate in length (~0.5 mm). Columella porous, papillose, intermediate in thickness (~0.4 mm). Calicular fossa shallow. Endothecal dissepiments thin, at 0.3–0.5 mm intervals.

Holotype.—USNM 93956 (Figs. 2, 3b, 5, 6); collected 3 Sep 1992, by H. M. Guzman, at 7-8.5 m depth on the upper reef slope along the northern tip of Isla Uraba, Bay of Panama (Fig. 1).

Material.—One colony: USNM 93956.

Comparison.—*Siderastrea glynni* is morphologically most similar to *S. radians* which also forms spheroidal, unattached colonies with small corallites. However, it differs from *S. radians* by having more numerous, thin septa that are equal in thickness. The

Table 1.—Morphologic characters distinguishing eight species of *Siderastrea.* References: 1 = Budd 1989; 2 = Budd et al. 1994; 3 = Foster 1980a; 4 = Foster 1980b; 5 = Laborel 1969; 6 = Laborel 1974; 7 = Scheer & Pillai 1983; 8 = Veron 1993; 9 = Yonge 1935.

Species	Distribution	Number of septa per corallite	Corallite diameter (mm)	Columella	Corallite wall	Additional references
S. glynni, new species	Recent; eastern Pacific	40–48	2.5–3.5	intermediate thickness, papillose; shallow fossa	intermediate thickness, 3–4 synap. rings; septa usually continuous between calices	—
S. radians (Pallas, 1766)	middle Pliocene to Recent; Caribbean, Bermuda, Brazil, w. Africa	30–40	2.5–3.5	thick, solid; intermediate fossa depth	thick, 2–3 synap. rings; septa usually continuous between calices	2, 4, 6, 9
S. siderea (Ellis & Solander, 1786)	early Miocene to Recent; Caribbean, ?w. Africa	44–50	3–5	thin, papillose; deep fossa	thin, 3–5 synap. rings; septa alternate between calices	2, 4, 6, 9
S. stellata Verrill, 1868	Recent; Brazil	~48	~3 (in series)	thin, papillose; very deep fossa	thin, 3–4 synap. rings; septa usually continuous between calices	5, 6
S. savignyana Milne Edwards & Haime, 1850	Recent; Red Sea, Indian Ocean	28–35	2.5–4	thick, solid; intermediate fossa depth	very thick, 2–3 synap. rings; septa continuous between calices	7, 8
S. mendenhalli Vaughan, 1917	early Miocene to early Pliocene; Dominican Republic, California	48–54	3–5	thick; shallow fossa	thick, 3–4 synap. rings; septa continuous between calices	1, 2, 3
S. silecensis Vaughan, 1919	early Miocene to early Pleistocene; Florida, Dominican Republic	48–>60	≫4.5	intermediate thickness; deep fossa	thin, 3–5 synap. rings; septa continuous between calices	1, 2
S. pliocenica Vaughan, 1919	middle Pliocene to early Pleistocene; Florida	40–48	4.5–5	thick, solid; shallow fossa	thick, 4–5 synap. rings; septa usually continuous between calices	2, 3

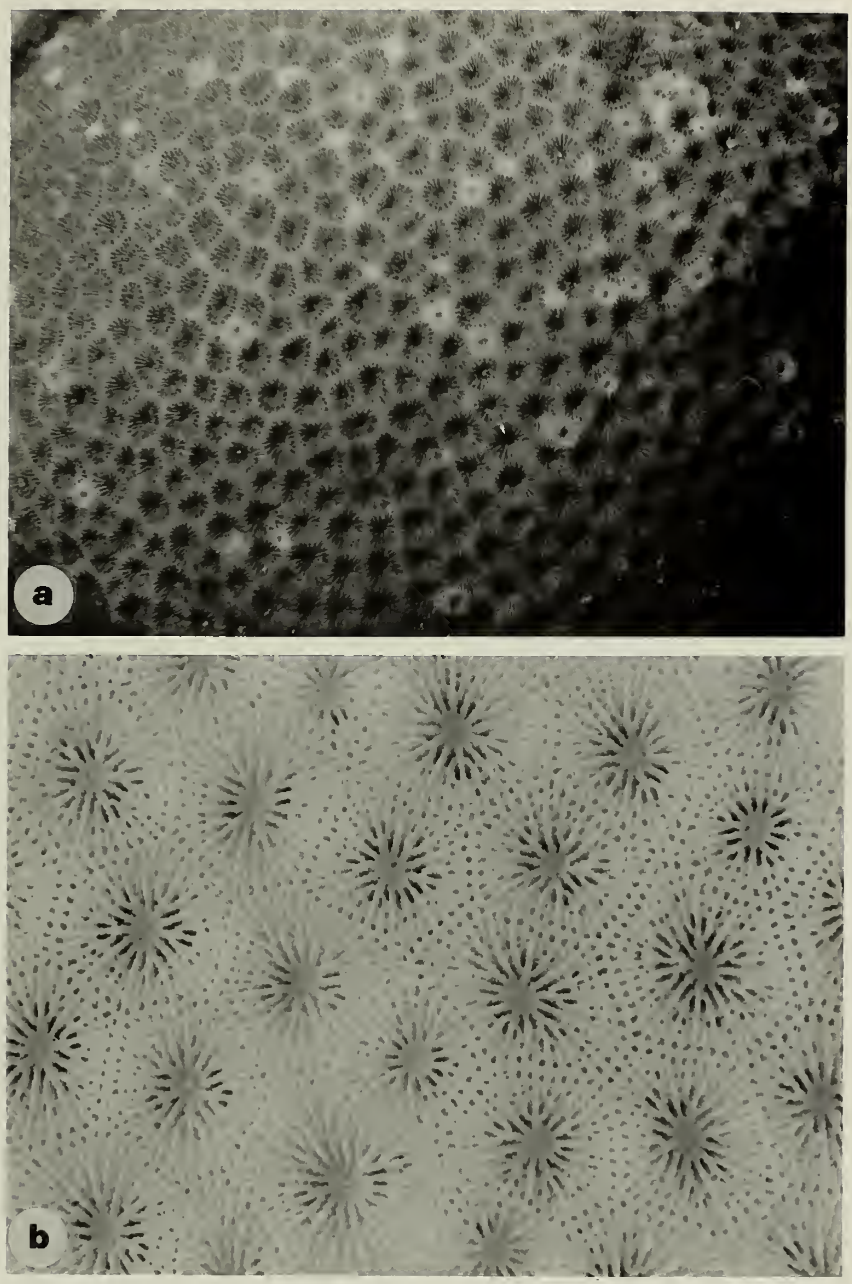

Fig. 3. *Siderastrea glynni.* (a) A closeup of a healthy colony in the field. (b) Holotype, USNM 93956. Calicular surface, ×8.

synapticulae of *S. glynni* are more numerous and regular, forming a diagnostic meshwork on the upper calical surface. Unlike most *S. radians,* calices are typically shallow, and columellae are not solid and prominent.

Distribution and ecology.—*Siderastrea glynni* is known only from Isla Uraba in the eastern Pacific, and it is extremely rare and possibly endangered. Colonies occurred clumped in a single patch in shallow reef rubble.

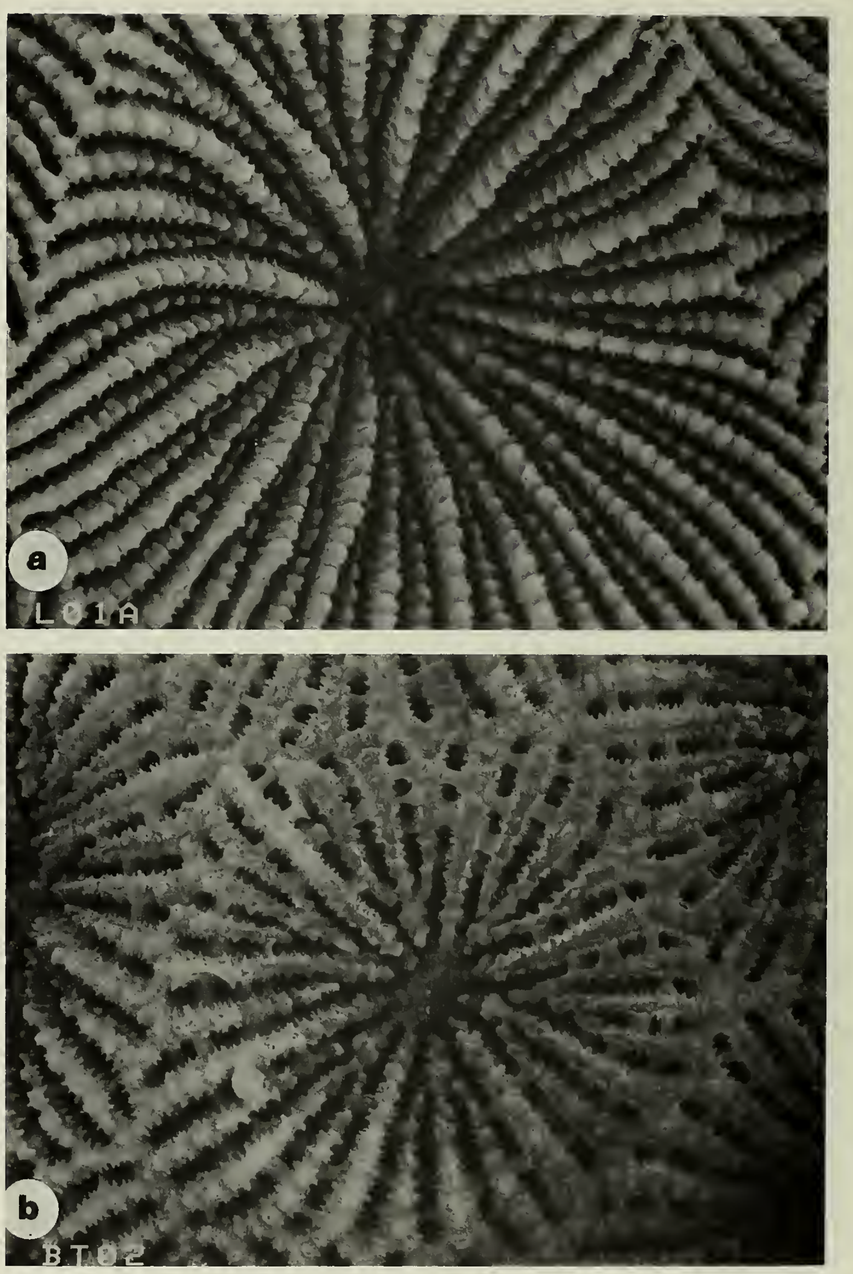

Fig. 4. SEM photos of calices of two common Caribbean species of *Siderastrea*. (a) *S. siderea*. USNM 93957. Recent, 20–25 m depth, Limones, San Blas Archipelago, Panama. ×20. (b) *S. radians*. SUI 84539. Recent, <1 m depth, southeast Cayos Zapatilla, Bocas del Toro, Panama. ×20.

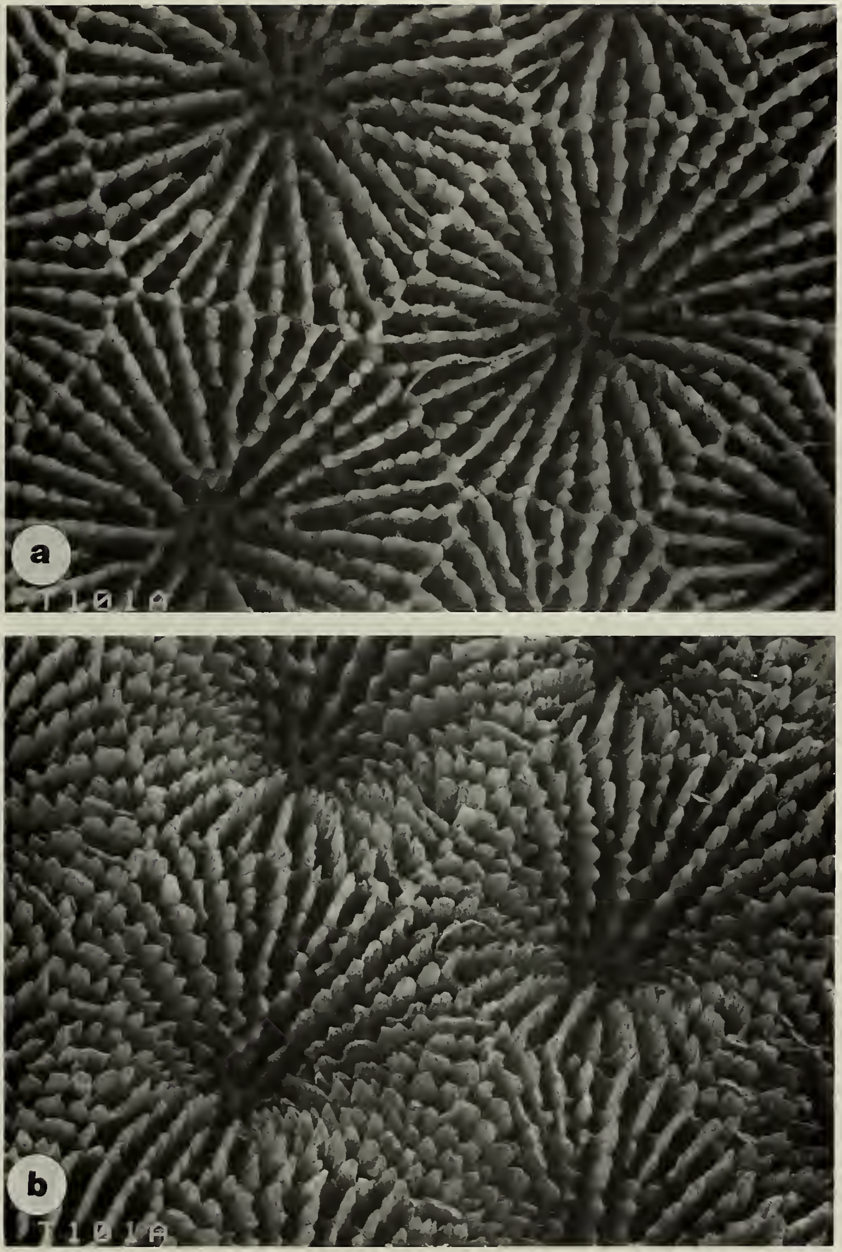

Fig. 5. (a, b). SEM photos of calices of the holotype of *Siderastrea glynni,* USNM 93956. ×20.

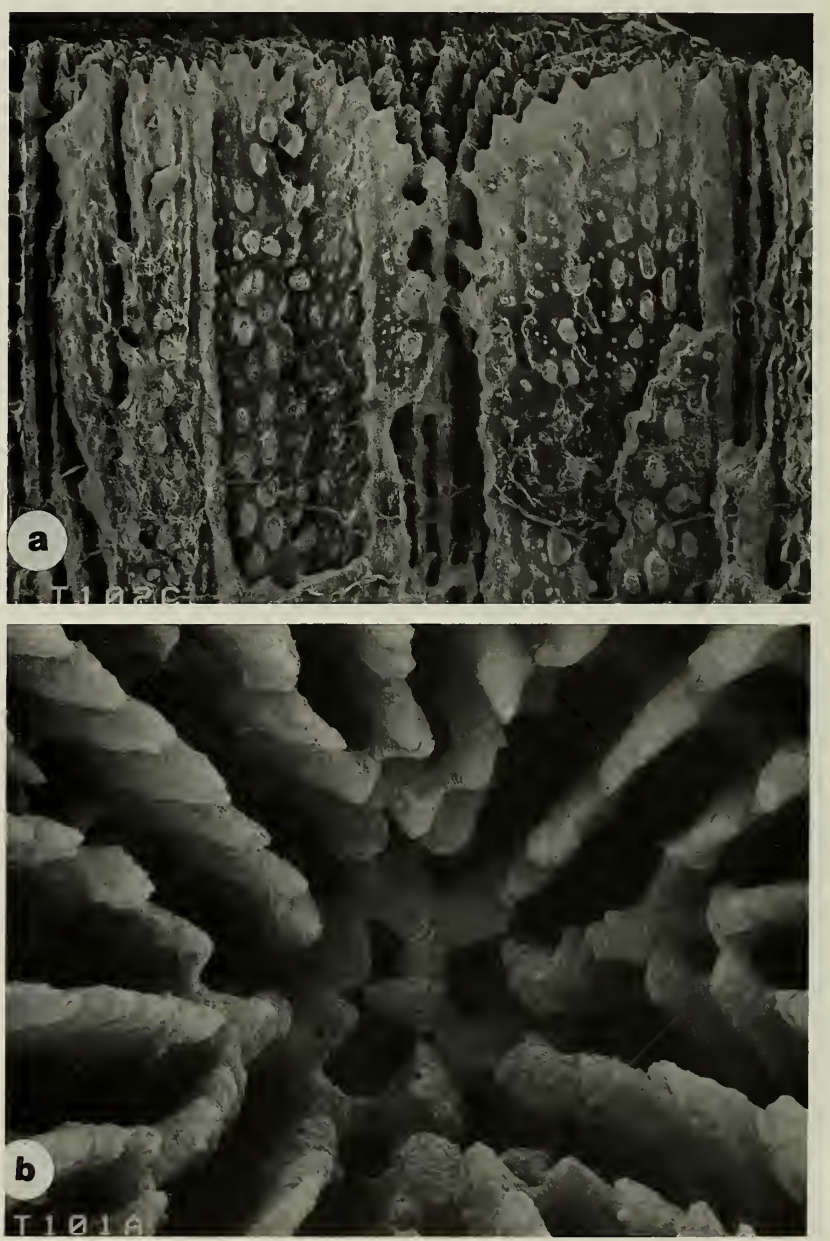

Fig. 6. SEM photos of the (a) wall (×20) and (b) columella (×80) on the holotype of *Siderastrea glynni,* USNM 93956.

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RESURRECTION OF *GLYPHOHESIONE* FRIEDRICH, 1950, WITH REDESCRIPTION OF *G. KLATTI* FRIEDRICH, 1950 AND DESCRIPTION OF *G. LONGOCIRRATA* (POLYCHAETA: HESIONIDAE)

Frank Licher

Abstract.—The formerly monotypic genus *Glyphohesione* Friedrich, 1950 is removed from synonymy with *Synelmis* Chamberlin, 1919 and emended. The type species, *G. klatti* Friedrich, 1950, from northern European waters, is redescribed, and *G. longocirrata,* a new species from the east coast of North America, is described. *Glyphohesione* is transferred from the Pilargidae to the Hesionidae, where it was originally placed, as the pilargid stem-species might have evolved from a hesionid species by progenesis.

Friedrich (1950) described the monotypic *Glyphohesione klatti* from Helgoland and recognized it as a hesionid. Eliason (1962a, 1962b), who reported the species from the Skagerrak and Öresund, considered it to be a pilargid belonging to the genus *Ancistrosyllis* McIntosh, 1879. Pettibone (1966) transferred it to the pilargid genus *Synelmis* Chamberlin, 1919. Comparison of brain morphology of different pilargid genera caused Fitzhugh & Wolf (1990) to doubt that specimens identified as *Synelmis klatti* in the collection of the U.S. National Museum, Washington, belong to this genus, and they suggested resurrecting the older taxon *Glyphohesione* for them. In a phylogenetic analysis of the Pilargidae (note: the correct spelling is Pilargidae, not Pilargiidae (see: International Commission on Zoological Nomenclature (1985): International Code of Zoological Nomenclature, art. 35 d (ii))), Licher & Westheide (1994) argued that the species of this family might form a monophyletic group within the Hesionidae. A subfamily Pilarginae beside the "Hesioninae" Hartmann-Schröder, 1971 and "Microphthalminae" Hartmann-Schröder, 1971 should not be erected until a comprehensive revision of the Hesionidae including pilargids has been made of the "true" hesionid taxa and is beyond the scope of the present study. The "Hesioninae" as well as the former "Hesionidae" ("Hesioninae" + "Microphthalminae") are very likely paraphyletic (Licher & Westheide 1994). The "Microphthalminae" represents a polyphyletic group (Westheide 1977). Reinvestigation of material of different species identified as *Synelmis klatti* in the course of the analysis of Licher & Westheide 1994 induced them to reestablish the old generic name.

The present paper emends the diagnosis of *Glyphohesione,* redescribes the European *G. klatti* and describes the eastern North American *Glyphohesione longocirrata,* new species.

Materials and Methods

For light microscopical preparations the fixed specimens (stored in 70% ethanol) were transferred into glycerine. Observations, drawings, and measurements were made by means of a LEITZ Diaplan microscope with interference-contrast optics and a camera lucida. For SEM investigations one specimen was dehydrated and critical-point dried with carbon dioxide. After sputtering with gold, it was analyzed with a JEOL JSM 820.

Material examined originates from the following museums: Gothenburg Natural History Museum (GNM); Senckenberg Museum, Frankfurt (SMF); U. S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Zoological Museum, University of Copenhagen (ZMUC).

Glyphohesione Friedrich, 1950, emended

Type species.—*Glyphohesione klatti* Friedrich, 1950, by monotypy and original designation.

Additional material examined.—The holotype of the type species of *Synelmis* Chamberlin, 1919, *S. simplex* Chamberlin, 1919 (USNM 19480, type) and some nontype specimens of *S. albini* (Langerhans, 1881) (type locality the Canary Islands, type material lost) from the Galapagos Islands (W. Westheide coll., Osnabrück) have been examined.

Diagnosis.—Hesionidae with body dorsoventrally flattened; some anterior segments distinctly wider, appearing somewhat inflated. Integument smooth, without papillae. Prostomium bilobed anteriorly, with two palps consisting of palpophores fused totally with prostomium and elongated palpostyles. Three slender antennae; lateral antennae located at anterior prostomial margin, close to palps; median antenna positioned at posterior margin. Pharynx unarmed. Peristomium achaetous, with two pairs of slender tentacular cirri. Parapodia biramous. Notopodia each with elongated dorsal cirrus, one notoacicula, and one stout emergent spine-like notochaeta, the latter in median and posterior segments only. Neuropodia well developed, each with slender ventral cirrus, one neuroacicula and simple chaetae only. Pygidium with two elongated anal cirri.

Remarks.—Eliason (1962a, 1962b) placed the monotypic *Glyphohesione* in *Ancistrosyllis* McIntosh, 1879, based on similarities with *Synelmis albini* (Langerhans, 1881) (=*Ancistrosyllis albini*). However, *Ancistrosyllis* possesses a hook-shaped notochaeta, not a straight one, which is characteristic for *Synelmis.* Pettibone (1966) transferred both *A. albini* and *A. klatti* to *Synelmis,* assuming *S. klatti* to be a juvenile of *S. albini.* Pearson (1970), Hartmann-Schröder (1971), and Katzmann et al. (1974) considered *S. klatti* to be a member of *Synelmis.* Fitzhugh & Wolf (1990) investigated American material identified as *Synelmis klatti* and suggested resurrecting the original generic name.

Glyphohesione Friedrich, 1950 clearly differs from *Synelmis* Chamberlin, 1919 in lacking the two emergent neuropodial spines which are apomorphic for *Synelmis* (Fitzhugh & Wolf 1990, Licher & Westheide 1994). In *Glyphohesione,* dorsal cirri are longer than ventral cirri, and the dorsal cirri of the first chaetiger are longer than those of the following ones, whereas in *Synelmis* dorsal and ventral cirri of all chaetigers are subequal. In addition, this taxon is known to possess nuchal organs, which were not found in *Synelmis,* and the brain is similar to that of *Sigambra* Müler, 1858 (Fitzhugh & Wolf 1990). *Glyphohesione* clearly differs from *Sigambra* in having notopodial spines and in lacking hook-shaped notochaetae.

Discussion.—Licher & Westheide (1994) conclude that there are good indications that the pilargid stem-species might have evolved by progenesis from a juvenile stage of a large-bodied hesionid species. This induced them to include the family Pilargidae in the Hesionidae, a view generally adopted by earlier authors (e.g., Ehlers 1908, Fauvel 1923, Augener 1927, Monro 1933, Treadwell 1941).

According to Licher & Westheide (1994), within the pilargids *Glyphohesione* is the taxon with the highest number of plesiomorphic characters shared with juvenile hesionids, e.g., (1) possession of elongated palpostyles, (2) lateral antennae located at the anterior prostomial margin, and (3) prostomial, peristomial, parapodial and pygidial appendages elongated and well developed.

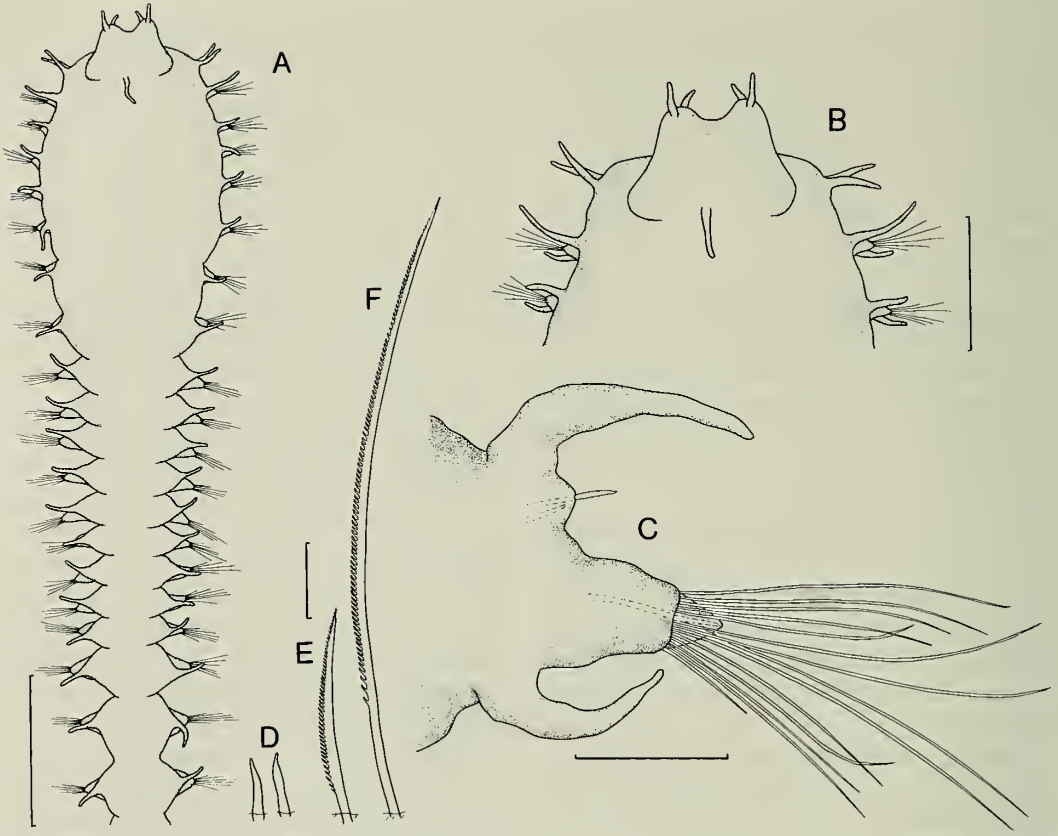

Fig. 1. *Glyphohesione klatti* Friedrich, 1950 (ZMUC POL-178). A. Anterior and median part of the body, dorsal view. B. Anterior end, dorsal view. C–F. Parapodium 21 (ZMUC POL-178-A): C. Parapodium, posterior view, half of neuropodial fascicle omitted. D. Emergent spine-like notochaetae. E. Ventralmost neurochaeta. F. Dorsalmost neurochaeta. Scales: A = 500 μm; B = 250 μm; C = 100 μm; D–F = 25 μm.

Glyphohesione is monophyletic and the adelphotaxon of the stem-species of all other pilargid genera (Licher & Westheide 1994).

Genus *Glyphohesione* Friedrich, 1950, resurrected

Glyphohesione klatti Friedrich, 1950
Figs. 1–2

Glyphohesione klatti Friedrich, 1950:171–173, figs. 1–2.
Ancistrosyllis klatti.—Eliason, 1962a:241; 1962b:29–32, fig. 3.
Synelmis klatti.—Pettibone, 1966:190–191.—Pearson, 1970:74–75, fig. 2b, c.—Hartmann-Schröder, 1971:144–145, fig. 49.—Katzmann et al., 1974:27–28. [Not *Synelmis klatti* of Wolf 1984; not Fitzhugh & Wolf 1990 (both = *G. longocirrata,* new species)].

Material examined.—Kattegatt: Off Skagen, Denmark, 58°01′N, 10°52′E, 190 m, fine mud, M. E. Petersen coll., 22 Sep 1968 (ZMUC POL-178, 5 incompl. specimens; ZMUC POL-178-B, 1 incompl. SEM preparation). Laholmsbukten, off Laholm, Sweden, St. 150/417, 21 m, stiff clay and some sand, "Akka," L. A. Jägerskiöld coll., 17 Jun 1933 (GNM 11347, 1 incompl. specimen).—Skagerrak: Saltkällefjord, off Gullmaren, Sweden, 56 m, P. Bagge coll., 24

Fig. 2. *Glyphohesione klatti* Friedrich, 1950 (ZMUC POL-178-B). A. Anterior end, lateral view. B. Parapodia of median region, right side, dorsal view. Scales: A–B = 100 μm.

Nov 1964 (GNM 12839, 1 incompl. specimen).—North Sea: Raunefjord, off Bergen, Norway, 245 m, sandy loam, Fosshagen coll., 05 Oct 1962 (GNM 12949, 2 incompl. specimens). German Bight, 54°40′N, 06°00′E, 43 m, silt and clay, M. Türkay coll., 24 May 1987 (SMF 4432, 1 incompl. specimen).—English Channel: Survey Sta. M 16T, 51°24.6′N, 08°05′W, 112 m, J. P. Hartley coll., Aug 1975 (USNM 58901, 2 incompl. specimens).

Type locality.—Tiefe Rinne off Helgoland, North Sea. Type material lost (H. Friedrich, pers. comm.).

Description.—Body robust, dorsoventrally flattened; anterior segments inflated, much wider than long, median segments about as wide as long, posterior segments longer than wide (Fig. 1A). Largest incomplete specimen (USNM 58901) with 40 segments and a length of 9.6 mm, 1.1 mm wide with parapodia (chaetiger 1), 0.8 mm wide without parapodia (chaetiger 5). (Up to 13 mm long, 0.5 mm wide for 71 segments according to Eliason 1962b:29). Color in ethanol brown. Living specimens with yellowish gut and transparent body with yellowish pigment in anterior region on posterior part of prostomium (M. E. Petersen, pers. comm.; see also fig. 3a, f in Eliason 1962b).

Prostomium slightly wider than long, divided anteriorly by a wide furrow into two lobes, lateral margins slightly concave (Figs. 1B, 2A). Palps with palpophores fused to prostomium and free elongate palpostyles, somewhat shorter than the lateral antennae, inserted anteroventrally. Three slender antennae, with slightly inflated bases. Lateral antennae slender, located at anterior prostomial margin; median antenna very slender, about 1.5–2 times as long as lateral ones, positioned at posterior prostomial margin. Eyes lacking. Nuchal organs not visible.

Peristomium almost as long as each of following anterior segments, dorsally fused with prostomium and encircling posterior half of latter. Two pairs subequal, slender tentacular cirri of similar shape and size as median antenna (Figs. 1B, 2A). Specimens in ethanol usually with two indistinctly delimited, brown-pigmented bulging areas on posterior part of peristomium.

Parapodia biramous, usually distinctly set apart from trunk except for some in inflated anterior region. Notopodia each with slender dorsal cirrus, extending slightly beyond tip of neuropodial lobe (Figs. 1C, 2B). Longest dorsal cirri (ca. 200 μm) occurring in first chaetiger. Following cirri much shorter, not longer than tentacular cirri. One thin notoacicula. Parapodia of median and posterior segments with one stout emergent spine-like notochaeta (first present on chaetigers 5–8) (Fig. 1C, D).

Neuropodia conical, each with a longer, triangular prechaetal lobe; a fan-shaped bundle of up to ca. 25 simple chaetae (Figs. 1C, 2B), decreasing in number posteriorly; and a shorter, distally truncate postchaetal lobe. Chaetae of different lengths, shorter ones stouter, all finely serrated, distally pointed with smooth, entire tips (Fig. 1E, F); serration becoming shorter distally and difficult to recognize. One neuroacicula present. Ventral cirri similar to dorsal ones but shorter, not extending beyond neuropodial lobe.

Posterior end lacking in all of the available specimens, but pygidium with two ventral filiform anal cirri according to Eliason (1962b:fig. 3j).

Distribution.—*Glyphohesione klatti* is known only from European waters: Öresund and Kattegat (Eliason 1962a, this paper); Skagerrak (Eliason 1962b, Bagge 1969, this paper); Tiefe Rinne off Helgoland, North Sea (Friedrich 1950); German Bight, North Sea (this paper); Loch Linnhe, Scotland (Pearson 1970); English Channel (this paper); and the Catalonian coast of the Mediterranean Sea (Katzmann et al. 1974). In northern Europe it has been taken at depths of 20–680 m and in the Mediterranean at depths of 10–185 m.

Glyphohesione longocirrata, new species
Fig. 3

Synelmis klatti.—Wolf, 1984:29–31 to 29–35, figs. 29–29 and 29–30 (USNM 86983, 86984, 86985, 86986, 86987); Fitzhugh & Wolf, 1990:1–16 (USNM 86986).

Material examined.—Gulf of Mexico: off Florida: SOFLA Sta. 20A, 25°17.20′N, 82°09.44′W, 22 m, coarse sand, Apr 1981 (USNM 86985, 1 compl. specimen, holotype); SOFLA Sta. 20C, 25°17.20′N, 82°09.44′W, 22 m, coarse sand, Nov 1980 (USNM 86986, 2 specimens, paratypes); SOFLA Sta. 20E, 25°17.20′N, 82°09.44′W, 22 m, Apr 1981 (USNM 86987, 1 specimen, paratype); MAFLA Sta. V-2531, 29°47.59′N, 86°09.29′W, 45 m, coarse sand, Aug 1977 (USNM 86983, 1 specimen, paratype).—Northwest North Atlantic Ocean: Gulf of Maine: Massachusetts, off Cape Cod: NEEB Sta. 41, 41°37.30′N, 69°15.42′W, 164 m, 27 Feb 1977 (USNM 91310, 5 specimens); NEEB Sta. 41, 41°37.34′N, 69°15.46′W, 165 m, 27 Feb 1977 (USNM 91311, 1 specimen); NEEB Sta. 41, 41°37.21′N, 69°14.54′W, 172 m, 27 Feb 1977 (USNM 91312, 1 specimen); NEEB Sta. 41, 41°37.00′N, 69°14.59′W, 165 m, 27 Feb 1977 (USNM 91313, 1 specimen); NEEB Sta. 41, 41°37.36′N, 69°15.49′W, 178 m, 17 May 1977 (USNM 91320, 1 specimen); NEEB Sta. 41, 41°36.58′N, 69°15.35′W, 175 m, 17 May 1977 (USNM 91321, 1 specimen); NEEB Sta. 42, 41°50.26′N, 69°29.30′W, 185 m, 26 Feb 1977 (USNM 91314, 1 specimen); NEEB Sta. 42, 41°50.10′N, 69°29.10′W, 185 m, 26 Feb 1977 (USNM 91315, 1 specimen); NEEB Sta. 42, 41°50.06′N, 69°29.09′W, 185 m, 26 Feb 1977 (USNM 91316, 1 specimen); NEEB Sta. 42, 41°49.53′N, 69°28.54′W, 191 m, 16 May 1977 (USNM 91322, 1 specimen); NEEB Sta. 42, 41°50.35′N, 69°29.28′W, 179 m, 16 May 1977 (USNM 91323, 2 specimens).—Georges Bank: Northern Slope: NEEB Sta. 35, 42°13.08′N, 67°34.20′W, 242 m, 19 May 1977 (USNM 91317, 1 specimen); NEEB Sta. 35, 42°13.05′N, 67°33.49′W, 243 m, 19 May 1977 (USNM 91318, 1 specimen); NEEB Sta. 35, 42°13.19′N, 67°34.36′W, 239 m, 19 May 1977 (USNM 91319, 1 specimen); Southern Slope: NEEB Sta. 16, 40°42.30′N, 67°34.26′W, 87 m, 19 Feb 1977 (USNM 91309, 1 specimen); Nantucket Shoals: NEEB Sta. 3, 40°39.38′N, 69°27.23′W, 56 m, 15 Feb 1977 (USNM 91308, 1 specimen).

Type locality.—Gulf of Mexico, off southern Florida, 22 m, coarse sand.

Description.—Body dorsoventrally flattened, with 2–4 inflated anterior segments (Fig. 3A). Largest complete specimen ex-

Fig. 3. *Glyphohesione longocirrata,* new species (USNM 86985, holotype). A. Anterior and median part of the body, dorsal view. B. Anterior end, dorsal view. C. Parapodium of median region, posterior view. D. Posterior end, lateral view. E–G. Posterior chaetiger: E. Emergent spine-like notochaetae. F. Ventralmost neurochaeta. G. Dorsalmost neurochaeta. Scales: A = 250 μm; B = 100 μm; C–D = 50 μm; E–G = 25 μm.

amined (USNM 86985, holotype) with 43 segments, 5.1 mm long, up to 0.5 mm wide including parapodia (chaetiger 4), 0.2–0.25 mm wide without parapodia. (Largest specimen examined by Wolf (1984) incomplete, with 53 segments, 12.0 mm long and 0.5 mm wide.) Color in ethanol light greyish yellow, nearly transparent.

Prostomium slightly wider than long, with concave lateral margins (Fig. 3B). Palps

Table 1.—Characters of *Glyphohesione klatti* Friedrich, 1950 and *G. longocirrata,* new species.

Characters	*Glyphohesione klatti* Friedrich, 1950	*G. longocirrata,* new species
Maximum length × width, no. of chaetigers	13 × 0.5 mm, 71 chaetiger (complete)	12+ × 0.5 mm, 53 chaetigers (incomplete)
Habitus; color	Robust; brown	Delicate; light greyish yellow
No. anterior inflated segments	ca. 8	2–4
Tentacular and dorsal cirri of anterior segments	At most one-fourth of body width	As long as body width
Notochaetae: first appearance of spines	Chaetigers 5–8	Chaetigers 10–15
Neurochaetae: structure, number per fascicle	Finely serrated with entire, curved tips; up to 25 per fascicle	Finely serrated with minutely bifid tips; up to 14 per fascicle
Distribution	Northern and southern Europe, 43–681 m	North American east coast and Gulf of Mexico, 22–243 m

consisting of two filiform palpostyles only, inserted anterolaterally at ventral side. Three filiform antennae; lateral ones near anterior prostomial margin, somewhat longer than palpostyles; median antenna longer than lateral ones, positioned at posterior prostomial margin. Eyes lacking. Nuchal organs not visible.

Peristomium shorter than following segments. Anterior peristomial margin slightly overlapped by prostomium. Two pairs subequal, filiform tentacular cirri, of similar shape as median antenna (Fig. 3B). Some specimens with two pigmented areas on posterior part of the peristomium (see also fig. 29–30a in Wolf 1984).

Parapodia biramous, usually distinctly set apart from trunk. Parapodia of second chaetiger usually smaller than those of first one. Notopodia each with filiform dorsal cirrus, extending far beyond tip of neuropodium (Fig. 3C). Dorsal cirri of anterior segments nearly as long as tentacular cirri. One thin and transparent notoacicula. Parapodia of median and posterior segments with one long stout emergent spine-like notochaeta (first present on chaetigers 10–15), nearly as long as shortest neurochaetae, decreasing in length posteriorly, distinctly bent in prepygidial segment (Fig. 3D, E).

Neuropodial lobe conical, with bundle of simple serrated and distally minutely bifid chaetae, 8–14 in anterior segment, 6–9 in posterior ones (Fig. 3C, F, G). One neuroacicula present. Ventral cirri similar to dorsal ones, extending slightly beyond tip of neuropodial lobe.

Pygidium rounded, with two long filiform anal cirri, about twice as long as median antenna (Fig. 3D).

Distribution.—*Glyphohesione longocirrata,* new species, is widely distributed off the east coast of North America: from the Gulf of Maine (off Massachusetts) to the Gulf of Mexico (off Florida and Alabama), at depths of 20–240 m, on bottoms of coarse to medium-fine sand, silty sand and clayey silt.

Remarks.—This species is assigned to the genus *Glyphohesione* because of the presence of simple chaetae, a straight spine-like notochaeta, elongated palpostyles, and the position of the lateral and median antennae. *Glyphohesione longocirrata,* new species, differs from *G. klatti* Friedrich, 1950 in possessing longer, more developed tentacular and dorsal cirri (Table 1). Dorsal cirri in anterior region in *G. longocirrata* are nearly as long as the body width; in *G. klatti* they are a quarter of the body width at most. In *G. longocirrata* the neurochaetae per fascicle are few and distally bifid (see Wolf 1984). Furthermore, specimens from North America have a more delicate body shape.

Etymology.—This species is named for its elongated tentacular and dorsal cirri.

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ADDITIONAL RECORDS OF POLYNOID POLYCHAETES FROM THE JUAN DE FUCA RIDGE

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Abstract.—Additional specimens of two polynoid polychaetes, *Bathycatalina filamentosa* (Moore) (Macellicephalinae), and *Harmothoe macnabi* Pettibone (Harmothoniae), were collected from a new vent site on the Juan de Fuca Ridge. Based on these materials, both the subfamily Macellicephalinae and genus *Bathycatalina* are emended, the former to include *Bathylevensteinia bicornis* (Levenstein) and *Gesiella jameensis* (Hartmann-Schröder), and the descriptions of *B. filamentosa* and *H. macnabi* supplemented.

A grab-sample of *Ridgia* tube-worms was taken from an isolated black smoker during the *Atlantic/Alvin* cruises to the Juan de Fuca Ridge in October 1993. Polynoid polychaetes obtained from the sample were sent to me for identification, and found to be *Bathycatalina filamentosa* (Moore) (Macellicephalinae), and *Harmothoe macnabi* Pettibone (Harmothoniae). Descriptions of both species are supplemented based on these additional materials. The genus *Bathycatalina* Pettibone is emended, and the Subfamily Macellicephalinae is also emended to include *Gesiella jameensis* (Hartmann-Schröder), and *Bathylevensteinia bicornis* (Levenstein).

Specimens are deposited in the Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution (USNM).

Family Polynoidae Kinberg, 1856

Subfamily Macellicephalinae Hartmann-Schröder, 1971, emended Pettibone, 1976.

Additions and emendations were added to the Subfamily Macellicephalinae Hartmann-Schröder, 1971, by Pettibone (1976: 6; 1985a:129; 1985b:740; 1989:159; & 1993: 679). Two new genera and species that were placed in the Subfamily Harmothoinae Horst, 1917, by Pettibone (1976:60) are herein included in the Subfamily Macellicephalinae, based on previous incorrect interpretations of the structures on the anterior lobes of the prostomia, as lateral antennae, rather than as anterior rounded-filiform extensions and not distinct lateral antennae. They include *Bathylevensteinia* Pettibone, 1976, with *B. bicornis* (Levenstein, 1962) and *Gesiella* Pettibone, 1976, with *G. jameensis* (Hartmann-Schröder, 1974).

Bathylevensteinia bicornis (Levenstein, 1962)

Macellicephala bicornis Levenstein, 1962: 1143, fig. 1.1), in Macellicephalinae.
Bathylevensteinia bicornis.—Pettibone, 1976:62, fig. 35a–e, in Harmothoinae.

Remarks.—*Bathylevensteinia bicornis* was incorrectly place in Harmothoinae, due to an incorrect interpretation of the so-called bifurcate frontal horns on the prostomium by Levenstein. Pettibone referred to the bilobed prostomium with subtriangular frontal horns, and, more medially, lateral antennae with cylindrical ceratophores with styles missing. However, the medial processes are on the same level as the lateral frontal horns, not ventral, and terminal styles are absent, thus not distinct lateral antennae.

Gesiella jameensis (Hartmann-Schröder, 1974)

Macellicephala (*Macellicephala*) *jameensis* Hartmann-Schröder, 1974:76, figs. 1–8, in Macellicephalinae.

Gesiella jameensis.—Pettibone, 1976:64, fig. 36a–j, in Harmothoinae.—Muir, 1982: 156, in Gesiellinae Muir, 1982.

Remarks.—The small spherical lobes with distal filaments on the prostomium are not to be considered as distinct lateral antennae, as indicated by Pettibone (1976:64). The presence of unique filamentous sensory organs on the cirrophores of the dorsal cirri, the basis for Gesiellinae by Muir (1982) does not seem to merit a separate Subfamily.

Genus *Bathycatalina* Pettibone, 1976, emended

Type species.—*Polynoe* (?) *filamentosa* Moore, 1910, by original designation and monotypy. Type locality: Southern California, off Santa Catalina Island, in 611–1097 m.

Remarks.—Based on an additional specimen from Juan de Fuca Ridge, referred herein to *B. filamentosa,* the genus is emended as follows: Body with 24 segments, last three small, with 11 pairs of elytrophores (not 12 pairs), on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21. Bilobed prostomium with rounded frontal processes and terminal filaments (not distinct lateral antennae, damaged on holotype); palps very long (missing on holotype). Pharynx with nine pairs of papillae (damaged on holotype).

Bathycatalina filamentosa (Moore, 1910)

Fig. 1

Polynoe (?) *filamentosa* Moore, 1910:366, pl. 31:figs. 52–56.

Bathycatalina filamentosa.—Pettibone, 1976:38, fig. 23a–e.

Material.—Juan de Fuca Ridge, 46°09.3′N, 129°48.4′W, 2059 m, *Alvin* Dive 2681 in 273°C Beard Chimney, 24 Oct 1993, C. van Dover, collector, from V. Tunnicliffe, 1 specimen (USNM 169153).

Description.—Length 15 mm, width with setae 8 mm, segments 24, last three very small. Elytra (all missing except very small elytra on segment 21) and bulbous elytrophores 11 pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21. Dorsal cirri on nonelytrigerous segments; cirrophores long, cylindrical, with long styles; dorsal tubercles elongate, forming digitiform ciliated brachial-like processes; some long clavate sensory papillae on dorsal cirrophores (Fig. 1A, B, F).

Prostomium deeply bilobed, rounded anterior lobes, with subconical processes and terminal filaments; ceratophore of median antenna in anterior notch of prostomium, large, cylindrical, style missing; palps very long; without eyes; tentaculophores of segment 1 lateral to prostomium, with few notosetae on inner sides and two pairs of tentacular cirri (missing) (Fig. 1A). Segment 2 with first pair of elytrophores, biramous parapodia, and long ventral buccal cirri, longer than following ventral cirri (Fig. 1A). Biramous parapodia with both notopodial and neuropodial rami subequal in size and length, with projecting acicular processes (Fig. 1C). Notosetae numerous, stout, forming radiating bundles, short and longer, some as long as neurosetae, with spinous rows and blunt bare tips (Fig. 1C, D). Neurosetae very numerous, forming dense brushlike bundles, thin, transparent, flattened distally, paddle-like, with serrated margins (Fig. 1C, E). Ventral cirri short, tapered (Fig. 1C). Posterior end with pygidium rounded, enclosed in small posterior parapodia (segments 22–24); cirrophores of dorsal cirri with clavate sensory papillae (Fig. 1B). Long extended pharynx encircled with nine pairs of dorsal and ventral papillae and two pairs of inner jaws (Fig. 1A). Groups of large yolky eggs attached to ventral surfaces of neuropodia on some posterior segments.

Distribution.—Northeastern Pacific, off Southern California (Santa Catalina Island),

Fig. 1. *Bathycatalina filamentosa* (USNM 169153): A, Dorsal view of anterior end, with pharynx fully extended; styles of median antenna, dorsal and ventral tentacular cirri, elytra of segment 2, and left dorsal cirrus of segment 3 missing; B, Dorsal view of posterior end (segments 21–24), dorsal cirri missing, long clavate sensory papillae on cirrophores; C, Left elytrigerous parapodium of segment 5, anterior view, acicula dotted, elytron missing; D, Short and distal tip of long notosetae from same; E, Distal tip of flattened neuroseta from same; F, Right cirrigerous notopodium, anterior view, showing cirrophore of dorsal cirrus with sensory clavate papilla (style missing) and ciliated branchial process on dorsal tubercle. Scales = 0.5 mm for C, F; 0.1 mm for D, E; A, B, not to scale.

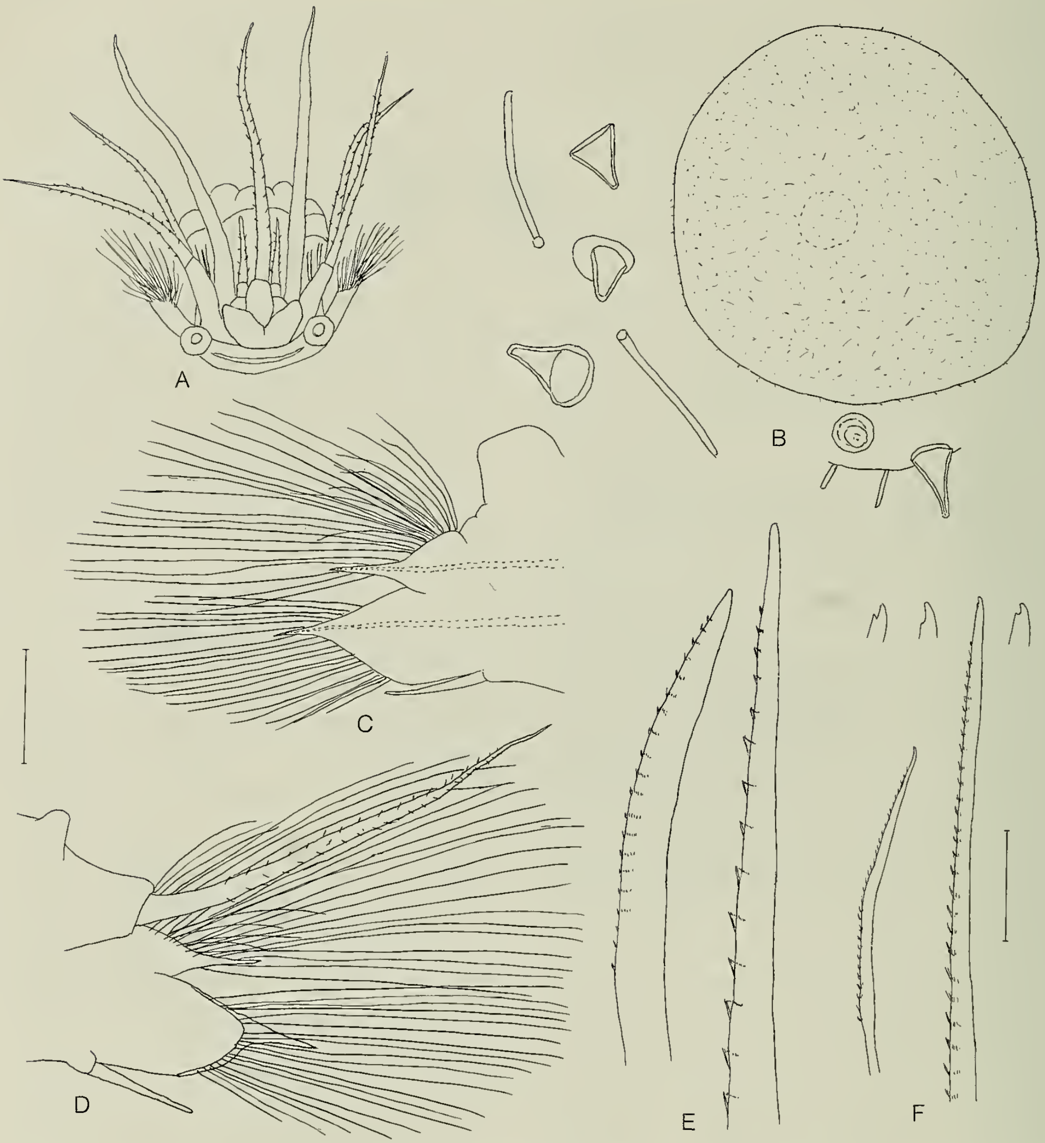

Fig. 2. *Harmothoe macnabi* (USNM 169154): A, Dorsal view of anterior end, pharynx partially extended; B, Right first elytron from segment 2, with detail of microtubercles, surface and border papillae; C, Right elytrigerous parapodium, anterior view, acicula dotted; D, Right cirrigerous parapodium, posterior view; E, Short and distal end of long notosetae from same; F, Lower and middle neurosetae from same, with detail of some tips. Scales = 0.5 mm for B–D; 0.1 mm for E, F; A, not to scale.

in 611–1097 m, and Juan de Fuca Ridge, off British Columbia, in 2059 m.

Remarks.—*Bathycatalina filamentosa* shows affinities to *Gesiella jameensis.* Both species have the unique clavate sensory papillae on the dorsal cirrophores of the cirrigerous segments. *G. jameensis* has fewer segments (18–19) and elytrophores (nine pairs) and the notopodia are much shorter than the neuropodia. Ciliated cirriform branchial structures on the dorsal tubercles of *B. filamentosa* are also found on *Bathy-*

fauvelia affinis (Fauvel) and *Bathybahamas charleneae* Pettibone. (See Key to the three species in Pettibone, 1985a;141). Dorsal tubercles are indistinct in *G. jameensis.*

Subfamily Harmothoinae Horst, 1917
Genus *Harmothoe* Kinberg, 1856
Harmothoe macnabi Pettibone, 1985
Fig. 2

Harmothoe macnabi Pettibone, 1985b:749, figs. 6, 7.

Material.—Juan de Fuca Ridge, 46°09.3'N, 129°48.4'W, 2059 m, *Alvin* Dive 2681 in 273° Beard Chimney, 24 Oct 1993, C. van Dover, collector, from V. Tunnicliffe, 2 specimens (USNM 169154).

Remarks.—The two specimens agree for the most part with the holotype from the Galapagos Rift in 2482 meters.

Description.—Complete specimen 12 mm long, 8 mm wide with setae, and 30 segments, last three very small; incomplete specimen 10+ mm long, 9 mm wide, and 15+ segments; (holotype much larger: 33 mm long, 14 mm wide with setae, and 31 segments, last three small). Body showing brownish pigmentation: on distal tips of buccal and ventral cirri, along lateral sides of ventral nerve cord, and dark pharynx showing through body wall.

Elytra and bulbous elytrophores 14 pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29. Elytra missing, except for first right elytron on segment 2 and very small elytra on segments 19 and 23; remaining large elytron round and covered with conical microtubercles and scattered long surface papillae and short border papillae (Fig. 2B). Dorsal cirri and non-elytrigerous segments, with short cylindrical cirrophores and long papillate styles extending beyond tips of setae; dorsal tubercles nodular (Fig. 2D).

Bilobed prostomium wider than long, with subtriangular cephalic peaks; median antenna with large ceratophore in anterior notch of prostomium; lateral antennae with distinct ceratophores inserted ventrally, styles papillate, about length of prostomium; without eyes; stout palps slightly longer than median antenna; tentaculophores (segment 1) lateral to prostomium, each with three or four setae on inner side and papillate dorsal and ventral tentacular cirri, slightly shorter than median antenna (Fig. 2A). Segment 2 with first pair of bulbous elytrophores, biramous parapodia, and long ventral papillate buccal cirri, much longer than following ventral cirri (Fig. 2A).

Biramous parapodia with notopodia rounded basally, with projecting acicular processes on lower sides, about as long as neuropodia; neuropodia with conical anterior lobes and projecting acicular processes and rounded posterior lobes (Fig. 2C, D). Notosetae numerous, forming radiating bundles, much stouter than neurosetae, short, slightly curved to longer, straight, with spinous rows and tapered bare tips (Fig. 2E). Neurosetae numerous, slender, with faint spinous rows and bare, slightly hooked tips with small subterminal tooth; lower ones with entire curved tips (Fig. 2F). Ventral cirri short, tapered, with slender tips (Fig. 2C, D). Some eggs in parapodia medial to bases of ventral cirri.

Distribution.—East Central Pacific in Galapagos Rift, in 2482 m and North Pacific in Juan de Fuca Ridge, 2059 m.

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A NEW GENUS AND SPECIES OF POLYCHAETE, *BOLLANDIA ANTIPATHICOLA* (NEREIDOIDEA: SYLLIDAE), FROM BLACK CORAL

Christopher J. Glasby

Abstract.—A new genus and species of syllid polychaete, *Bollandia antipathicola,* is described. This is the first syllid species to be found in association with an antipatharian coral. It differs from other Syllidae in having one pair of peristomial cirri and two pairs of tentacular cirri (i.e., a total of three pairs of cirri on the anterior end), lacking palps and antennae, and in having few specialized stout setae. The species is hermaphroditic and possesses many paired ventral reproductive papillae that may be used in copulation or for ejecting spermatophores.

Routine sorting of a collection of benthic invertebrates from 52–61 m off Okinawa, Japan, yielded an unusual polychaete that was attached to Black Coral, *Antipathes* sp. The species clearly belonged to the order Phyllodocida as it had a muscular, axial type of eversible pharynx, unlike the ventral type found in other polychaete orders having a pharynx such as the Eunicida and Amphinomida (Dales 1962, Orrhage 1973). Further, the species was suspected of belonging to the Nereidoidea as it had at least two pairs of tentacular cirri presumably resulting from the cephalization of the parapodia of the first two segments, as for example in some species of the Hesionidae (Glasby 1993). The Nereidoidea currently contain six families: the Chrysopetalidae, Hesionidae, Nautiliniellidae, Nereididae, Pilargidae, and Syllidae (Glasby 1993; Glasby & Fauchald 1991). The species could not initially be assigned to any of these based on external features; however, a histological study revealed an axial pharynx that was fully differentiated (sensu Glasby 1993), that is one having a proventriculus and muscular ventriculus, a synapomorphy of the Syllidae.

The association between the new syllid polychaete and the *Antipathes* may be commensal, although there is insufficient information available on the biology of either organism to be certain. Commensalism has been reported previously among the Syllidae with species associated with poriferan hosts (Cognetti 1957, Pearse 1934), ophiuroid hosts (e.g., Hendler & Meyer 1982) and a eunicid polychaete (Hempelmann 1931). Although there are several records of cnidarian hosts (Utinomi 1956, Hartmann-Schröder 1960, Laubier 1960, Wright & Woodwick 1977, Hartmann-Schröder 1991, 1992) there appear to be no previous records of syllids being associated with antipatharian corals (Anthozoa: Ceriantharia). However, Pettibone (1991) recorded four polynoid species from antipatharians. Further, Pettibone (and references therein) found that the commensal annelids could induce the formation of tunnels in the coenenchyme of the main stems of the coral: tunnels were formed by anastomosed twigs. No such modification to the coral was observed in the present study.

Other commensal nereidoids include *Antonbruunia viridis* Hartman & Boss, recently moved to the Pilargidae (Glasby 1993) and species of the Nautiliniellidae all of which are commensals or parasites of bivalve molluscs (Hartman & Boss 1965, Miura & Laubier 1989, Blake 1993).

Specimens described in this paper have been deposited with the National Museum of Natural History, Smithsonian Institution (USNM), Natural History Museum, London (BMNH), and the Australian Museum (AM).

Family Syllidae Grube, 1850

Bollandia, new genus

Type species.—*Bollandia antipathicola,* new species.

Diagnosis.—Antennae absent; palps absent; nuchal organs not externally exposed (sensu Glasby 1993); three pairs of appendages on anterior end, most probably representing one pair of peristomial cirri and two pairs of tentacular cirri (i.e., parapodia of segments 1 & 2 cephalized during ontogeny; but see Remarks); pharyngeal apparatus consisting of sinuous, unarmed pharynx, and a barrel-shaped proventriculus; notopodia and notosetae absent; neurosetae simple, occur in the sub-acicular position only; anal cirri paired.

Etymology.—The genus has feminine gender, and is named in honor of R.F. Bolland who collected the specimens. The specific name refers to the genus of Black Coral, *Antipathes,* on which the new species was found.

Bollandia antipathicola, new species

(Figs. 1A–H; 2A–D)

Material examined.—All material from Japan, Okinawa, Horseshoe Cliffs, 1 km WNW Onna village, 26°30.0′N, 127°50.9′E, coll. R. F. Bolland. Holotype: Stn RFB 1240, 61 m, coll. 5 Aug 1984 (USNM 169157). Paratypes: Stn RFB 1240, 61 m, coll. 5 Aug 1984, 7 specimens (USNM 169158), 2 specimens mounted for SEM (USNM 169159), 2 specimens sectioned (USNM 169160), 2 specimens (AM W21804), 2 specimens (BMNH 1994.3202–3203); Stn RFB 1235, 57.9 m, coll. 3 Aug 1984, 2 specimens (USNM 169161); Stn 1243, 64.0 m, coll. 10 Aug 1984, 6 specimens (USNM 169162); Stn RFB 1276, 51.8 m, coll. 10 Oct 1984, 1 specimen (USNM 169163); Stn RFB 1974, 61 m, coll. 28 Aug 1988, 2 specimens (USNM 169164), 1 specimen mounted for SEM (USNM 169165).

Description.—Holotype 73 setigers, 6.0 mm long, 0.4 mm wide. Paratype material ranged in size from 16 setigers, 1.3 mm long, 0.2 mm wide (USNM 169165) to 47 setigers, 6.2 mm long, 0.3 mm wide (USNM 169160). Body approximately uniform in width throughout, highly arched dorsally particularly over setigers 1–4 (Figs. 1A, C) which carry the pharyngeal apparatus, flat-concave ventrally with parapodia directed ventrolaterally (Figs. 1B, 2D). Preserved material with diffuse brown pigment on ventral surface of setiger 4 (absent in smaller paratypes) and from setiger 8 to near pygidium, particularly intense around base of ventral cirri. Dorsum, parapodia and cirri covered with clumps of long cilia (Fig. 1A).

Prostomium small, ill-defined, directed anteroventrally, lacking antennae or palps (Figs. 1B, 2D). Eyes very small, red, two pairs, posterior pair slightly further apart than anterior pair. Peristomium indistinct, carrying a pair of smooth peristomial cirri (C1), about twice width of prostomium, directed anteriorly (Fig. 2D). First two segments cephalized, fused together and with peristomium, ventral surface slightly raised above level of succeeding segments (Fig. 1B); first pair of tentacular cirri (C2) smooth, lacking aciculae, slightly dorsally displaced, similar in shape though slightly longer than peristomial cirri, basally with pair of minute vestigial ventral cirri (V1; not visible in holotype); second pair of tentacular cirri (C3) also smooth and lacking aciculae, similar in size and shape to C2, basally with a pair of small vestigal ventral cirri (V2; Figs. 1B, 2D).

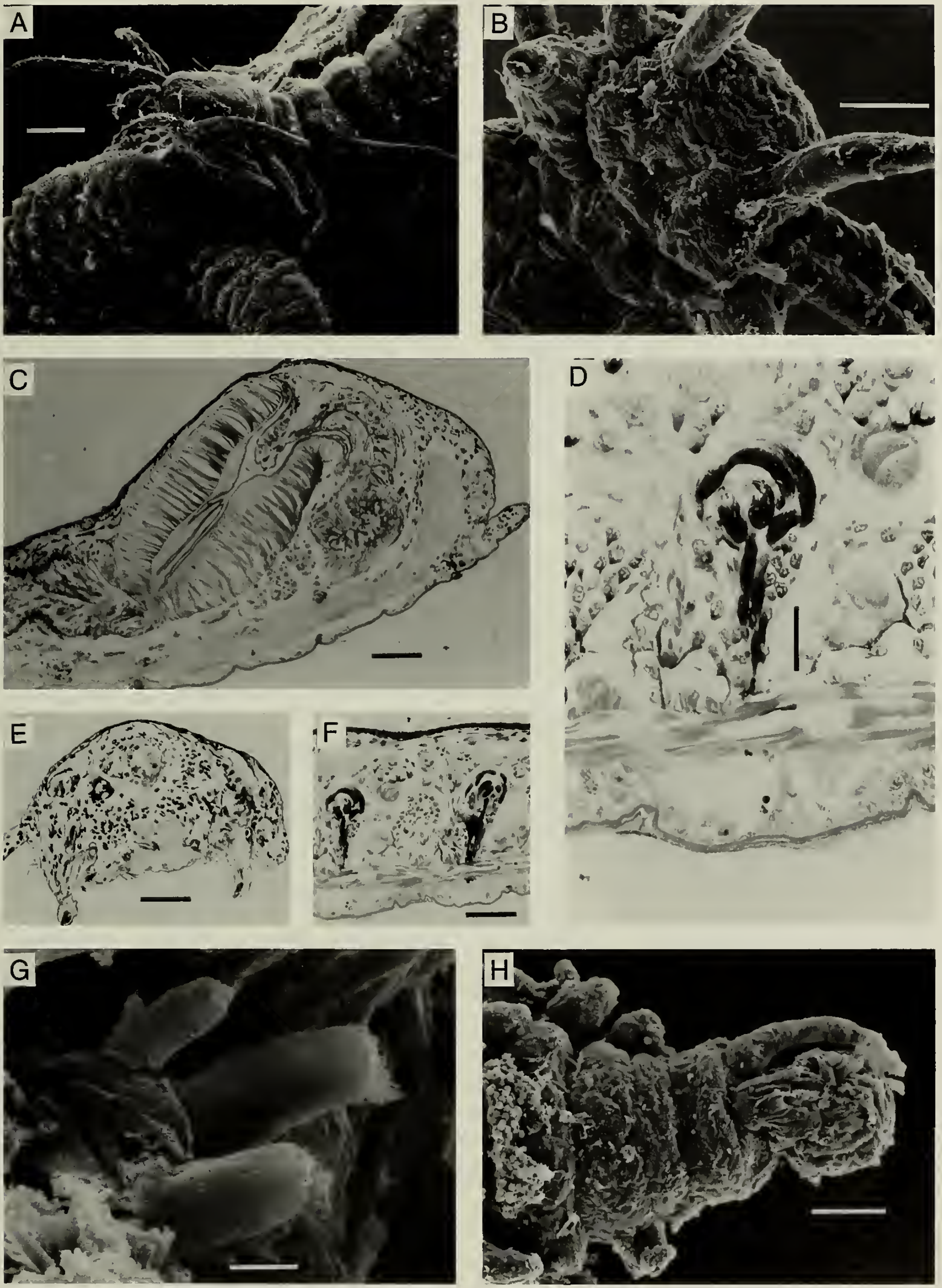

Fig. 1. A–H: *Bollandia antipathicola,* new genus, new species, Paratypes (USNM 169160): A, in situ on *Antipathes* sp.; B, anterior end, anteroventral view; C, anterior end, longitudinal section; D, midbody, longitudinal section; E, midbody, transverse section; F, sperm containing tubules, midbody; G, reproductive papillae, midbody; H, posterior end, ventral view. Scale bars: 100 μm (A, C, D, E), 40 μm (B, H), 20 μm (F), 5 μm (G).

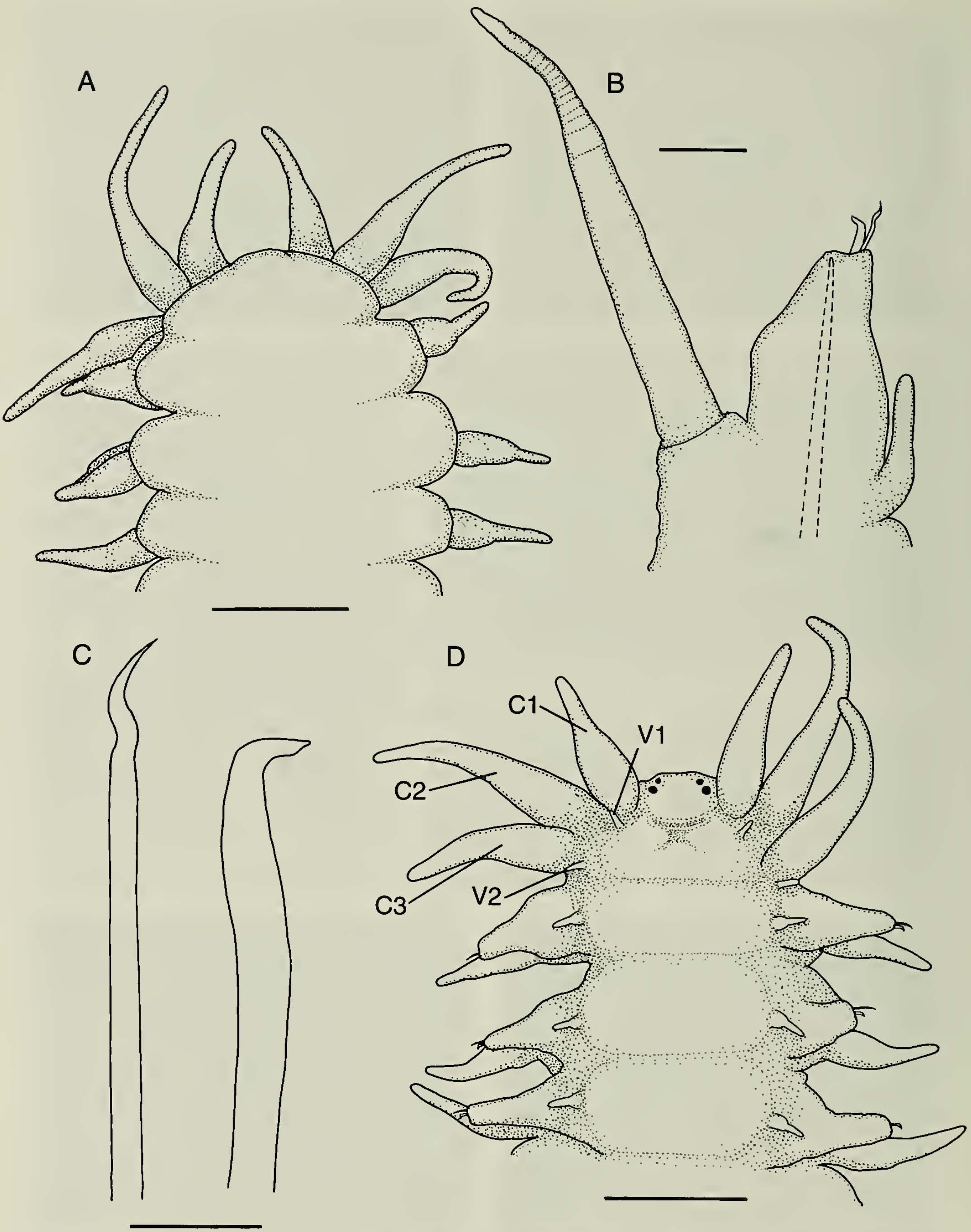

Fig. 2. A–D: *Bollandia antipathicola,* new genus, new species: A, Paratype (USNM 169158) anterior end, dorsal view; B, Holotype, parapodium from midbody, anterior view; C, Holotype, setae from parapodia of midbody; D, anterior end, ventral view, composite illustration compiled from 3 paratypes (USNM 169158) [C1 = peristomial cirri; C2, C3 = tentacular cirri; V1–3 = ventral cirri]. Scale bars: 0.10 mm (A, D), 0.05 mm (B), 0.02 mm (C).

Pharyngeal apparatus housed in anterior dorsally vaulted region (Fig. 1C). Pharynx cylindrical, extending back to about second setiger, sinuous, apparently unarmed (although not dissected). Proventriculus barrel-shaped, extending from pharynx back to about setiger 4, with about 28–35 groups of radial muscle columns (Fig. 1C).

Segment 3 first setigerous. Parapodia consisting of a single conical neuropodial lobe supported by one acicula and carrying two setae (Figs. 2B, D). Dorsal cirri atop very short cirrophore, tapered, faintly articulated distally, with very closely spaced articles; about equal in length to neuropodial lobe. Ventral cirri very slender, adpressed to parapodia, about ½ (¼–½) length of neuropodial lobe (Figs. 2B, D). Subsequent parapodia similar to first, except length of dorsal cirri 1–3 times length of corresponding neuropodial lobes, generally increasing slightly in length posteriorly, though longer ones occurring every 4–7 segments. Setae of two types, both only slightly less stout than corresponding acicula: highly tapered flail-tipped setae, slightly bent near tip; and slightly stouter setae, distally bent at right-angles forming beak-like tip (Fig. 2C).

Pygidium swollen, glandular, pair of conical ventrolateral anal cirri (Fig. 1H; absent in holotype).

Reproductive papillae present on elevated pads at ventral base of parapodia (Fig. 1G); resemble ventral cirri in both size and shape. Beginning on setigers 2–5 reproductive papillae extend posteriorly to last setigers. Papillae fed by internal tubules filled with mature sperm (Figs. 1D–F). Perhaps also early stages of sperm present, but not classical spermatids and no intermediate stages between these early stages and mature stages. Oocytes spherical, unpigmented, ranged in diameter from about 10–50 μm (1 specimen, USNM 169163), present in all specimens in posterior half of body from setigers 9–11 to near pygidium.

Remarks.—The species is hermaphroditic, although it is difficult to estimate from so few specimens whether it is a sequential or a simultaneous hermaphrodite. Although resembling some types of seminal receptacles (spermathecae), the 'internal tubules' are more likely to represent seminal vesicles or testes since they appear to empty to the exterior via reproductive papillae. Reproductive papillae may be used for direct copulation, as in *Pisione remota* (Stecher 1968), although no gametal pores could be identified on any specimen. Alternatively they may function for ejecting spermatophores that could be fixed to (and later penetrate) the body of another individual, as in *Hesionides arenaria* (Westheide 1967).

The precise nature of the anterior end appendages is uncertain, since the distinction between anterior segments, peristomium and prostomium is unclear. However, long, slender appendages in the Nereidoidea are more likely to represent cirri, either of peristomial or segmental origin, than antennae or palps. Assuming that the presence of the vestigial ventral cirri (Fig. 2D) at the ventral base of the anterior end cirri indicates a segmental origin, then clearly two segments have been cephalized. The question is whether the first pair of ventral cirri (V1) is associated with the first (C1) or the second (C2) pair of cirri. If associated with C1 then the first pair are tentacular cirri derived from segment 1 and the second and third pairs (C2, C3) are also tentacular cirri perhaps both derived from segment 2 (Fig. 2D). If this were the case then *Bollandia* would lack peristomial cirri. However, a more likely hypothesis, and the one proposed here, is that V1 is associated with C2, implying that C1 are peristomial cirri and the C2 and C3 are derived from segments 1 and 2 respectively.

Most Syllidae have one or two pairs of anterior end cirri (Fauchald 1977, Garwood 1991). Strictly speaking the cirri are peristomial in origin and should therefore be referred to as peristomial cirri (Glasby

1993), although the term tentacular cirri has also been used in the literature. Exceptions are those genera that lack peristomial cirri altogether, including *Exogonella* Hartman, *Fauvelia* Gravier, *Haplosyllides* Augener, and *Nudisyllis* Knox & Cameron; *Irmula* Ehlers supposedly has six pairs of tentacular cirri. *Bollandia antipathicola,* new species, differs from these and other species of Syllidae in having one pair of peristomial cirri and two pairs of tentacular cirri (=three pairs of anterior end cirri). In addition it lacks antennae and palps and has few specialized stout setae. The lack of palps appears to have been recorded for only one other syllid genus, *Haplosyllides* Augener. *Haplosyllides* differs from *Bollandia* in having three antennae and lacking both peristomial and tentacular cirri (Augener 1922).

Most Syllidae undergo some form of structural (epitokous) modification associated with sexual maturity (Garwood 1991). Neither schizogamy, in which sexual individuals are budded off from the adult, nor epigamy, in which the whole animal undergoes modification were observed in the present specimens of *Bollandia.* Like the new *Bollandia* species, palps are often absent in epigamous (=epitokous) syllids (Estapé & San Martín 1991). However, the new species can not represent an epitokous syllid since epitokes generally lack peristomial cirri, have enlarged eyes and many capillary (swimming) setae and their bodies are often turgid with gametes.

The species resembles most closely those of the subfamily Eusyllinae, which was recently defined by Garwood (1991). In common with the Eusyllinae, *Bollandia* has smooth or indistinctly articulated dorsal cirri and cirri of the anterior end, the presence of ventral cirri, and segmental ciliation that is retained in adults. It differs from the Eusyllinae however, in having 3 pairs of anterior end cirri (cf. two pairs, according to Garwood) and in lacking palps, although other members of the Eusyllinae may have reduced palps (Garwood 1991).

In my opinion the subfamilial groupings within the Syllidae remain controversial (see also Fauchald 1977) despite the findings of Garwood (1991), which support the traditional four subfamilial groupings. The Syllidae have never been subject to any sort of rigorous phylogenetic analysis and therefore the Eusyllinae, along with other syllid subfamilies, may not constitute a monophyletic group. Until monophyletic groups within the Syllidae can be identified, the phylogenetic relationships of *Bollandia* must remain obscure.

Acknowledgments

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NEW SPECIES OF *DIPLOCARDIA* AND *ARGILOPHILUS* (ANNELIDA: OLIGOCHAETA: MEGASCOLECIDAE) FROM SOUTHERN CALIFORNIA

Samuel W. James

Abstract.—Five new species of megascolecid earthworms, *Diplocardia californiana, D. woodi, D. montana, Argilophilus woodi,* and *A. margaritae* are described from material collected in various wildland habitats in the mountains neighboring the Los Angeles Basin. No other native earthworms were previously known from the region. The *Diplocardia* species are related to *D. keyesi,* known from Baja California, and all occur to the south of Los Angeles. Other *Argilophilus* are known from sites farther north; those described here are found to the north of the greater Los Angeles area. The northern limit of *Diplocardia* in California appears to be the San Gorgonio Pass. This may also be the southern limit of *Argilophilus* in California, but further collecting will be needed for confirmation.

It has been almost a century since anyone made an organized attempt to study terrestrial Oligochaeta in Southern California. The species presented here came to light as a result of the industriousness of Hulton B. "Hutch" Wood during his preliminary investigations of biotic factors affecting soils in the San Dimas Experimental Forest. Together we collected extensively in the mountains and wildlands surrounding the Los Angeles Basin. It may come as a surprise to learn that an area noted for a long dry period would support indigenous earthworms in unirrigated land. Though many sites were in riparian zones or adjacent to other sources of water, several were not so favored and not located at elevations where precipitation is abundant. A full account of the sites visited, their soils and vegetation, and the earthworm species encountered is in Wood & James (1993). Five species are new and are described here. Additional material was collected in early 1993, and further data on the new species were taken from these collections. There is also one more new species from the 1993 collections.

All specimens were obtained by digging and handsorting, and were killed in 50% ethanol and fixed in 5% formalin. Examinations were conducted by dorsal dissection under a stereomicroscope with a drawing tube.

Diplocardia californiana, new species
Fig. 1A–C

Type material.—Holotype: USNM 169803, In grass/lupine meadow near vernal pool on Mesa de Colorado, Santa Rosa Plateau, near Temecula, Riverside Co., California, 5 Apr 1990, S. W. James, H. B. Wood, K. L. Olivier, collectors; Paratypes: USNM 169804, same locality as holotype.

Additional material.—In grass pasture of Love Valley, Cleveland National Forest, 22 Apr 1991, S. W. James and H. B. Wood, collectors; In grass among pines, Upper French Valley near Mt. Palomar Observatory, 22 Apr 1991, S. W. James and H. B. Wood, collectors; In grass adjacent to live oak grove, Falcon Camp, Cleveland National Forest, 24 Apr 1991, S. W. James and H. B. Wood, collectors; Long Canyon, Cleveland National Forest, near California Highway 74 in grassy area among oaks, 24 Apr 1991, S. W. James and H. B. Wood, collectors; In grass/geranium mix and oak chaparral near Tenaja Creek, Cleveland National Forest, 24 Apr 1991, S. W. James and H. B. Wood, collectors. In grass/geranium mix and oak chaparral near Tenaja Creek, Cleveland National Forest, 6 Apr 1993, K. L. Olivier and H. B. Wood, collectors. Miller Mountain, in the bowl, basalt rock substrate with clay soil, grass, 15 Apr 1993, K. L. Olivier and R. Mees, collectors.

Description.—External characteristics: Dimensions 58–85 mm by 2.4–3.0 mm at segment xxx, 2.8–3.3 mm at vii; body cylindrical throughout, segments 106–164. Setae closely paired throughout; setal formula AA:AB:BC:CD = 3:1:4:1.3 at x, 3.5:1:3:1 at xxx, DD > ½ circumference throughout. Prostomium epilobous to nearly tanylobous, segments with postsetal secondary annulus v, pre- and postsetal annuli vi–end, in x+ each third has tertiary annulus. Brown pigmentation present in i–v, vi, vii, denser dorsally; sometimes also present in male field area. Nephridiopores at D, first dorsal pore 9/10 or 10/11, spermathecal pores at leading edges of viii, ix lateral to A. Ovipores presetal median to A in xiv; male pores at 21/22; prostatic pores and penial setae at ends of seminal grooves in AB in xxi–xxiii. Clitellum xii–xxi, xxii, saddle-shaped; no genital markings (Fig. 1A).

Internal characteristics: Septa 5/6–11/12 muscular, greatest thickness at 8/9; 5/6 only faintly muscular. Alimentary canal with two gizzards in v, vi; appearing as one unit without substantial demarkation; esophagous with pebbly internal texture ix–xiii, low longitudinal folds 13/14–xviii, ventral esophageal ridge xi–xvii, esophagous valvular in xviii, xix, intestinal origin xx; typhlosole a simple fold originating over xxiii–xxv, height less than one tenth lumen diameter. No calciferous glands. Stomate meganephridia 2 per segment, exoic with duct entering body wall in CD, avesiculate, tubules in elongate flat coil over AD.

Vascular system with ventral trunk, single dorsal trunk, these connected by lateral trunks in v–ix, latero-esophageal hearts in x–xii. Extra-esophageal vessel from pharyngeal glands, along ventral-lateral face of gizzard, ventral face of esophagous v–xiii, in xiii branching out to body wall of xiii–xx. Supra-esophageal vessel x–xiii.

Fan-shaped ovaries composed of long strings, with funnels in xiii; paired spermathecae in viii, ix, each an ovoid ampulla with sessile diverticulum composed of 3–6 internal lobes arranged in one row (Fig. 1B); ampulla under esophagous, ampulla long axis usually perpendicular to duct axis.

Male sexual system holandric, testes and funnels free in x, xi; acinous equal-sized seminal vesicles in ix, xii; vasa deferentia superficial, very thin, enter body wall at 21/22; tubular prostates with very short slightly muscular ducts, gland in several folds within segments of origin (xxi, xxiii); penial setal follicles just anterior to ducts. Penial setae 0.25–0.3 mm by 0.015 mm, nearly straight, gradually tapering to blunt tip (Fig. 1C); genital setae lacking.

Diagnosis.—*Diplocardia* with male field in xxi–xxiii.

Remarks.—Specimens from Love Valley, Tenaja Creek and Falcon Camp had abundant melanocytes in the linings of the body cavity, on blood vessels, nephridia, and other organs in the region xi–xxv. External pigmentation was slightly variable among sites, the darkest being those of Mesa de Colorado and the lightest coming from Falcon Camp and Upper French Valley. Oil droplets were abundant in the coeloms of worms from Long Canyon and Love Valley. Much of the material showed evidence of reduction in male functions. Seminal vesicles varied from partly filled to very small to rudimentary, even in fully clitellate individuals. Iridescence of male funnels was uncommon, and iridescence of spermathecal diverticula was seen only in the 1993 Tenaja Creek material. Prostates were quite small for *Diplocardia,* and penial setae were little more than straightened ambulatory setae. Some of the lack of male development could be season-

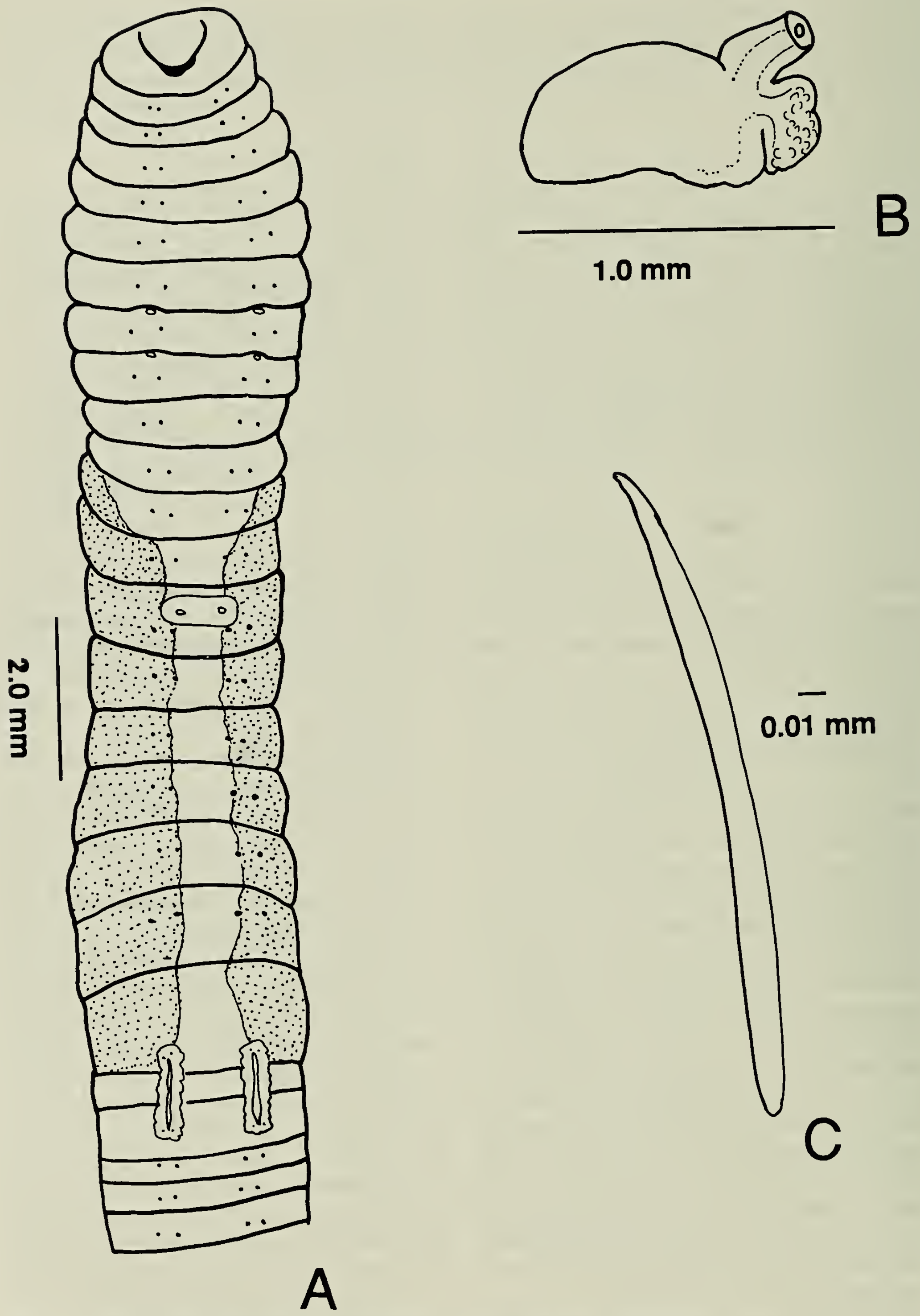

Fig. 1. *Diplocardia californiana*: A. ventral view, B. spermatheca, C. penial seta.

al, many of the sites having been at high elevations. However, all material examined was fully clitellate except the worms from Upper French Valley, the highest elevation site.

Diplocardia californiana is referred to as *Diplocardia* CA1 in Wood & James (1993).

Diplocardia keyesi Eisen, 1900 has the male field in xx–xxii. This would place it as the nearest relative of the new *Diplocardia* described here. *Diplocardia keyesi* is known only from a single location in northern Baja California, near Ensenada. The location of the male field or male pores is usually very conservative in earthworms, but is quite variable in *Diplocardia.*

Diplocardia woodi, new species

Fig. 2A, 2B

Type material.—Holotype: USNM 169806, Mesa de Burro, Santa Rosa Plateau, Riverside Co., California. 1 Apr 1993, K. L. Olivier, collector; Paratypes: USNM 169807, same locality as holotype.

Additional material.—Mesa de Burro, Santa Rosa Plateau, Riverside Co., California. 5 Apr 1990, S. W. James, H. B. Wood and K. L. Olivier, collectors.

Description.—External characteristics: Dimensions 63–78 mm by 2.7–2.9 mm at segment xxx, 3.2 mm at ix; body cylindrical throughout, segments 134–153. Pigmentation lacking or present as slight rings of brown pigment at segmental equators of some or all of ii–v. Setae closely paired throughout; setal formula AA:AB:BC:CD = 3.5:1:3:1.3 at x, 4:1:3.5:1.3 at xxx, DD > ½ circumference throughout.

Prostomium epilobous, segments with postsetal secondary annulus vi–vii, pre- and postsetal annuli viii–end, in xxii+ postsetal third has tertiary annulus. Nephridiopores not seen, first dorsal pore 9/10 or 10/11, spermathecal pores at leading edges of viii, ix lateral to A. Ovipores presetal median to A in xiv; male pores at 21/22; prostatic pores and penial setae at ends of seminal grooves in AB in xxi–xxiii. Clitellum saddle-shaped, interrupted at mid-ventral line, xii-xxi; no genital markings (Fig. 2A).

Internal characteristics: Septa 6/7–11/12 muscular, greatest thickness at 8/9; 13/14 only faintly muscular. Alimentary canal with two gizzards in v, vi; appearing as one unit with thin region at 5/6; esophagous with pebbly internal texture ix–xviii, ventral esophageal ridge 12–18, valvular in xix, intestinal origin xx; typhlosole simple fold originating over xxiii–xxv, height one fifth lumen diameter. No calciferous glands. Stomate meganephridia 2 per segment, exoic with duct entering body wall in CD, avesiculate, tubules in elongate flat coil over BD.

Vascular system with ventral trunk, single dorsal trunk, these connected by lateral trunks in v–ix, latero-esophageal hearts in x–xii. Extra-esophageal vessel from pharyngeal glands, along ventral-lateral face of gizzard, ventral face of esophagous v–xiii, in xiii branching out to body wall of xiii–xx. Supra-esophageal vessel ix–or x–xiii.

Fan-shaped ovaries composed of long strings, with funnels in xiii; paired spermathecae in viii, ix, each an ovoid ampulla with sessile diverticulum composed of 1–3 internal lobes (Fig. 2B).

Male sexual system holandric, testes and funnels free in x, xi; seminal vesicles in ix, xii, both quite small; vasa deferentia superficial, very thin, enter body wall at 21/22; tubular prostates with very short slender ducts less than one-tenth gland length, gland in several folds within segments of origin (xxi, xxiii); penial setal follicles just anterior to ducts, penial setae not enlarged (4) or lacking (1); genital setae lacking.

Diagnosis.—*Diplocardia* with male field in xxi–xxiii, and distinguished from *D. californiana* by the greater height of the typhlosole, smaller nephridia, fewer lobes of the spermathecal diverticulum, lack of mus-

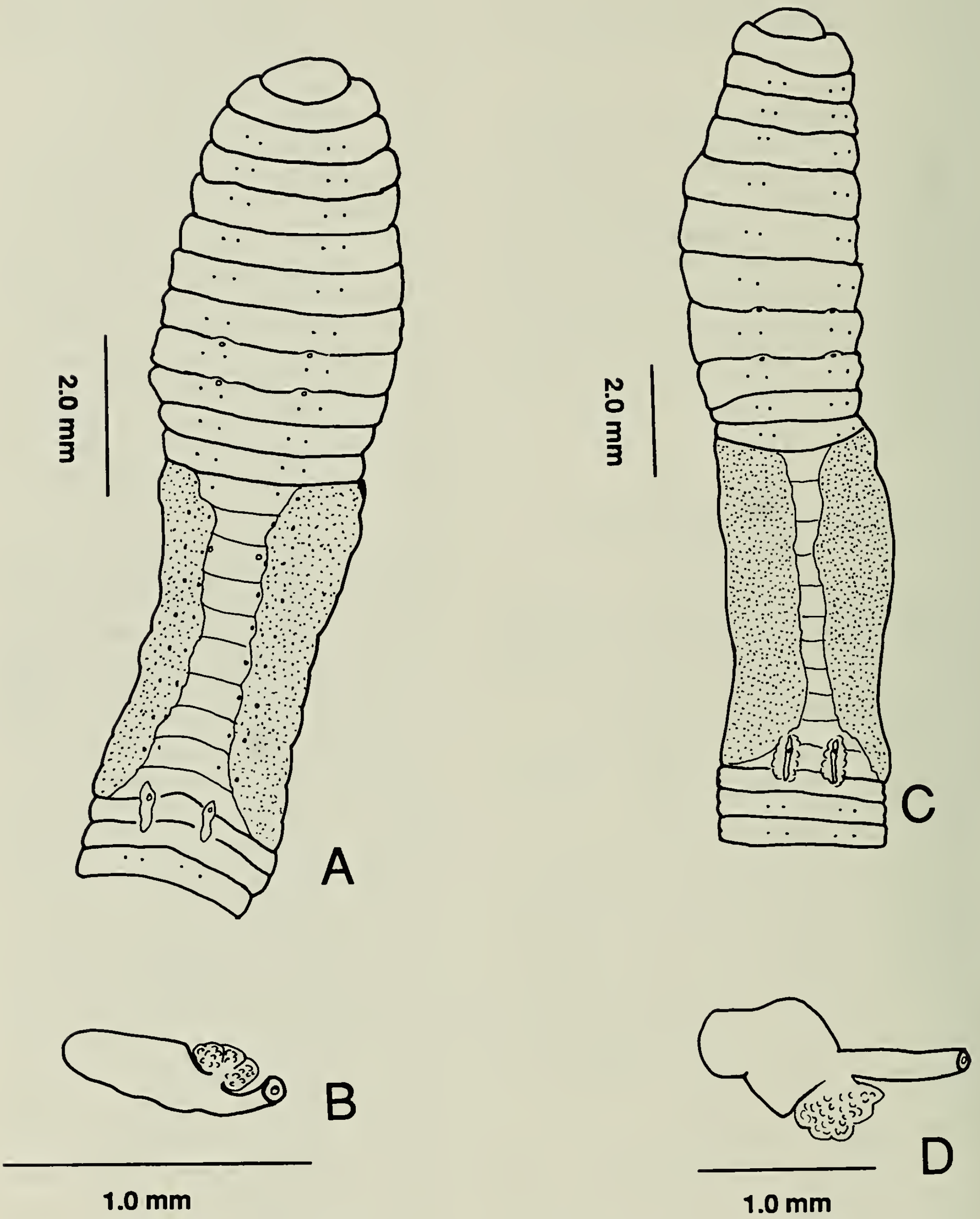

Fig. 2. *Diplocardia woodi*: A. ventral view, B. spermatheca. *Diplocardia montana*: C. ventral view, D. spermatheca.

cularity of prostatic ducts, and lack of development of penial setae.

Remarks.—Iridescence of the male funnels was detected on one individual from the 1993 material, though coagulum was present in segments x and xi of all material examined. Spermathecal diverticula of the 1993 material were iridescent, but those of the 1990 material were not. The species is named after Hulton B. Wood. It is referred to as "*Diplocardia* CA2" in Wood & James (1993).

Diplocardia montana, new species

Fig. 2C, 2D

Type material.—Holotype USNM 169805, Miller Mountain, San Diego Co. California, top end of jeep trail, 900 m elev., clay loam soil and grass; 15 Apr 1993, K. L. Olivier and R. Mees, collectors.

Description.—External characteristics: Dimensions 103 mm by 3.5 mm at segment xxx, 4 mm at ix; body cylindrical throughout, segments 152. Pigmentation present as slight rings of brown pigment at segmental equators on ii–viii. Setae closely paired throughout; setal formula AA:AB:BC:CD = 4:1.3:4:1 at x, 3:1:4:1.2 at xxx, DD > ½ circumference throughout. Prostomium prolobous, segments with postsetal secondary annulus vi–vii, pre- and postsetal annuli viii–end, in xxii+ postsetal third has tertiary annulus. Nephridiopores not seen, first dorsal pore 10/11, spermathecal pores on small bumps at leading edges of viii, ix in A. Ovipores presetal median to A in xiv; male pores at 21/22; prostatic pores at ends of seminal grooves in AB in xxi–xxiii. Clitellum saddle-shaped, interrupted at midventral line, xii–xxii; no genital markings (Fig. 2C).

Internal characteristics: Septa 6/7–11/12 muscular, greatest thickness at 8/9; 12/13 only faintly muscular. Alimentary canal with two gizzards in v, vi; appearing as one unit with thin region at 5/6; esophagous with pebbly internal texture ix–xviii, paired ventral esophageal ridges xiii–xviii, valvular in xix, intestinal origin xx; typhlosole simple fold originating 22/23, height one tenth lumen diameter or less. No calciferous glands. Stomate meganephridia 2 per segment, exoic with duct entering body wall in CD, avesiculate, tubules in elongate flat coil over BD.

Vascular system with ventral trunk, single dorsal trunk, these connected by lateral trunks in v–ix, latero-esophageal hearts in x–xii. Extra-esophageal vessel from pharyngeal glands, along ventral-lateral face of gizzard, ventral face of esophagous v–xiii, in xiii branching out to body wall of xiii–xx. Ventral esophageal ridges contain blood vessels connected to extra-esophageals. Supra-esophageal vessel x–xiii.

Fan-shaped ovaries composed of long strings, with funnels in xiii; paired spermathecae in viii, ix, each an ovoid ampulla with sessile diverticulum composed of 1–3 internal lobes (Fig. 2D).

Male sexual system metandric, testes and funnels free in xi; seminal vesicles in xii; vasa deferentia superficial, very thin, enter body wall at 21/22; tubular prostates with very short slender ducts so that prostates are nearly sessile, gland in several folds within segments of origin (xxi, xxiii) or one adjacent segment; penial setal follicles just anterior to ducts, penial setae vestigial; genital setae lacking.

Diagnosis.—*Diplocardia* with metandric reduction of the male gonads, male field in xxi–xxiii.

Remarks.—Apart from the metandric condition, *D. montana* is very similar to its southern California congeners. However, its one pair of male funnels and its spermathecal diverticula were iridescent, and there was no other evidence of reduction of male functions. It is also somewhat larger than the other species. So far it is the only known metandric *Diplocardia.*

Argilophilus woodi, new species
Fig. 3A–C

Type material.—Holotype, USNM 169799. Type locality: in oaks and sagebrush, 1300 m elev., near milepost 41.50, California Hwy. 33, Ventura Co. California, 4 Apr 1990, S. W. James and H. B. Wood, collectors. Paratypes (USNM 169800) from same locality, three adults, 4 Apr 1990, S. W. James and H. B. Wood, collectors.

Description.—External characteristics: Dimensions 51–58 mm by 3.5–4 mm (strongly contracted), width at segment xxx, body cylindrical throughout, segments 125–140. Pigmentation lacking. Setae ab closely paired throughout; setal formula AA:AB:BC:CD = 3.5:1:2.5:2.5 at xxx, DD > ½ circumference throughout. Prostomium epilobous, segments with postsetal secondary annulus vi–ix, pre- and postsetal annuli x–xii. Nephridiopores not seen, first apparent dorsal pore 18/19, but dorsal pores merely thin spots in body wall, few if any actually open; spermathecal pores at leading edges of viii, ix at B. Ovipores presetal median to A in xiv; male pores in xviii on small papillae; penial setae emerge from papillae in xviii. Clitellum annular xiii–xviii, no genital markings (Fig. 3A).

Internal characteristics: Septa 6/7–13/14 muscular, greatest thickness 8/9–11/12; 13/14 only faintly muscular. Alimentary canal with gizzard in vi; esophagous with pebbly internal texture x–xiv, low longitudinal folds xv; ventral esophageal ridge x–xv, valvular in xvi, intestinal origin xvii, no caecum; typhlosole simple fold originating over 20/21–xxv, terminates in region lxxxiv–ci, height one-fourth lumen diameter. No calciferous glands. Stomate meganephridia 2 per segment, exoic with duct entering body wall in CD, avesiculate, tubules in elongate flat coil over BC.

Vascular system with ventral trunk, single dorsal trunk, these connected by lateral trunks in vi–x, esophageal hearts in xi–xiii. Lateral trunk of vi with branch to gizzard, in v trunk from dorsal vessel to gizzard. Extra-esophageal vessel present but not traceable. Supra-esophageal vessel x–xiii.

Fan-shaped ovaries composed of long strings, with funnels in xiii; paired spermathecae in viii, ix, each an ovoid ampulla with one or two sessile hemispherical diverticula (Fig. 3B).

Male sexual system holandric, testes and funnels free in x, xi; seminal vesicles in xi, xii, that of xii twice size of seminal vesicle in xi; vasa deferentia superficial, enter distal end of tubular prostate glands in xviii; prostates with slender ducts about one quarter length of glandular portion; penial setal follicles just anterior to ducts, penial setae bowed, 540 × 12 microns (Fig. 3C).

Diagnosis.—*Argilophilus* with last hearts in xiii, gizzard in vi, no genital markings or papillae other than those of male pores.

Remarks.—*Argilophilus woodi* is most similar to the new species described below, and otherwise seems close to *A. sierrae* Michaelsen, 1921 based on somatic characters. The material used to describe *A. sierrae* was immature, so comparisons are difficult. However, that species does have much larger and more ornamented penial setae, adiverticulate spermathecae, a midventral papilla in xviii, and only one pair of seminal vesicles (Michaelsen 1921). *Argilophilus woodi* differs from previously published species in having the diagnostic combination given above. The species *A. panuliris* MacNab & McKey-Fender, 1959, *A. marmoratus* Eisen, 1893, *A. papillifer* Eisen, 1893 and *A. collinus* Eisen, 1900 all have the last hearts in xii (except *A. papillifer* which also has last hearts in xiii) and gizzard in v and vi (the first) or in v only (the last three) (Eisen 1894, 1900; Gates 1941, 1962, 1977; MacNab & McKey-Fender 1959; McKey-Fender 1970). There are other differences, such as the clitellae of most of these species being saddle-shaped, and there being genital markings on some part of the body in each. *Argilophilus hammondi* McKey-Fender, 1970 has its gizzard in v and an earlier intestinal origin than *A. woodi*, a saddle-shaped clitellum, several sets of

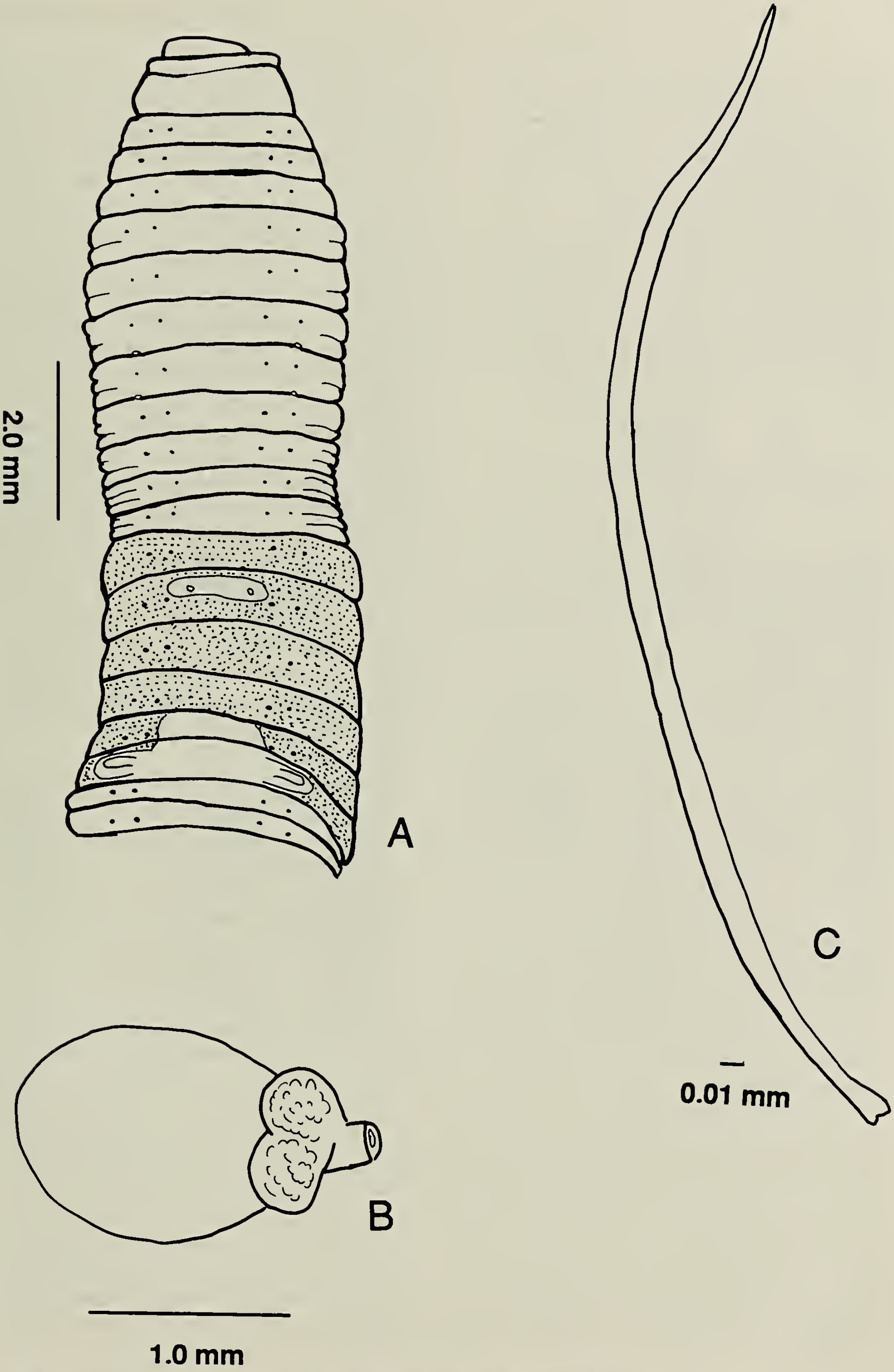

Fig. 3. *Argilophilus woodi*: A. ventral view, B. spermatheca, C. penial seta.

paired genital markings, a longer typhlosole and longer penial setae (McKey-Fender 1970). *Argilophilus garloughi* Smith, 1937 has last hearts in xiii but also has calciferous lamellae, a later intestinal origin and the gizzard in v (Smith 1937).

The species is named for Hulton B. Wood, whose interest in earthworms led to its discovery, and who was the first to come up with a specimen in a seemingly unlikely spot for earthworms. It is referred to as "*Argilophilus 1*" in Wood & James (1993).

Argilophilus margaritae, new species
Fig. 4A–C

Type material.—Holotype USNM 169801 and Paratypes USNM 169802, in canyon live oak and bay forest, Sec. 13 R12W, T2N along Forest Service Road 2N24, 2 Apr 1990, S. W. James and H. B. Wood, collectors.

Additional material.—Oak-sycamore riparian forest, West Fork San Gabriel River, 2 Apr 1990, S. W. James and H. B. Wood, collectors. Canyon live oaks on north-facing slope of San Gabriel River valley, Forest Service Road 2N24, 2 Apr 1990, S. W James and H. B. Wood, collectors. Oak and Coulter Pine with grass understorey, 1670 m. elev., 5 km west of Running Springs on California Hwy. 330, 23 Apr 1991, S. W. James and H. B. Wood, collectors. Ponderosa pine-oak forest with grass understorey at milepost 33.93 on California Hwy. 138 east of Crestline, 23 Apr 1991, S. W. James and H. B. Wood, collectors.

Description.—External characteristics: Dimensions 45–78 mm by 4–5 mm, width at segment xxx, generally strongly contracted during fixation; body cylindrical throughout, segments 124–148. Pigmentation lacking. Setae ab closely paired throughout; setal formula AA:AB:BC:CD = 3.7:1:3:2.3 at xxx, DD > ½ circumference throughout. Prostomium epilobous, segments with postsetal secondary annulus vi–x, pre- and postsetal annuli x–xii. Nephridiopores not seen, first dorsal pore 12/13–19/20 but dorsal pores mostly merely thin spots in body wall, few actually open; spermathecal pores at leading edges of viii, ix at B. Ovipores presetal median to A in xiv; male pores in xviii. Clitellum xiii–xviii, annular only over xiii–xiv, genital marking at 9/10 broad oval intersegmental papilla in BB or genital markings lacking (Fig. 4A).

Internal characteristics: Septa 6/7–11/12 muscular, greatest thickness 8/9–10/11; 12/13 only faintly muscular. Alimentary canal with gizzard in vi; esophagous with pebbly internal texture xi–xiii, low longitudinal folds xiv–xv; sometimes a ventral esophageal ridge xii–xiv, valvular in xvi, intestinal origin xvii or one-half xvii, no caecum; typhlosole simple fold originating over 20/21–xxiv,xxv, terminates li–lvii; height one third lumen diameter or less. No calciferous glands. Stomate meganephridia 2 per segment, exoic with duct entering body wall in CD, avesiculate, tubules in rounded flat coil over BC.

Vascular system with ventral trunk, single dorsal trunk, these connected by lateral trunks in vi–x, esophageal hearts in xi–xiii. Lateral trunk of vi with branch to gizzard, in v trunk from dorsal vessel to gizzard. Extra-esophageal vessel from under pharynx, along ventral-lateral face of gizzard, ventral face of esophagous iv–xiii, in xiii branching out to body wall of xiii–xviii. Supra-esophageal vessel xi–xiii, with lateral bulges to points of attachment of hearts.

Fan-shaped ovaries composed of long strings, with funnels in xiii; paired spermathecae in viii, ix, each an ovoid ampulla with 2–3 lobed sessile diverticulum broadly attached to spermathecal duct (Fig. 4B).

Male sexual system holandric, testes and funnels free in x, xi; seminal vesicles in xi, xii, that of xii slightly larger; vasa deferentia superficial, enter distal ends of tubular prostate glands in xviii; prostates with slender

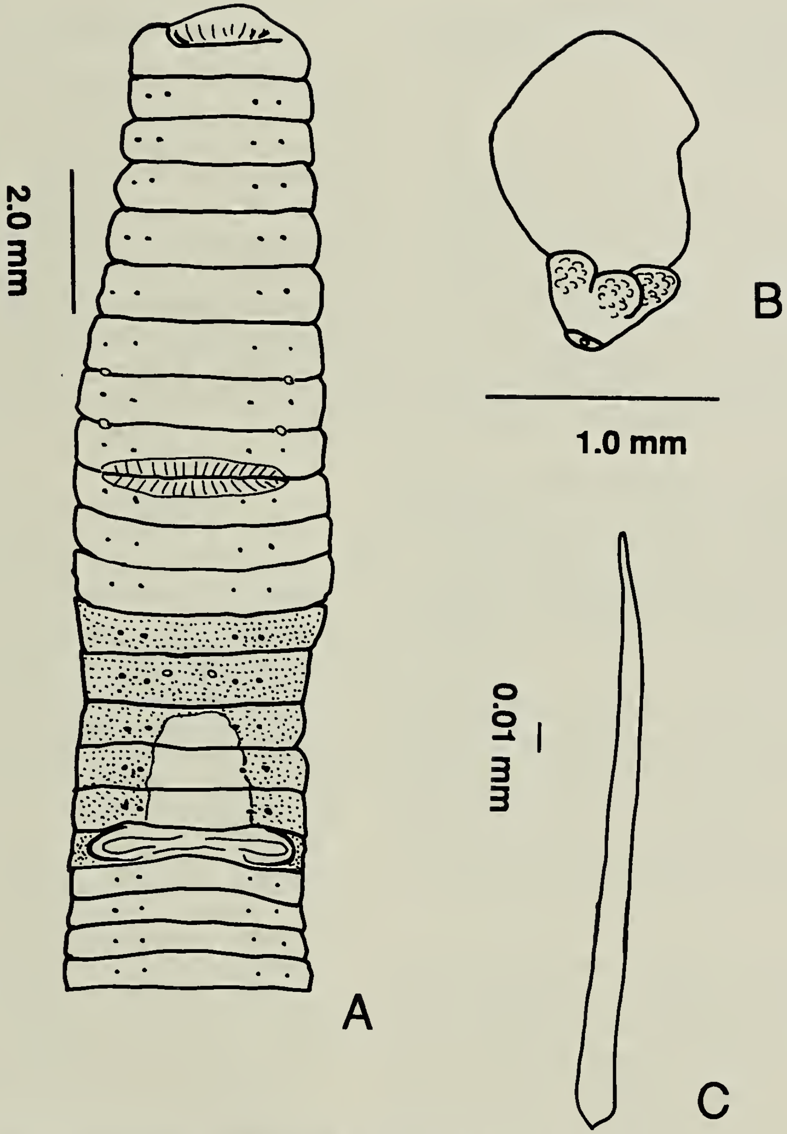

Fig. 4. *Argilophilus margaritae*: A. ventral view, B. spermatheca, C. penial seta.

ducts about one tenth length of glandular portion or shorter; penial setae absent or setae ab of xviii not differentiated from ambulatory setae (Fig. 4C).

Diagnosis.—Argilophilus with last hearts in xiii, gizzard in vi, no penial setae, one genital marking at 9/10 or none, partially annular clitellum.

Remarks.—This species differs from its previously published congeners in the same ways as *A. woodi,* with the sometime exception of the presence of a genital marking. It differs from *A. woodi* in having a lesser extent of annularity in the clitellum, a shorter typhlosole, no penial setae, and a prostatic duct that is shorter relative to the length of the prostate gland. The configuration of the spermathecal diverticula is also different.

Argilophilus margaritae, under the name "*Argilophilus 2*" was found in a variety of habitats and soil types, ranging from fine- to coarse-textured (Wood & James 1993).

The species name is the genitive case Latin equivalent of the name of the author's older daughter.

In Wood & James (1993) we noted that *Argilophilus* species were absent from the region south of 34°N latitude, coinciding with San Gorgonio Pass. This low desert and the lowlands to the west (presently the Los Angeles metropolitan area) may have presented a barrier to the dispersal of earthworms.

Diplocardia species were found to the south of this boundary, except for the San Jacinto Peak region which appears not to harbor any native earthworms. Exotic Lumbricidae are present there as there are in many of the sites sampled, so there is nothing inherently inimical to earthworms about the highlands around San Jacinto Peak. However, south of the boundary we collected one immature specimen of a megascolecid worm with a single gizzard in one segment, greatly resembling a young *Argilophilus.* Reserving judgment on that record until more material can be obtained, the range of *Argilophilus* is now extended south to 34°N latitude.

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PEOSIDRILOIDES, A NEW GENUS, AND NEW RECORDS OF *PEOSIDRILUS* (OLIGOCHAETA: TUBIFICIDAE) FROM THE UNITED STATES, WITH THE DESCRIPTION OF A NEW SPECIES FROM THE GULF OF MEXICO

Christer Erséus and Michael R. Milligan

Abstract.—*Peosidrilus biprostatus* Baker & Erséus, 1979, is recorded from the Gulf of Mexico, *P. coeloprostatus* (Cook, 1969) from Maine, and both *P. biprostatus* and *P. acochlearis* (Erséus & Loden, 1981) are reported from bathyal depths (off North Carolina) for the first time. *Peosidriloides,* new genus, does not have lateral spermathecal pores, the feature regarded as an autapomorphy of *Peosidrilus* Baker & Erséus, 1979. *Peosidriloides hornensis,* new species, from the northern Gulf of Mexico, shares some apomorphic features (a short clitellum, long vasa deferentia) with *Peosidriloides flabellifer* (Erséus, 1984), new combination, but is distinguished from that species by its more numerous anterior setae, its more ventral spermathecal pores, its wider vasa deferentia, and its possession of penial organs.

The marine tubificid genus *Peosidrilus* was established by Baker & Erséus (1979) to accommodate one species, *P. biprostatus* Baker & Erséus, 1979, from the east coast of the United States (New Jersey and North Carolina). Although this species was transferred to *Phallodrilus* Pierantoni, 1902 in a subsequent paper by Erséus (1984), *Peosidrilus* was resurrected when the paraphyletic taxon *Phallodrilus* was split into a number of genera (Erséus 1992). *Peosidrilus* was then recognized by the assumedly autapomorphic, lateral, position of the spermathecal pores, and was enlarged to include fourteen species; however, one species (*P. flabellifer* Erséus, 1984) with spermathecal pores located in line with the ventral setae was included in this genus too.

Many species of *Peosidrilus* are recorded from shallow-water or continental shelf bottoms of the northwestern part of the Atlantic Ocean; one, *P. simplidentatus* (Erséus, 1979a), is a High Arctic deep-sea form. An Atlantic origin of the genus has therefore been suggested (Erséus 1992).

The present paper presents geographic as well as bathymetric range extensions of three North Atlantic species. *Peosidrilus biprostatus* and *P. acochlearis* (Erséus & Loden, 1981) are recorded from the continental slope off North Carolina, *P. biprostatus* also from the Gulf of Mexico, and *P. coeloprostatus* (Cook, 1969) is reported from as far north as Maine. Moreover, a new species, described from the northern Gulf of Mexico, as well as *P. flabellifer,* are attributed to a new genus.

The new material studied originates from three sources: (1) the Study of Biological Resources on the U.S. South Atlantic Continental Slope and Rise (Blake et al. 1987), supported by contract number 14-12-0001-30064 from the U.S. Department of Interior, Minerals Management Service, to Battelle New England Research Laboratory, Woods Hole Oceanographic Institution, and Lamont-Doherty Geological Observatory (courtesy Dr. Nancy Maciolek-Blake), (2) oligochaetes collected at Perdido Key, near Pensacola, northwestern Florida, and Horn

Island, off the coast of Mississippi, by Dr. J. McLelland, Gulf Coast Research Laboratory, Ocean Springs, Mississippi, and (3) material from a study of trophic coupling and benthos in Sheepscot River, Maine (Dr. L. Watling and Dr. R. Langton, principal investigators; courtesy also Ms. L. McCann; University of Maine, Darling Marine Center).

The specimens were stained in paracarmine and mounted whole in Canada balsam. Material of the species is deposited in the United States Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C., the Swedish Museum of Natural History (SMNH), Stockholm, and in the reference collection of Darling Marine Center.

Peosidrilus Baker & Erséus, 1979

Peosidrilus Baker & Erséus, 1979:505–506.—(In part) Erséus 1992:27.

Adelodrilus Cook (in part).—Erséus & Loden 1981:823.

Phallodrilus Pierantoni (in part); Erséus 1979a:203.—Erséus 1984:823.—Erséus 1990:54.

Diagnosis (modified after Erséus 1992) (assumed autapomorphy in italics).—Marine tubificids. Somatic setae bifid, with upper tooth thinner and shorter than lower. Penial setae, when present, generally with clubbed ectal ends, each bearing an apical hook; however, in some species the 'clubs' are indistinct, or even absent. Penial setae small, generally straight, and numerous in bundle. *Spermathecal pores lateral,* or in line with dorsal setae [*P. dorsospermatheca*]. Vasa deferentia ciliated, narrow in all but one species [vasa much dilated in *P. acochlearis*], entering apical ends of atria. Atria generally somewhat elongate, more or less horizontal and curved; occasionally short and almost erect. Each atrium with two prostate glands, anterior one attached at entrance of vas deferens, posterior one attached to ectal end of atrium. Atria either opening directly to exterior through simple pores, small male projections, or true pendent penes; copulatory sacs absent or present. Spermathecae of varying shape; spermathecal vestibules present in a few species.

Type species.—Peosidrilus biprostatus Baker & Erséus, 1979.

Other species.—Twelve species listed by Erséus (1992); i.e., excluding *P. flabellifer,* which is transferred to *Peosidriloides,* new genus, below.

Remarks.—Peosidrilus was revised by Erséus (1992) to include a number of species formerly regarded as members of *Phallodrilus,* primarily those species that have clubbed, apically hooked penial setae, and lateral spermathecal pores, the latter feature considered as a possible autapomorphy of *Peosidrilus.* However, the genus is heterogeneous. Due to the lack of distinct synapomorphies, other species have been included on the basis of overall (partly symplesiomorphic) similarity with the more typical members. With the removal of *Peosidriloides flabellifer,* new combination, however, *Peosidrilus* is now more unambiguously diagnosed by its lateral spermathecal pores. The dorsal position of the pores in *P. dorsospermatheca* can be regarded as a secondary transformation from the lateral position.

Peosidrilus may have to be revised again when new information becomes available. Other taxa with clubbed, apically hooked penial setae (*Adelodrilus* Cook, 1969, *Bermudrilus* Erséus, 1979b) will then also have to be considered (see Erséus 1992).

Peosidrilus biprostatus
Baker & Erséus, 1979

Peosidrilus biprostatus Baker & Erséus, 1979: 506–508, figs. 1–2.—Erséus & Loden 1981:819–820.—Erséus 1992:27, fig. 12F.

Phallodrilus biprostatus; Erséus 1984:819–820.—Erséus 1986:296–297.—Davis 1985:table 1.

New material.—USNM 169815, 1 specimen from off Cape Fear, North Carolina, U.S.A., 32°32.22′N, 77°15.31′W, 605 m, sand, South Atlantic cruise 5, station 14A, box core 3 (20 Sep 1985; see Blake et al. 1987). USNM 169816, 1 specimen from 800 m off Perdido Key (Gulf of Mexico), near Pensacola, Florida, U.S.A., about 6 m, sand, station A 0920C89C (collected by J. McLelland, October 1989).

Remarks.—The specimen from 605 m depth off North Carolina represents the deepest record of this species; *P. biprostatus* has never been found deeper than 73 m before (Baker & Erséus 1979). The worm is not complete. It is 3.5 mm long, comprising anterior 21 segments only. Its penial setae are about 9 per bundle.

The Perdido Key material provides the first record of *P. biprostatus* from the Gulf of Mexico. The single worm is the smallest (complete, and sexually mature) individual of the species reported to date; it is 4.5 mm long, with about 38 segments. The penial setae appear to be 6 on one side of worm, whereas the penial setae and male efferent duct are not developed on the other side.

Distribution and habitat.—NW Florida (first record for Gulf of Mexico), eastern United States (Florida through Massachusetts). Largely coarse sand, known from 5.5–605 m depth.

Peosidrilus acochlearis (Erséus & Loden, 1981)

Adelodrilus acochlearis Erséus & Loden, 1981:821–823, figs. 1B–C, 2.—Erséus 1983:77–78.
Phallodrilus acochlearis; Erséus 1986:297–298, fig. 7.
Peosidrilus acochlearis; Erséus 1992:27.

New material.—USNM 169817–169818, 2 specimens from off Cape Fear, North Carolina, U.S.A., 32°32.22′N, 77°15.31′W, 605 m, sand, South Atlantic cruise 5, station 14A, box core 3 (20 Sep 1985; see Blake et al. 1987).

Remarks.—One of the two specimens is complete: 3.6 mm long, with 36 segments. This specimen has a few modified bifid setae, with much prolonged lower teeth, in some dorsal bundles of the posteriormost segments (see Erséus & Loden 1981:fig. 1C). The new material conforms to the previous descriptions in other characters too, but one individual appears to have at least 15 penial setae per bundle. Previously described material had maximally 14 such setae per bundle (Erséus 1986).

This species had not been collected deeper than 11 m before. The present record is from a continental slope station.

Distribution and habitat.—East coast of the United States (Florida through North Carolina). Sand, known from 5.5–605 m depth.

Peosidrilus coeloprostatus (Cook, 1969)

Phallodrilus coeloprostatus Cook, 1969:16–17, fig. 5.—Erséus 1979a:189–190, fig. 4.—Erséus 1984:813–815, fig. 1.
Peosidrilus coeloprostatus; Erséus 1992:27.

New material.—USNM 169819–169823 (5 specimens) and Darling Marine Center reference collection (3 specimens), all from Outer Sheepscot Bay, Maine, 43°43.10′N, 69°43.40′W, Station B7, 37 m, coarse sand and gravel with a large amount of vascular plant detritus, annual salinity range 32.4–33.2‰ (collected by L. Watling, 8 Sep 1988). SMNH Main coll. 1414, 4 specimens from same area, kind of sediment, collector and date, but 43°42.85′N, 69°43.65′W (Station B9), 38 m.

Remarks.—The new material from Sheepscot River conforms well to the previous descriptions. The specimens are 3.9–7.2 mm long, with 38–78 segments. Their penial setae are about 35–50 μm long, (8)9–15(16) per bundle.

This species has been reported from as far south as Maryland/Delaware (Diaz et al. 1987), but not north of Massachusetts (Cook 1969) before.

Distribution and habitat.—East coast of United States (Maryland through Maine; new record for Maine). Sand, known from 3.4–78 m depth.

Peosidriloides, new genus

Phallodrilus Pierantoni (in part); Erséus 1984:823.
Peosidrilus Baker & Erséus (in part); Erséus 1992:27.

Etymology.—Named for its resemblance (*-oides* Greek for 'resembling') to *Peosidrilus.* The type species was previously classified as a member of that genus.

Diagnosis.—(assumed autapomorphies in italics).—Marine tubificids. Somatic setae bifid. *Clitellum short, maximally extending over posterior third of segment X, whole XI, and anterior two thirds of XII.* Somatic setae bifid, with upper tooth thinner and shorter than lower. Penial setae with single-pointed, curved tips (tips also somewhat clubbed in *P. flabellifer*). Penial setae small, numerous, densely packed, generally over 10 per bundle. Spermathecal pores in line with ventral setae, or even ventral to this line. *Vasa deferentia* ciliated, narrow, *several times longer than atria,* entering apical ends of atria. Atria cylindrical or somewhat spindle-shaped, horizontal, but slightly curved towards male pores; latter simple (*P. flabellifer*) or as penis-like organs (*P. hornensis*). Each atrium with two prostate glands, anterior one attached at entrance of vas deferens, posterior one attached to ectal end of atrium. Spermathecae with discrete ducts and thin-walled ampullae; spermathecal vestibules not distinct.

Type species.—*Phallodrilus flabellifer* Erséus, 1984.

Other species.—*Peosidriloides hornensis,* new species.

Remarks.—The inclusion of *Phallodrilus flabellifer* in *Peosidrilus* was problematic as this species does not have lateral spermathecal pores, which is the assumed autapomorphy of *Peosidrilus* (see Erséus 1992; and above). With regard to the (ventral) location of the spermathecal pores, the new genus *Peosidriloides* is plesiomorphic.

The penial setae of *Peosidriloides hornensis* and *P. flabellifer* have tips that are either unmodified (Erséus 1992: fig. 1D, state 0), or with indistinct ectal swellings (Erséus 1992: fig. 1D, state 3), both relatively plesiomorphic conditions vis-á-vìs the distinctly clubbed penial setae (Erséus 1992: fig. 1D, state 4) found in most species of *Peosidrilus, Adelodrilus* and *Bermudrilus.* The new genus therefore may be phylogenetically separated from these other genera. Monophyly of *Peosidriloides* is supported by the unusually short clitellum, and the very long vasa deferentia.

Both species of *Peosidriloides* are from the Northwest Atlantic.

Peosidriloides flabellifer (Erséus, 1984), new combination

Phallodrilus flabellifer Erséus, 1984:818–819, fig. 4.
Peosidrilus flabellifer; Erséus 1992:27.

Remarks.—As argued above, this species is better placed outside *Peosidrilus.* The distinguishing features of *P. flabellifer* and *P. hornensis* are noted in Remarks for the latter below.

Distribution and habitat.—Georges Bank, off Massachusetts (Northwest Atlantic). Coarse sand, 78–79 m depth.

Peosidriloides hornensis, new species
Fig. 1

Holotype.—USNM 169824, whole-mounted specimen.

Type locality.—N shore of about the middle of Horn Island, about 11 km off the coast of the state of Mississippi, northern Gulf of Mexico, swash and supratidal zones in an area severely impacted by an oil spill, Station no. 11 (collected by J. McLelland, 21 Sep 1989).

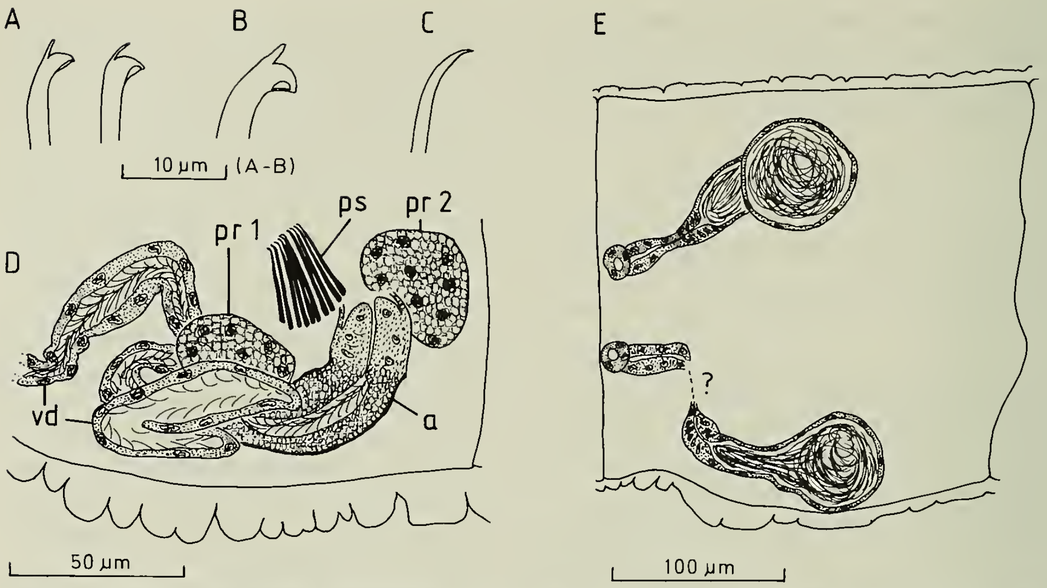

Fig. 1. *Peosidriloides hornensis,* new species. A, Free-hand drawing of anterior somatic setae; B, Free-hand drawing of postclitellar somatic seta; C, Free-hand drawing of penial seta; D, Male genitalia in segment XI; E, Spermathecae in segment X (one spermatheca slightly damaged). Abbreviations: a, atrium; pr1, anterior prostate gland; pr2, posterior prostate gland; ps, penial seta; vd, vas deferens.

Paratypes.—USNM 169825 and SMNH Type coll. 4632, 2, whole-mounted specimens from type locality.

Etymology.—Named for Horn Island.

Description.—Length of two USNM specimens, 8.2 and 6.1 mm, 59 and 60 segments respectively (SMNH specimen not complete). Width at clitellum (fixed, compressed specimens) 0.32–0.39 mm. Prostomium rounded, well set off from peristomium. Clitellum extending over ⅔X–⅔XII, well developed in all specimens. Somatic setae (Fig. 1A–B) bifid, with upper tooth shorter and distinctly thinner than lower, and with subdental ligaments. These setae generally 35–50 µm long, 2.5–3.5 µm thick (smaller in a few anteriormost segments), two or three (occasionally four) per bundle anteriorly, two per bundle in postclitellar segments. Penial setae (Fig. 1C; D, *ps*) single-pointed, 25–35 µm long, 1–2 µm thick, about 7–12 per bundle (exact numbers difficult to establish), with curved, thin tips (details not clear); setae densely packed within bundle. Male and spermathecal pores paired, both pairs ventral to lines of ventral setae; pores thus rather close to each other within each pair (see Fig. 1E). Male pores posteriorly in segment XI, spermathecal pores in most anterior part of X.

Pharyngeal glands in segments IV–V. Male genitalia (Fig. 1D) paired. Vas deferens variably wide (ectal part dilated, up to about 15–20 µm wide), coiled, several times longer than atrium, appear to enter apical end of latter (details not clear). Atrium cylindrical or somewhat spindle-shaped, slightly curved, 45–60 µm long, 20–22 µm wide, with very thin outer (muscle) lining, and granulated and ciliated inner epithelium. Atrium terminating in simple copulatory organ; probably a penis, but difficult to see whether organ is fully pendent within a penial sac. Copulatory organ 23–28 µm long, 23–28 µm wide. Two small, compact prostate glands present; anterior one attached near junction between vas deferens and atrium, posterior one located near penial organ.

Spermathecae (Fig. 1E) totally about 135–160 long, with slender duct-like, at middle somewhat constricted, part, and pear-shaped, thin-walled ampullae; latter 55–70 μm wide, filled with non-organized sperm. Typical spermathecal vestibules not present, but outer (somewhat swollen) parts of ducts possibly homologous to such structures.

Remarks.—This new species differs from *Peosidriloides flabellifer* in several aspects. It has up to three or four setae in some anterior segments (setae two per bundle throughout body in *P. flabellifer*), its spermathecal pores are closer together ventrally (pores in line with ventral setae in *P. flabellifer*), its vasa deferentia appear dilated (vasa narrow throughout in *P. flabellifer*), and it has penis-like copulatory organs (atria opening directly to the exterior through simple pores in *P. flabellifer*).

With regard to the dilation of the vasa deferentia and the possession of penial organs, *P. hornensis* is similar to *Peosidrilus acochlearis* (Erséus & Loden, 1981), but the latter taxon is in other respects (with numerous somatic setae, distinctly clubbed penial setae, clitellum and vasa deferentia of normal length, and lateral spermathecal pores) a typical member of *Peosidrilus.* The resemblance may therefore be due to convergence.

Distribution and habitat.—Known only from Horn Island (northern Gulf of Mexico). Inter- and supratidal sand.

Discussion

Peosidrilus and *Peosidriloides* are both taxa with a more or less Northwest Atlantic distribution, at least by conclusion from the present records. Their general appearance seems to indicate phylogenetic membership in a larger group of phallodriline genera extending across the North Atlantic to Europe and the Mediterranean and Black Seas; this larger group contains also *Adelodrilus* and *Bermudrilus.* The character patterns within this larger group are, however, confusing, and it is probable that there is homoplasy (both convergence and reversal) in the location of spermathecal pores as well as in the morphology of penial setae (Erséus 1992).

Twelve of the thirteen species of *Peosidrilus* are known only from the east coast of the United States, including the Gulf of Mexico, and from the Caribbean (Erséus 1992; present paper). The genus thus appears to have undergone a unique radiation in this part of the Northwest Atlantic.

All previous records of *Peosidrilus* have been from either intertidal or continental shelf habitats. The present records of *P. biprostatus* and *P. acochlearis* from a station 605 m deep indicate that the genus also occurs at bathyal depths.

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A NEW AMERICAN FAIRY SHRIMP, *LINDERIELLA SANTAROSAE* (CRUSTACEA: ANOSTRACA: LINDERIELLIDAE), FROM VERNAL POOLS OF CALIFORNIA, U.S.A.

Alain Thiéry and Michael Fugate

Abstract.—A new species of fairy shrimp, *Linderiella santarosae* (Anostraca: Linderiellidae), is described from vernal pools on the Santa Rosa Plateau Reserve, Riverside Co., California, U.S.A. The form of the basal outgrowth on antenna 2 of males and the spines on the resting eggs are the primary characters which distinguish *L. santarosae* from the other *Linderiella* species of western North America, northwestern Africa and southwestern Europe. *Linderiella santarosae* is also distinguished from *L. occidentalis,* the other Californian species, by fixed differences at two electrophoretic loci (PGM and PEP-D). The distribution of the five known species, each locally endemic to Mediterranean climatic regions, may be linked to a wider distribution of the genus in the past across the Laurasian continent.

Brtek (1964) erected the family Linderiellidae and the genus *Linderiella* based on an enigmatic anostracan (*Linderiella occidentalis* Dodds, 1923) from a lake (Lagunita) on the Stanford University Campus in Palo Alto, Santa Clara Co., California, U.S.A. Dodds (1923) originally placed *L. occidentalis* in the genus *Branchinecta,* and Linder (1941), in his review of the Anostraca, transferred it to the family Chirocephalidae and the genus *Pristicephalus.* Brtek (1964) separated *L. occidentalis* from the Chirocephalidae based on differences in the male reproductive structures.

The genus *Linderiella* is currently restricted to regions with a Mediterranean climate in the Northern Hemisphere. Species are found in Morocco (*Linderiella africana* Thiéry, 1986), France (*Linderiella massaliensis* Thiéry & Champeau, 1988), Spain (Alonso 1985) and California, U.S.A. (*L. occidentalis* Dodds, 1923). The genus inhabits pools and ponds with low mineralization that fill after winter rains (Alonso 1985, Thiéry & Champeau 1988, Eng et al. 1990).

During fieldwork in California from 1988 to 1991, one of us (MF) collected two species of anostracans from several vernal ponds and pools within the Nature Conservancy Reserve on the Santa Rosa Plateau, Riverside Co., California. One of the species was *Branchinecta lynchi* Eng et al., 1990, and the other was the new species in the genus *Linderiella* described in this paper.

Methods

Specimens were fixed in 10% formalin and preserved in 70% ethanol. Antennae, thoracic appendages and penes to be illustrated were removed under a WILD M7 stereomicroscope and observed with a WILD M20 compound microscope, both equipped with camera lucida. Measurements are given to the nearest 0.1 mm for the adults and to the nearest 2 mm for the diameter of the resting eggs. Total length includes the distal setae of the cercopods. Specimens observed on the scanning electron microscope (SEM) were dehydrated through a graded ethanol series to absolute ethanol, critical-point

Fig. 1. California collection sites for populations of *Linderiella* used in this study. Open star indicates the type locality of *Linderiella santarosae,* n. sp.; solid star, the type locality of *Linderiella occidentalis* (Palo Alto); solid circle, Fields Rd. and Tim Bell Rd.; solid square, Prairie City OHV; open circle, sites sampled by Eng et al. (1990), open triangles, DB. 430 population and solid triangle, Marin Co. (DB. 878).

dried and coated with gold-palladium for observation in a Cambridge Stereoscan 360. Specimens of related species used for morphological comparisons are from the personal collections of A. Thiéry (*L. africana*: Daya Azigza, 6 Mar 1985, Middle Atlas, Morocco and *L. massaliensis*: pond of Saint Maximin, 7 Feb 1988, France) and D. Belk (*L. occidentalis*: California, DB, 430). Additional specimens of *L. occidentalis* either were collected in the field or lab-reared from dry mud (see locations on Fig. 1): Lagunita, Stanford University, Palo Alto, type locality of *L. occidentalis* (soil sample collected Nov 1989, C. Sassaman): 4 ♂, length, 8.8–10.9 mm, 3 ♀ (1 ovigerous), length, 9.5–10.0 mm; Tim Bell Road (12 Mar 1988, coll. S. Morey): 5 ♂, length, 9.7–11.2 mm, 4 ♀ (2 ovigerous), length, 11.0–13.3 mm; Fields Road (12 Mar 1988, coll. S. Morey): 7 ♂, length, 9.7–10.6 mm; 7 ♀ (5 ovigerous), length, 9.6–12.0 mm; Prairie City OHV. (2 Feb 1990 coll. M. Fugate): 21 ♂, length, 10.0–13.2 mm, 25 ♀ (20 ovigerous), length, 12.6–18.0 mm, and Tehama Co. DB. 430 (28 Mar 1982): 8 ♂, length, 10.1–12.4 mm, 9 ♀ (9 ovigerous), length, 10.2–14.6 mm.

Allele frequencies were determined using starch gel electrophoresis (see Fugate 1992 for detailed methods) for three populations (Fields Road, 14 individuals; Tim Bell Road, 6 individuals; Lagunita, 10 individuals) of *Linderiella occidentalis,* one population (Mesa de Burro, 14 individuals) of *Linderiella santarosae* and one population of (7 individuals from Connecticut Valley Biological Supply) *Eubranchipus vernalis* (Verrill, 1869) at the following eight loci: malic enzyme (ME), phosphoglucomutase (PGM), glucose-6-phosphate isomerase (PGI), phenylalanyl-proline peptidase (PEP-D), leucyl-alanine peptidase (PEP-C), Glucose-6-phosphate dehydrogenase (G6PD), isocitrate dehydrogenase (IDH), and aspartate aminotransferase (AAT). Nei's pairwise genetic distances (D) were calculated from the allele frequency data and clustered with the UPGMA method using PHYLIP 3.4 (Felsenstein 1989). Nei's genetic distance (D) is an estimate of the number of allelic substitutions per locus between two populations (Nei 1987 chap. 9).

Linderiella santarosae, new species
Figs. 2–10

Material examined.—Holotype ♂, USNM 266798, allotype ♀, USNM 266797 and 20

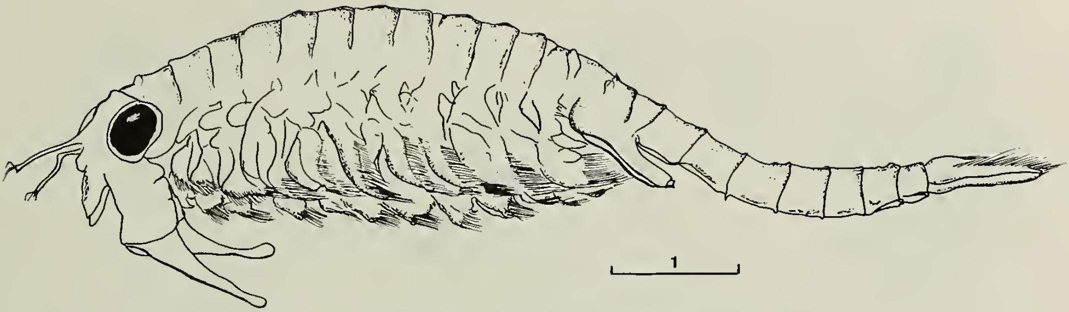

Fig. 2. *Linderiella santarosae*, n. sp.: habitus male, left lateral view (scale in mm).

paratypes, USNM 266796, Mesa de Burro; 18 paratypes, USNM 266795, Mesa de Colorado; 4 paratypes, Mesa de Colorado, Museum National d'Histoire Naturelle, Paris (MNHN Bp. 549). Additional specimens, fixed 1 August 1989 from Mesa de Colorado, also were used for the description. These individuals were lab-reared from soil samples collected 3 May 1988.

Type locality.—Vernal pools on the Santa Rosa Plateau Reserve, Riverside Co., California (Fig. 1). The reserve, located 6.5 km southwest of Interstate 15 on Clinton Keith Road (33°32′N, 117°17′W), is bordered on the northwest by the Santa Ana Mountains and on the east by agricultural and urban development surrounding the cities of Murrieta and Temecula.

Etymology.—The species is named after the type locality, the Santa Rosa Plateau, Riverside Co., California.

Male.—Length, 10.1 mm; to telson, 9.0 mm. Habitus (Fig. 2). Lengths of males examined 6.4–10.2 mm. Antenna 2 in form of claspers without frontal process. Distal segment of antenna 2 slender, slightly curved, with row of transverse ridges on inner surface (Fig. 6a, f, h). Tip of segment slightly inflated and bent medially (Fig. 6a, g). Basal portion of row slightly sinuous, contiguous to external edge on distal half of segment (Fig. 10h), not reaching tip. Basal segment of antenna 2 stout with dorsomedially projecting basomedial outgrowth (Figs. 3A, 5F, 6a). Outgrowth with slender, laterally curving tip and spinose plateau on inner face (Figs. 3B, C, 6a, 7a, f). Spines on plateau smooth and slightly recurved (Fig. 7a, f). Maxilla 2 of common type with single stiff seta on tip and 2–3 soft setae toward base (Cannon & Leak 1933, Linder 1941). Preepipodites of thoracic appendages serrated (Fig. 3E). Endopodite rounded with small spines at the base of setulose setae (Fig. 3D). Penes rectilinear, parallel. Basal part non-retractile, square in cross section, reaching end of third abdominal segment, with slightly curved medially-directed spur ornamented with 3–5 curved spines on inner side (Figs. 3F, 8a, c). Eversible tip of penes with smoothly tapered spine (Fig. 8b). Abdomen with dorsal and ventral setae 60–70 mm long (Fig. 8g, h). Cercopods with fine setae on surface and setulated setae along edges (Fig. 8e, f).

Female.—Length 11.1 mm, 10.0 mm to telson, ovigerous. Lengths of females examined 7.2–11.3 mm. Antenna 2 with straight horn-like process originating from inner side of basal segment (Fig. 4A, B). Process with thick base, denticulate on distal half (Fig. 4B). Anterior surface of basal segment hirsute, bearing irregular row of setae at base of the inner process (Fig. 4A, B). Distal segment of antenna 2 small, tapering to point. Brood pouch globular, 1.2 times wider than long, extending to abdominal segment 3. Pore opens subdistally and ventrally (Fig. 4C, D). Resting eggs (=cysts) spherical, with numerous short, tulip-shaped spines (Figs. 9a–i, 10a, c); diameter 230–283 μm, mean diameter, 260.7 ± 13.8 μm,

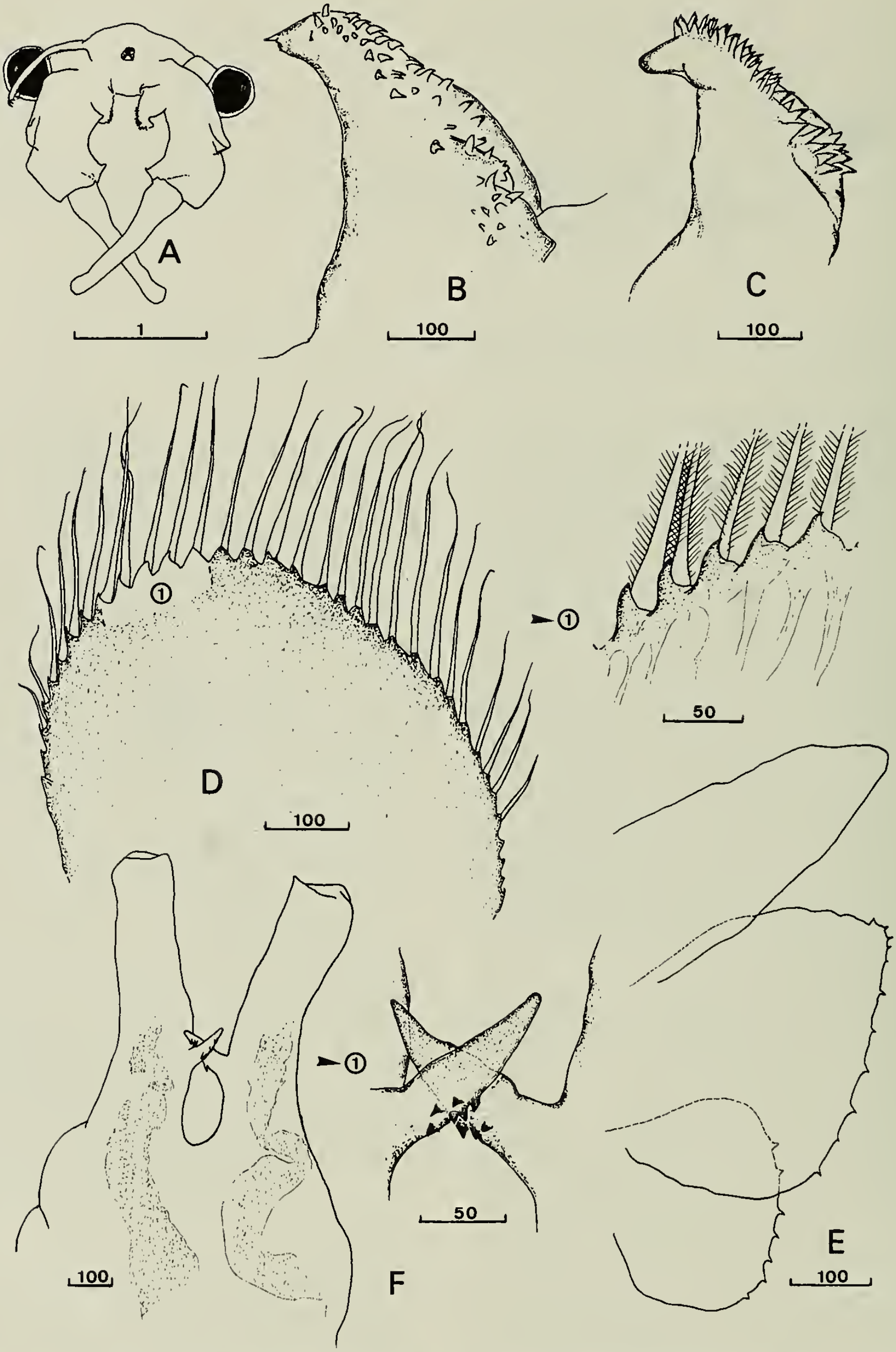

Fig. 3. *Linderiella santarosae,* n. sp. male: (A) head frontal view; (B) & (C) detail of the basomedial outgrowth; (D) shape of the endopodite of the appendage 7 with an enlarged detail; (E) shape of the preepipodites of the appendage 7; (F) penes in ventral view, tip not everted, with detail of the spurs of the basal nonretractile part (scales in μm, except for (A) in mm).

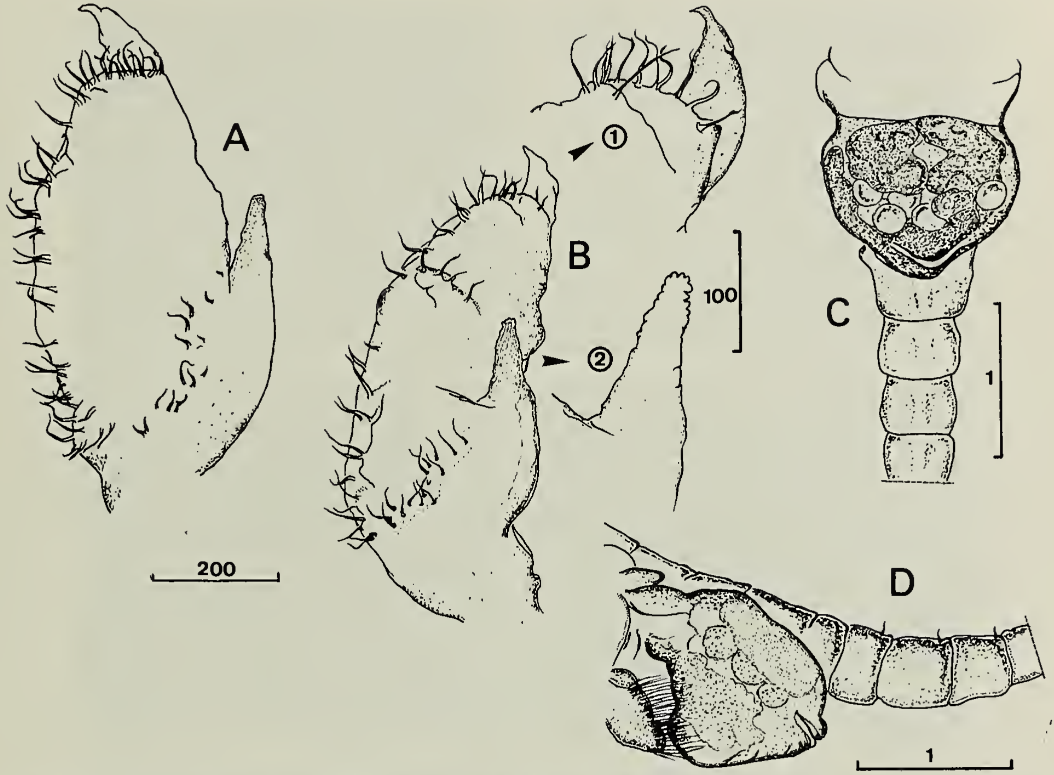

Fig. 4. *Linderiella santarosae,* n. sp. female: (A) & (B) second antenna dorsal view; (C) brood pouch ventral view; (D) brood pouch left lateral view (scales (A) & (B) in mm & (C) (D) in μm).

$n = 35$ from three mature females. Spines, 18–23 μm long, with flat tops, 5–16 μm wide (Fig. 9d–i). Most tops open with no pore visible at base of spines. Irregularly, spines fused at bases in twos or threes, making short walls not reaching more than half of total length of spine (Fig. 9a, b). Spinose outer layer surrounding spongy inner layer (Fig. 10d). One of largest mature females (8.2 mm) with 14 eggs in brood pouch.

Females larger than males through same cohort as previously observed for other *Linderiella* species (Dodds 1923, Heath 1924, Thiéry 1986a, Thiéry & Champeau 1988). Living fairy shrimps white, sometimes pale green or blue, quite translucent, with dark red eyes and reddish orange cercopods. Brood pouch of mature female with white shell glands and gold yellow to dark bronze resting eggs.

Remarks.—The five species in the genus *Linderiella* are distinguished from one another by only minor morphological differences (Thiéry & Champeau 1988). The undescribed Spanish *Linderiella* was initially identified as *L. occidentalis* (Alonso 1985) and *Linderiella santarosae* was as well in a recent survey of Californian anostracans (Eng et al. 1990). The form of the male antenna 2 and the resting egg are the two most reliable characters for distinguishing *L. santarosae* and *L. occidentalis* (Figs. 5–10), but minor differences are also found in the form of the medial spur on the penis (Fig. 8a–d). The row of transverse ridges on the distal segment of the male antenna 2 of *L. occidentalis* is more sinuous and the tip of the segment is neither sharply bent nor slightly inflated (Figs. 6 & 10h, i). The paired basomedial outgrowths on the basal segment

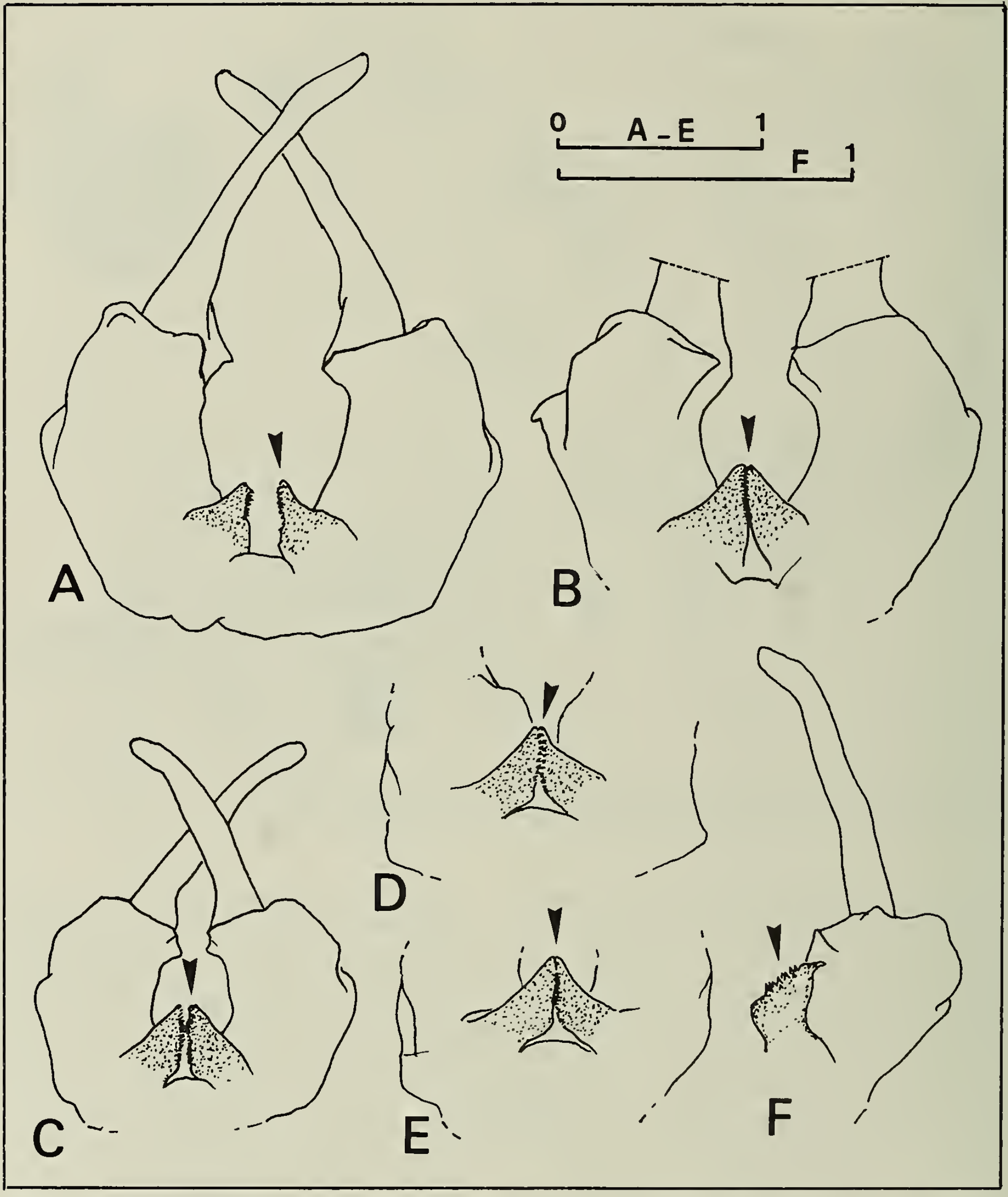

Fig. 5. Comparison of basomedial outgrowth of basal segment of male second antenna between *Linderiella santarosae,* n. sp. and different populations of *Linderiella occidentalis* (Dodds): *L. occidentalis,* (a) Tim Bell Rd.; (b) Olsen Rd.; (c) Lagunita Palo Alto; (d) Prairie City OHV; (e) DB. 430; *Linderiella santarosae,* n. sp.; (f) Santa Rosa Plateau, type locality (scale in mm).

of the male antennae 2 of *L. occidentalis* are similar in form to those of *L. santarosae,* but lack the slender, outward curving tips (Figs. 5, 6a–c, & 7). The resting eggs of *L. occidentalis* have acute spines instead of short, tulip-shaped (less than 2% of the spines of *L. occidentalis* eggs have a flat top) and the spines are longer in *L. occidentalis* (27–33 μm) than in *L. santarosae* (18–23 μm).

Fig. 6. SEM-micrographs in male second antenna. (a) *L. santarosae,* n. sp., lateral view; (b) inner view of *L. occidentalis* (DB. 430); (c) inner view of *L. occidentalis* (Prairie City); (d) inner view of *L. africana* (Daya Azigza, 6 March 1985, Middle Atlas Morocco); (e) inner view of *L. massaliensis* (pond of St. Maximin, 7 February 1988, France); (f) *L. santarosae,* n. sp., detail of row of transverse ridges, medial part of second segment, lateral view; (g) *L. santarosae,* n. sp., inner view of second segment; (h) *L. santarosae,* n. sp., detail of row of transverse ridges, apical view (scales in μm).

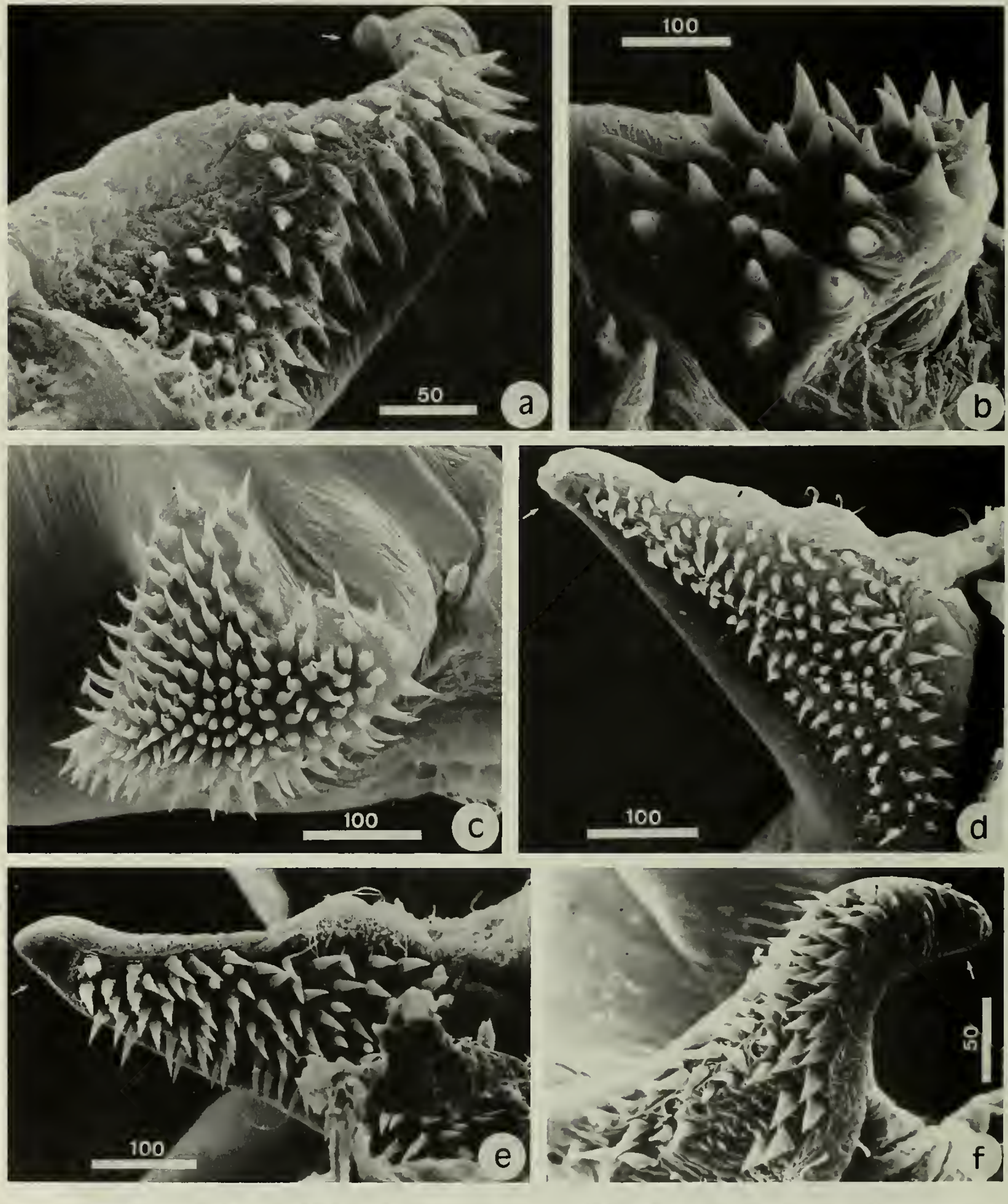

Fig. 7. SEM-micrographs of basomedial outgrowth on inner side of second antennae of males (inner views). (a) *L. santarosae,* n. sp.; (b) *L. africana*; (c) *L. massaliensis*; (d) *L. occidentalis* (DB. 430); (e) *L. occidentalis* (Prairie City); (f) *L. santarosae,* n. sp. (scales in μm). Arrows on (a), (d), (e), (f) indicate the straith or curved tip of the basomedial outgrowth.

Linderiella africana and *L. massaliensis* (the Spanish *Linderiella* is still undescribed) also differ from *L. santarosae* in the form of the basomedial outgrowth on antenna 2 of the male (Fig. 7) and the spines of the resting eggs (Mura & Thiéry 1986, Thiéry & Champeau 1988). The resting eggs of the Spanish *Linderiella* resemble those of *L.*

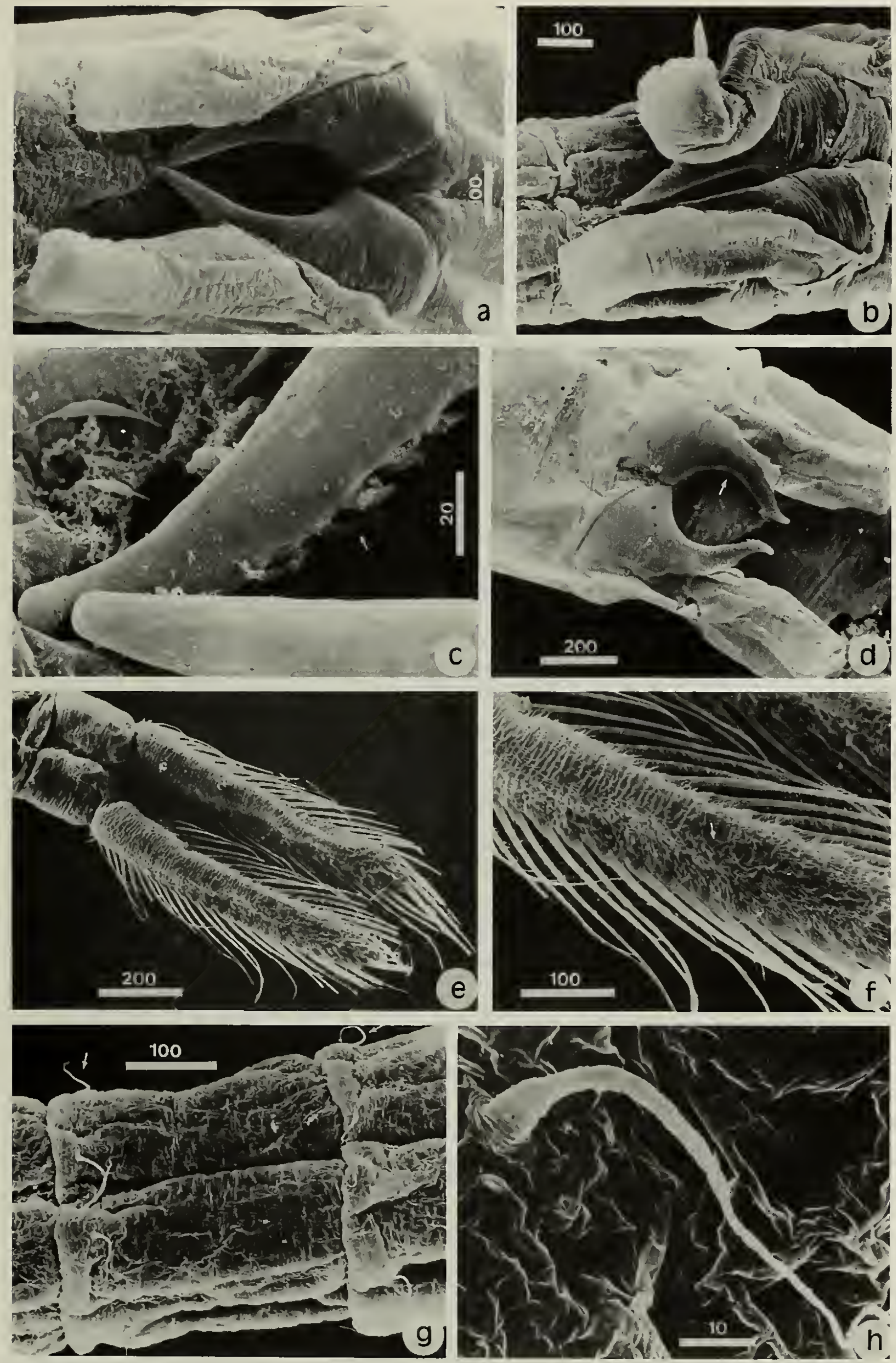

Fig. 8. SEM-micrographs of genital and abdominal segments of males. *Linderiella santarosae,* n. sp. (a–c) & (e–h); (a) ventral view of genital segments of abdomen, nonretractile structures and invaginate penes; (b) idem, with devaginate penes; (c) detail of nonretractile structure, with teeth on inner side (arrow); *Linderiella occidentalis* (DB. 430): (d) ventral view of genital segments of abdomen, with nonretractile parts and invaginate penes (arrow indicates curved inner edge); *Linderiella santarosae,* n. sp.; (e) ventral view of telson and cercopods; (f) detail of cercopods with hirsute surface (arrow); (g) ventral view of abdomen with setae (arrows); (h) detail of an abdominal seta (scales in μm).

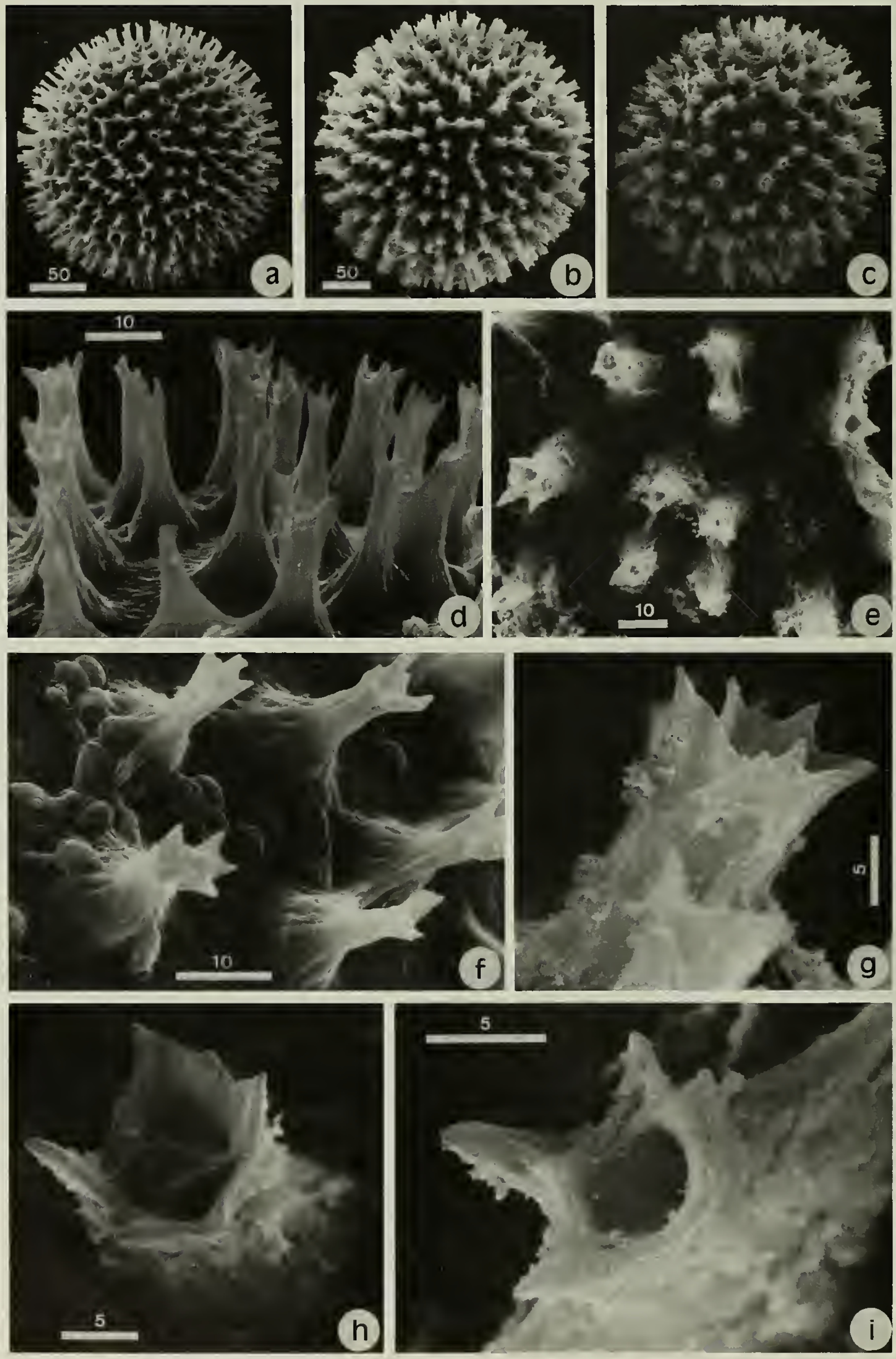

Fig. 9. *Linderiella santarosae,* n. sp. SEM-micrographs of resting eggs, (a) egg from single female, collected 1 January 1989, (b) & (c) eggs from two different females, collected 1 January 1988; (d) detail of spines, lateral view; (e) detail of spines, apical view; (f) idem, lateral view; (g) detail of a characteristic flat tip, lateral view; (h) detail of a flat tip in apical view; (i) idem, with opened spine (scales in μm).

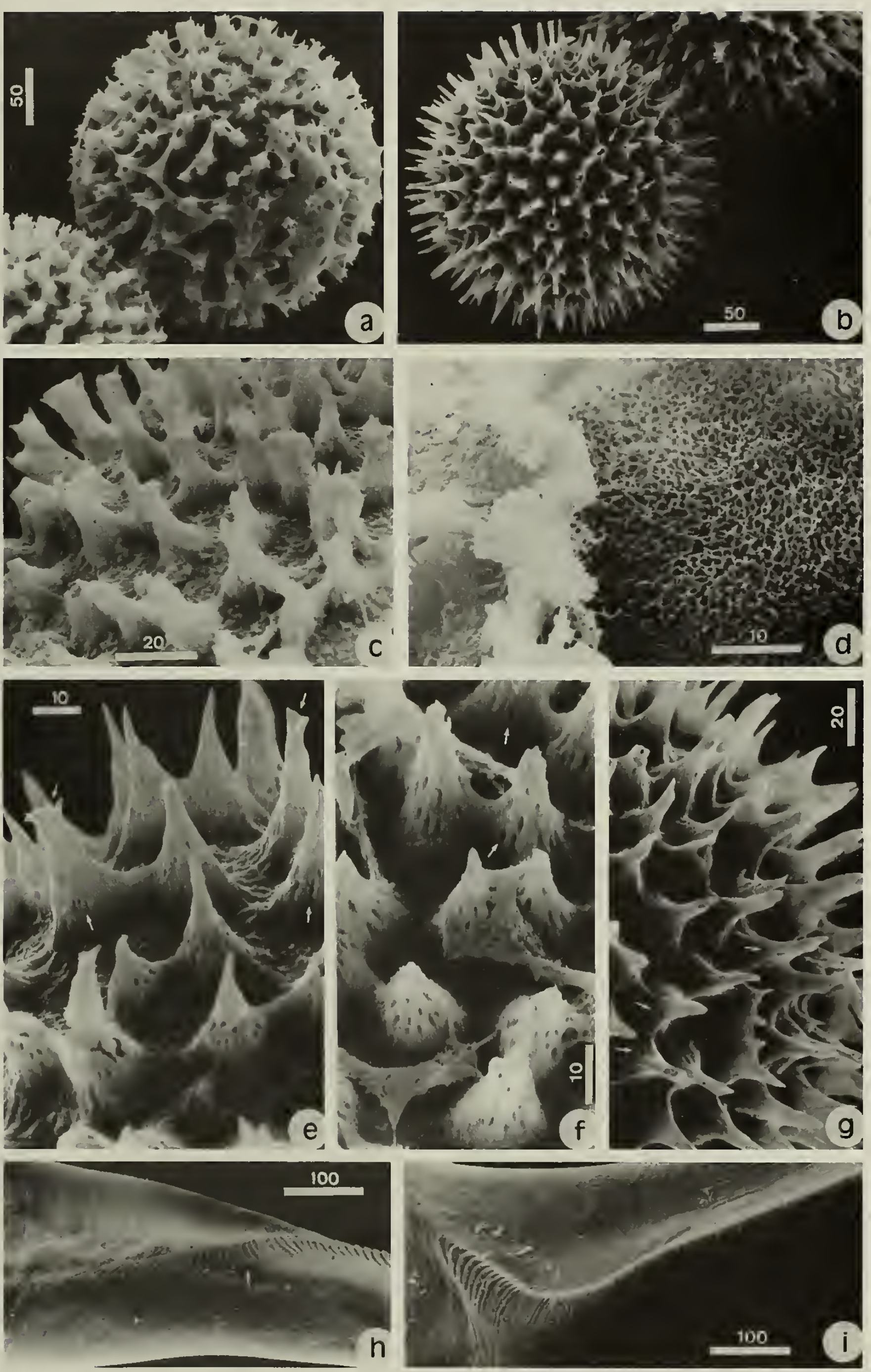

Fig. 10. *Linderiella santarosae*, n. sp. (a), (c), (d), (h) and *L. occidentalis* (b) & (e)—Lagunita. Palo Alto, (f)—Prairie City OHV, (g)—DB. 430; (a) whole egg entangled with mucus; (b) whole egg, with some broken spines (arrows)—(a) & (b) same scale; (c) lateral view of flat top spines; (d) detail of spongy inner layer of egg; (e–g), three detail of acute spines of *L. occidentalis* eggs, with some pores at their bases (arrows indicate pores and some flat top spines); (h) inner view of basal part of second antenna of male (*L. santarosae*, n. sp.) note—slightly sinuous line of rows (arrow); (i) idem, *L. occidentalis*, note the sinuous line more marked (arrow) (scales in μm).

Table 1.—Allele frequencies for populations of *Linderiella santarosae,* new species (1 = Mesa de Burro). *Linderiella occidentalis* (2 = Fields Rd., 3 = Tim Bell Rd., 4 = Lagunita), and *Eubranchipus vernalis* (5).

		Population				
Locus		1 (14)	2 (14)	3 (6)	4 (10)	5 (7)
PEP-C	a	0.143	0.000	0.000	0.100	0.000
	b	0.857	1.000	1.000	0.900	1.000
PGI	a	0.000	0.000	0.000	0.100	0.000
	b	1.000	1.000	0.833	0.900	0.000
	c	0.000	0.000	0.167	0.000	1.000
PGM	a	1.000	0.000	0.000	0.000	0.571
	b	0.000	0.000	0.167	0.500	0.429
	c	0.000	1.000	0.833	0.500	0.000
G6PD	a	0.000	0.000	0.000	0.000	0.500
	b	0.000	0.000	0.000	0.000	0.500
	c	0.000	0.000	0.333	0.100	0.000
	d	1.000	1.000	0.667	0.900	0.000
PEP-D	a	0.000	0.071	0.333	0.100	0.000
	b	0.000	0.857	0.667	0.900	0.000
	c	0.000	0.071	0.000	0.000	0.000
	d	1.000	0.000	0.000	0.000	0.000
	e	0.000	0.000	0.000	0.000	0.571
	f	0.000	0.000	0.000	0.000	0.429
ME	a	0.000	0.000	0.000	0.000	0.786
	b	0.000	0.000	0.000	0.000	0.214
	c	1.000	0.429	0.500	0.100	0.000
	d	0.000	0.571	0.500	0.900	0.000
IDH	a	0.000	0.000	0.000	0.100	1.000
	b	1.000	1.000	1.000	0.800	0.000
	c	0.000	0.000	0.000	0.100	0.000
AAT	a	0.000	0.000	0.000	0.000	0.929
	b	1.000	1.000	1.000	1.000	0.071

santarosae; this undescribed species also has tulip-shaped spines (Alonso & Alcaraz 1984, Thiéry & Champeau 1988). These differences in resting egg morphology confirm previous studies on the taxonomic value of resting egg ornamentation as a tool for identification of most anostracans (see review in Thiéry & Gasc, 1991, and Mura 1991, 1992a, 1992b).

A preliminary electrophoretic survey potentially provides two additional characters for distinguishing between *L. santarosae* and *L. occidentalis.* Although samples sizes are small (14 *L. santarosae* & 30 *L. occidentalis*), two loci (PEP-D & PGM) show fixed allelic differences (Table 1). Additional sampling may show these allelic differences to be incompletely fixed, but its unlikely to substantially alter the large genetic distances between the two species. The average D within *Linderiella occidentalis* (3 populations) is 0.054 and between *L. occidentalis* and *L. santarosae* is 0.378 (Fig. 11). These genetic differences are similar to those found between closely related species in the anostracan genus *Branchinecta* (Fugate 1992). For example, *Branchinecta lynchi* and *Branchinecta sandiegonensis* Fugate, 1993 have ranges similar to *L. occidentalis* and *L. santarosae,* respectively (Eng et al. 1990, Fugate 1992, 1993). The average D within *B. lynchi* is 0.154 (9 populations) and between *B. lynchi* and *B. sandiegonensis* (3 populations) is 0.477. A limitation in the electrophoretic analysis arises due to the limited range of *L. santarosae*; the close proximity of the pools on the plateau (<5 km) allows water birds to freely move resting eggs from pool to pool and makes the entire range of the species effectively one population.

Distribution and habitat.—*Linderiella santarosae* is currently known only from vernal pools on the Santa Rosa Plateau Reserve, Riverside Co., California. The Santa Rosa Plateau is approximately 300 km southeast of the nearest known populations of *Linderiella* in southern California (Cachuma Canyon, Santa Barbara Co., 34°42′N, 119°54′W, personal collection of Clyde Eriksen, A2-25; Sulfur Mountain, Ventura Co., 34°26′N, 119°06′W, personal collection of Denton Belk DB. 693). These two populations have not been studied electrophoretically, but morphologically appear to be *Linderiella occidentalis.* Another pool, one mile northwest of Olema, Marin Co. and across the road from the Visitors Center at Point Reyes National Seashore, 38°03′N/122°48′W (coll. Gary M. Fellers, collection DB. 878), is reported to have individuals that "look like *L. occidentalis,* but have eggs with some short flat-topped spines" (D. Belk,

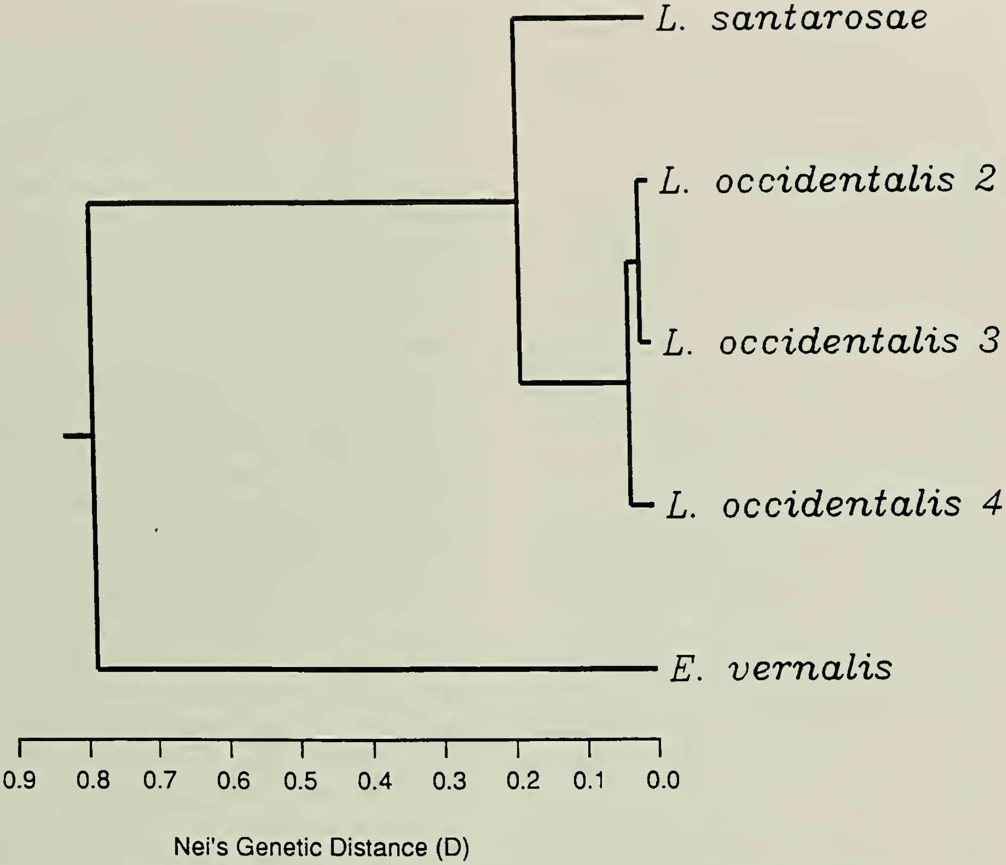

Fig. 11. UPGMA tree of Nei's pairwise genetic distances between populations of *Linderiella occidentalis* and *L. santarosae. Linderiella santarosae* 1—Mesa de Burro, *L. occidentalis* 2—Fields Rd., 3—Tim Bell Rd., 4—Lagunita, *Eubranchipus vernalis* 5—Connecticut Valley Biological Supply.

in litt.). We have not seen these individuals, but it would appear unlikely that these are individuals of *L. santarosae.*

The Santa Rosa Plateau Reserve is an isolated unit of grassland and oak-woodland-chaparral in southeastern Riverside Co., California, owned and managed by the Nature Conservancy (Lathrop & Thorne 1968, 1978). Two large (~3 km^2), flat-topped mesas of volcanic origin are prominent features of the reserve and contain thirteen vernal pools ranging in size from 25 m^2 to over 100,000 m^2. The mesas are capped by olivine basalt lavas that have weathered to form soils of the Murrieta series. The average elevation of the plateau is 610 m (Lathrop & Thorne 1976a, 1976b, 1983).

Collie & Lathrop (1976) report that pools on the Santa Rosa Plateau normally fill after winter rains (November to April) totaling 30–40 cm. The physico-chemical features of the 13 vernal pools are similar to those of pools containing *L. occidentalis* in other parts of the state (Eng et al. 1990); the conductivity of the water is low (147-189 μmhos cm^{-1} in February to 500–1050 in June), the pH is near 7.0 and water temperatures are usually below 20°C when *L. santarosae* is present (Collie & Lathrop 1976). *Linderiella occidentalis* is also commonly found at temperatures below 20°C and higher temperatures may be limiting to adults (Lanway 1974, Patton 1984, Eng et al. 1990).

The flora of the reserve was listed by Munz

& Keck (1959) and later was characterized in a series of papers by Lathrop (1976), Lathrop & Thorne (1968, 1976a, b, 1978, 1983) and Thorne & Lathrop (1969, 1970). Kopecko & Lathrop (1975) quantified the vegetation in and around the vernal pools on the reserve and reported the following genera and species, also common in pools containing *Linderiella* from France, Spain and Morocco: *Isoetes, Eleocharis, Callitriche, Juncus, Marsilea* and *Ranunculus aquatilis* (Maire 1924, Barbero et al. 1982, Alonso 1985, Thiéry 1987). These genera have been labeled "typical" vernal pool plants in California (Jain 1976).

The fauna of vernal pools on the Santa Rosa Plateau is poorly characterized (Pequegnat 1951), but the branchiopod diversity is much lower than that found associated with the other four *Linderiella* species (Alonso 1985, Thiéry 1986a, Thiéry & Champeau 1988). The other four species are often found in pools containing notostracans and conchostracans, but neither are present in pools on the plateau. Two amphibians are known to breed in the pools (*Bufo* sp. and *Hyla* sp.), and the following invertebrates are also present after winter rains: *Branchinecta lynchi* (Anostraca), *Moina* sp. (Cladocera), calanoid copepods, Ostracoda, Rotifera and Platyhelminthes.

Discussion

The modern disjunct distribution of the genus *Linderiella* has been the subject of some speculation (Belk 1984, Thiéry 1986a, 1986b; Thiéry & Champeau 1988, Banarescu 1990). These authors, using indirect evidence from a variety of sources, have attributed the disjunction to a vicariance event (sensu Bernardi 1986, Wiley 1988) involving the fragmentation of an ancestral taxon distributed across Laurasia. A number of other animal and plant taxa with similar ecologies have either modern or fossil distributions across the Holarctic (e.g., Raven 1971, DiCastri & Mooney 1973, Banarescu 1990). The limited fossil records of branchiopods indicates that modern genera may have been formed before the Cretaceous (Trusheim 1938, Tasch 1969, Trusova 1971, Jell & Duncan 1986). Also, dispersal is passive, limited, and more likely to occur in a north-south rather than an east-west direction (Proctor 1964, Proctor & Malone 1965, Cruden 1966, Proctor et al. 1967, Boileau et al. 1992, Fugate 1992, Saunders et al. 1993).

Although the vicariance hypothesis is consistent with the evidence for both ancientness and limited dispersal, the alternative hypothesis of long-distance dispersal cannot be fully eliminated due to the lack of a fossil record and an inadequate understanding of phylogenetic relationships within the Anostraca. The lack of a fossil record is difficult to surmount, but a phylogeny could be reconstructed using morphological, biochemical or molecular characters. The phylogeny could then be employed to test the coincidence between the history of the species within the genus and the history of the geographic regions in which they are currently found (Brooks 1990, Wiley et al. 1991). Until such a test is performed, the vicariance hypothesis will remain speculative.

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TWO NEW MARINE INTERSTITIAL OSTRACODA (CRUSTACEA: PUSSELLIDAE) FROM FIJI

Shinichi Hiruta

Abstract.—*Danipussella rhamphodes* and *Pussella fijiensis* (Podocopida, Bairdiacea) are described based upon specimens collected from coarse intertidal sand on the coral reef in Viti Levu, Fiji. These two species are discernible from congeneric species, mainly in the morphology of carapace and/or copulatory appendage.

Marine interstitial ostracods are one of the useful animal groups in reconstructing historical biogeography (Danielopol & Wouters 1992). However, our knowledge of them is still poor in respect to tropical environments, especially the coral reefs (Danielopol & Hartmann 1986). The present paper deals with two new marine interstitial species of the genera *Danipussella* Wouters, 1988 and *Pussella* Danielopol, 1973 (Pussellidae: Bairdidacea: Podocopida) from Fiji. Several pussellid species including an as yet undescribed new one are known from the southwestern Pacific (Cabioch et al. 1986, Danielopol & Wouters 1992). The ostracods were collected during the survey for marine invertebrates, which was carried out by Dr. Ken-Ichi Tajika, during the Koshida Team Expedition, a part of ODMT (the Research and Exchange Program of Osaka University in the South Pacific Region), in 1985 (Koshida et al. 1986).

Four pussellid specimens were discovered in samples from coarse intertidal sand on the coral reef of the Suva Barrier Reef in the vicinity of Suva in Viti Levu, Fiji. Two of them, possibly a female and a juvenile, sustained damage to the carapace and appendages. Two other, male specimens belonging to the above-mentioned genera were found in good condition. The male holotypes of the two new species are deposited in the National Science Museum, Tokyo (NSMT).

Superfamily Bairdiacea Sars, 1865
Family Pussellidae Danielopol, 1976
Genus *Danipussella* Wouters, 1988
Danipussella rhamphodes, new species
(Figs. 1, 2)

Specimen examined.—Holotype male: Fiji (NSMT-Cr11412). Specimen was collected by Dr. Ken-Ichi Tajika from the Suva Barrier Reef in the vicinity of Suva in Viti Levu, 16 Oct 1985.

Etymology.—The specific name is derived from Greek *rhamphodes* meaning beaklike, in reference to the beak shape of the ventral process of the copulatory appendage.

Description.—Female unknown. Male (holotype). Carapace (Fig. 1-1–3; Fig. 2-1–4) elongate, thin, 0.568 (both valves) mm long, 0.205 (right) mm high; dorsal margin evenly arched (Fig. 1-1 somewhat deformed), connected smoothly with posterior rounded margin; ventral margin concave in the middle; posteroventral margin convex; anterior margin straight, connected with dorsal and ventral margins at almost right angles; anterior surface of valve near anterior margin with two large processes which are triangular in lateral view and have terminal stout spines: internally these processes are connected with the vestibulum. Surface smooth, with some long hairs along the ventral margin. Inner margin parallel to anterior margin; posterior inner lamella

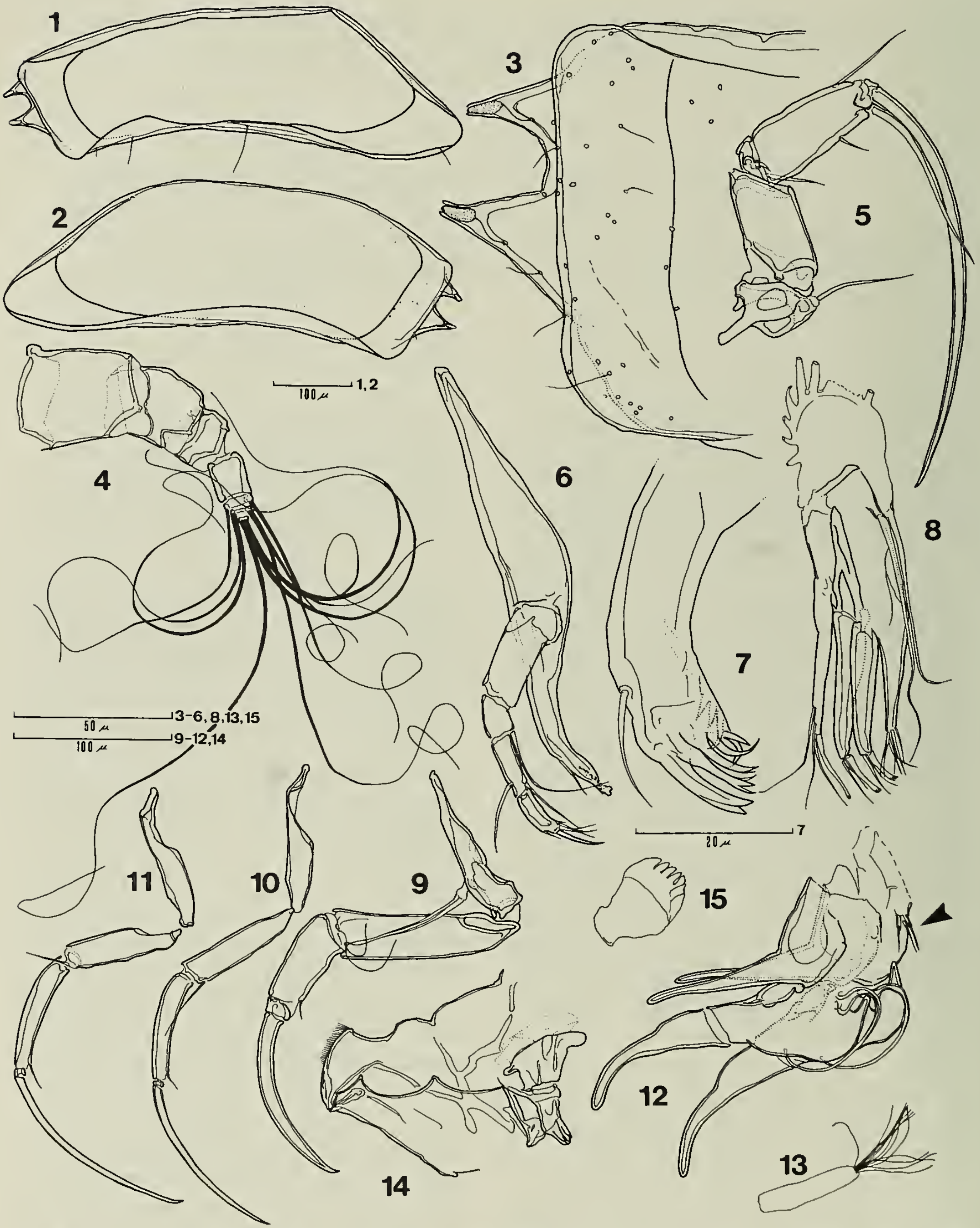

Fig. 1. *Danipussella rhamphodes,* new species. Male (holotype: NSMT-Cr11412). 1. internal view of right valve; 2. internal view of left valve; 3. internal view of anterior part of right valve; 4. right first antenna; 5. right second antenna; 6. right mandible; 7. idem, distal part; 8. right maxillula; 9. left first walking leg; 10. left second walking leg; 11. left third walking leg; 12. furca (arrow), abdominal bristle, and copulatory appendage; 13. brush-like organ; 14. lip; 15. Oesophagal chewing apparatus.

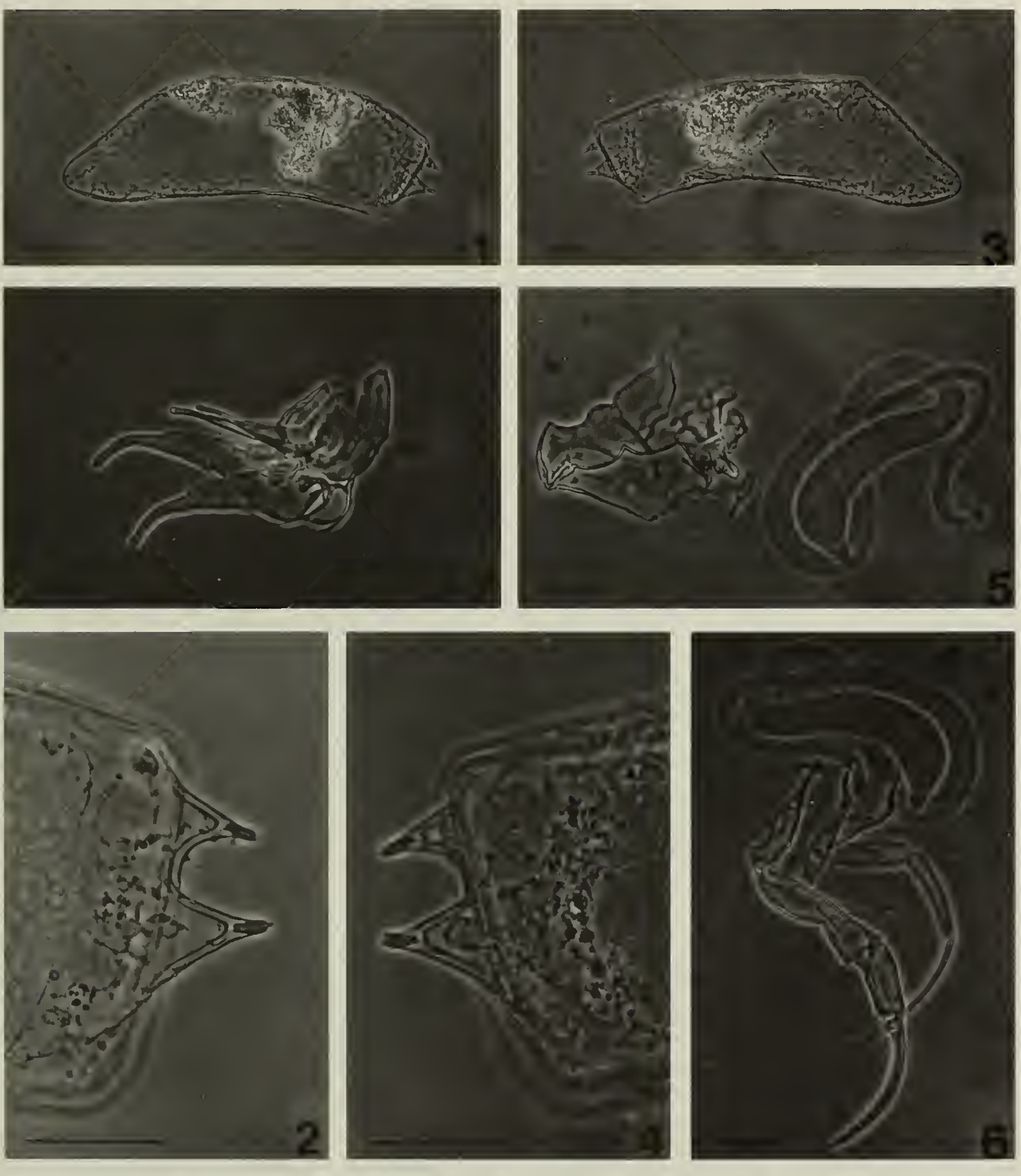

Fig. 2. *Danipussella rhamphodes,* new species. Male (holotype: NSMT-Cr11412). 1. internal view of left valve; 2. idem, anterior part; 3. internal view of right valve; 4. idem, anterior part; 5. lip and testis; 6. legs (leg 2 broken) and testis; 7. furca (arrow) and copulatory appendage. Each bar represents 0.05 mm.

broad, forming a large vestibulum. Adductor muscle scar pattern not clearly visible. Normal pore cannals scattered.

First antenna (Fig. 1-4) seven-segmented; first to third segments gradually decreasing in size; fourth segment quadrangular in lateral view; fifth to seventh segments very short, each with three, four, and three long setae respectively.

Second antenna (Fig. 1-5) five-segmented; first segment short, with a long ventrodistal seta; second segment somewhat shorter than fourth segment; third segment (basis) short, with a long mediolateral seta and a very small exopodite which is one-segmented and has one short terminal seta; fourth segment (first endopodite segment) with a long dorsal subterminal seta, a short ventral seta arising from the distal third of the ventral margin, and a long ventrodistal seta which is 1.6 times as long as the fourth segment; terminal segment small, about one-seventh the length of fourth segment, with a short thin seta and a strong long claw, which is 3.75 times as long as the fourth segment.

Mandible (Fig. 1-6, 7). Masticatory process with a short seta on the anterior margin; distal edge toothed, with nine teeth, of which some teeth are bifurcate or trifurcate. Palp four-segmented; first segment as long as second and third segments combined; second segment about one-half the length of third, with a long posterodistal seta; third segment with two setae, an anterior subterminal one and a posterodistal one; fourth segment robust, having a thicker cuticle than preceding three segments, and as long as third segment, with a short anterior subterminal seta, at least four distal setae of which the anteriormost is longer and stronger than the others, and one very short posterior subterminal seta.

Maxillula (Fig. 1-8) furnished with three masticatory lobes; first and second lobes articulated with basal part, with three and four terminal setae respectively of which the ventral one is thicker than the others, and furnished with minute some terminal short teeth; third lobe connected with basal part, with seven terminal setae. Palp unsegmented, with two setiferous ledges along dorsodistal part, each with one long seta, and two long distal setae of which the ventral one is thicker than the other and furnished with minute terminal teeth. Two long mouthward directed setae present. Respiratory plate with about ten setae.

First walking leg (Fig. 1-9; Fig. 2-6) four-segmented; first segment with two long ventral setae arising from a short process on the ventral margin as illustrated; third segment with a short anterodistal seta; length ratio of first to fourth segments and terminal claw 10:11.25:6:1:11.25. Second walking leg (Fig. 1-10) slender, with an anterodistal seta on second and third segments; length ratio of segments and terminal claw 35:30:25:1:45. Third walking leg (Fig. 1-11; Fig. 2-6) slender, with an anterodistal seta on second and third segments; length ratio of segments and terminal claw 17.5:15:13.5:1:25.

Furca and abdominal bristle (sensu Wouters 1988) (Fig. 1-12; Fig. 2-7: arrow). Furca consisting of a pair of proximally thickened short setae. Abdominal bristle forming a short thin seta.

Copulatory appendage (Fig. 1-12; Fig. 2-7). Each hemipenis with two anteriorly directed large processes, terminating in a round tip; dorsal process straight, tapered; ventral process beaklike, articulated with basal part, having a thick proximal part and a thin distal part which is slightly curved ventrally. Basal posterodorsal part with a small dorsally pointing process and a long recurved tube, whose proximal part is thickened, near preceding process. Testis (Fig. 2-5, 6) as shown in figures. Brush-shaped organ (Fig. 1-13) located near the base of the first walking leg, consisting of a pair of lobes, whose length is about five times as long as wide; each lobe with long filaments.

Lip (Fig. 1-14; Fig. 2-5) with hairs along anterior margin and several teeth-like structures, as illustrated. Oesophagal chewing apparatus (Fig. 1-15) present near the base of lip.

Remarks.—Wouters (1988) established the genus *Danipussella* based upon the materials from the Comoros as a monotypic genus within the family Pussellidae, containing three genera: *Anchistrocheles, Pussella,* and *Danipussella.* In this connection, Warne (1990) proposed the classification of the family Bythocyprididae (Bairdiacea), in which he considered Pussellinae as a subfamily of the family, and assigned *Orlovibairdia* McKenzie, 1978 and the new genus *Bythopussella* to the Pussellinae. Further, Danielopol and Wouters (1992) mention an as yet undescribed new pussellid genus from Papua New Guinea. Further study on the pussellid ostracods is needed.

The type species *Danipussella serpentina* and the present new species are quite similar to each other in morphology of both hard and soft parts. Furthermore, the size of the present new species (0.568 mm) is almost the same as in *D. serpentina* (0.59 mm), which is much larger than *Pussella*-species (0.26 mm). As Wouters (1988:87) predicted, this character seems to have taxonomic value. While the structure of the copulatory appendage of both species is basically similar, the morphology of the ventral process is a useful character in differentiating between them. *D. serpentina* has a long snakelike ventral process, while *D. rhamphodes* has a beaklike one.

Since these two *Danipussella*-species were found at remote distance from each other (the Comoros and Fiji), other species of the genus might be distributed widely in tropical seas.

Pussella fijiensis, new species
(Figs. 3, 4)

Specimen examined.—Holotype, male: Fiji (NSMT-Cr11413). The specimen was collected by Dr. Ken-Ichi Tajika from the Suva Barrier Reef in the vicinity of Suva in Viti Levu, 16 Oct 1985.

Description.—Female unknown. Male (holotype). Carapace (Fig. 3-1, 2; Fig. 4-1–6) thin, 0.452 (right), 0.445 (left) mm long, 0.181 (right), 0.177 (left) mm high. Dorsal and ventral margins arched, almost parallel to each other in anterior two-thirds of the length; posterodorsal margin strongly arched, terminating in a blunt triangular tip where ventral and dorsal margins meet; posteroventral margin with a large posteriorly pointing process, which is connected with vestibulum, and has a wide base and a terminal spine; anterior margin truncate, weakly arched; anterior surface near anterior margin with two large anteriorly pointing processes; upper one smaller than lower one, both connected with vestibulum and furnished with terminal spine. Surface of carapace smooth, with scattered normal pore canals; radial pore canals with short hairs and some long hairs. Inner margin almost parallel to anterior, ventral, and posterodorsal margins; anterior inner lammella broad. Hingement indistinct, but a small round process detected at the anterodistal edge of the right hinge. Adductor muscle scar (Fig. 4-7) consisting of four scars of different sizes as illustrated.

First antenna (Fig. 3-3) seven-segmented; first to third segments gradually decreasing in size; fourth segment quadrangular in lateral view; fifth to seventh segments very small, with three, four, and three long setae respectively.

Second antenna (Fig. 3-4) five-segmented; first segment with a long ventrodistal seta; second segment somewhat longer than fourth; third segment (basis) short, with a ventrodistal seta and a very small exopodite consisting of one segment, terminating in a short seta; fourth segment (first endopodite segment) with two subterminal setae, a long distal one, and a short ventral one, and a short ventrodistal claw-like seta; terminal segment small, about one-seventh of the length of fourth, with a short ventrodistal seta and a long claw which is about 3 times as long as the fourth and fifth segments combined.

Mandible (Fig. 3-5) similar to preceding species; fourth segment of palp with four distal setae of different lengths.

Maxillula (Fig. 3-6) furnished with three masticatory lobes; first and second lobes separated from base of maxillula, with two terminal setae, the ventral one being thicker than the other, and furnished with some short terminal teeth; third lobe connected with the body, with four distal setae. Palp unsegmented, with one long dorsal seta and two long distal setae, the ventral one thicker than the other, and furnished with some

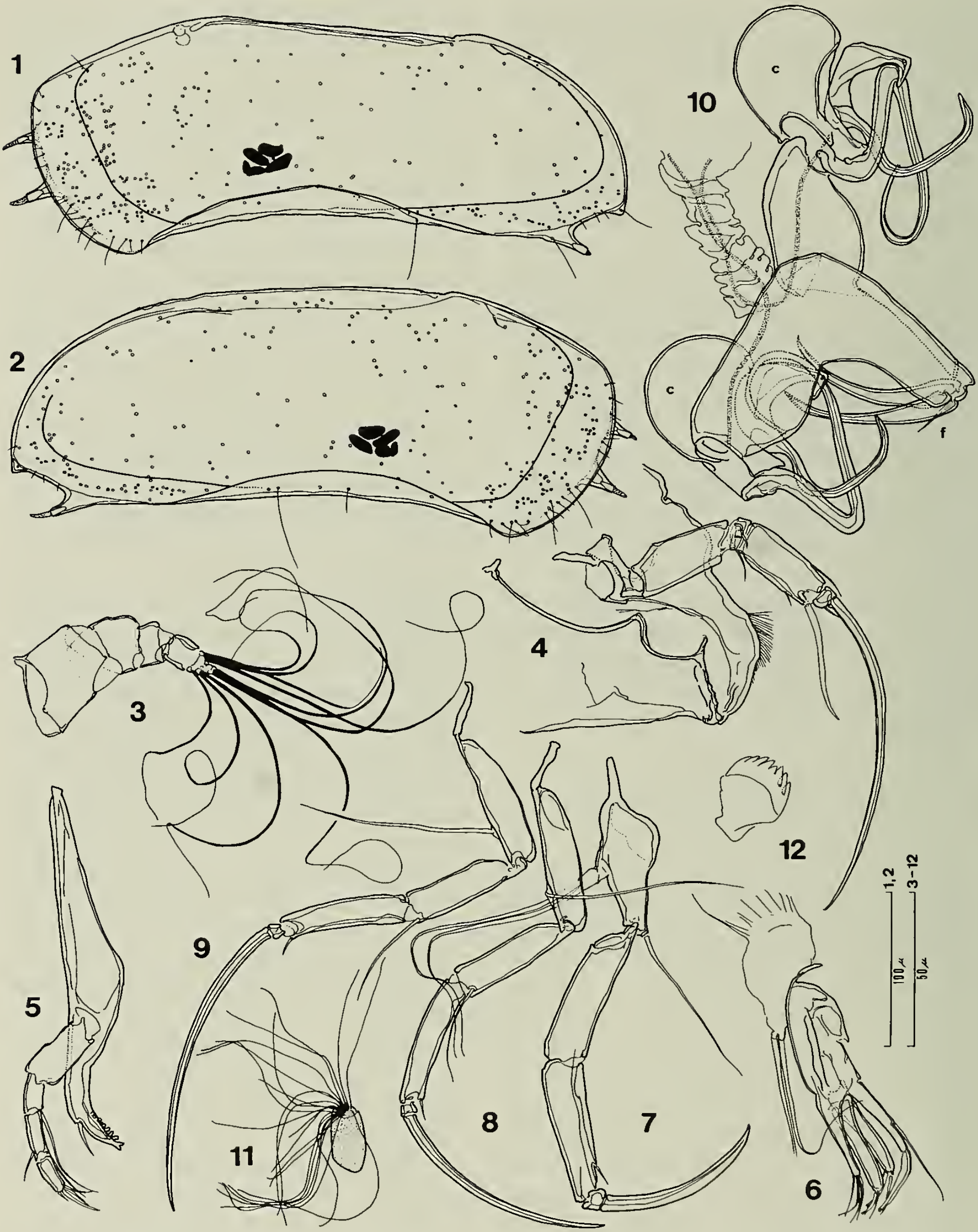

Fig. 3. *Pussella fijiensis,* new species. Male (holotype: NSMT-Cr11413). 1. internal view of right valve; 2. internal view of left valve; 3. right first antenna; 4. right second antenna and lip; 5. right mandible; 6. right maxillula; 7. right first walking leg; 8. right second walking leg; 9. right third walking leg; 10. furca (f) and copulatory appendage (c); 11. brush-like organ; 12. oesophagal chewing apparatus.

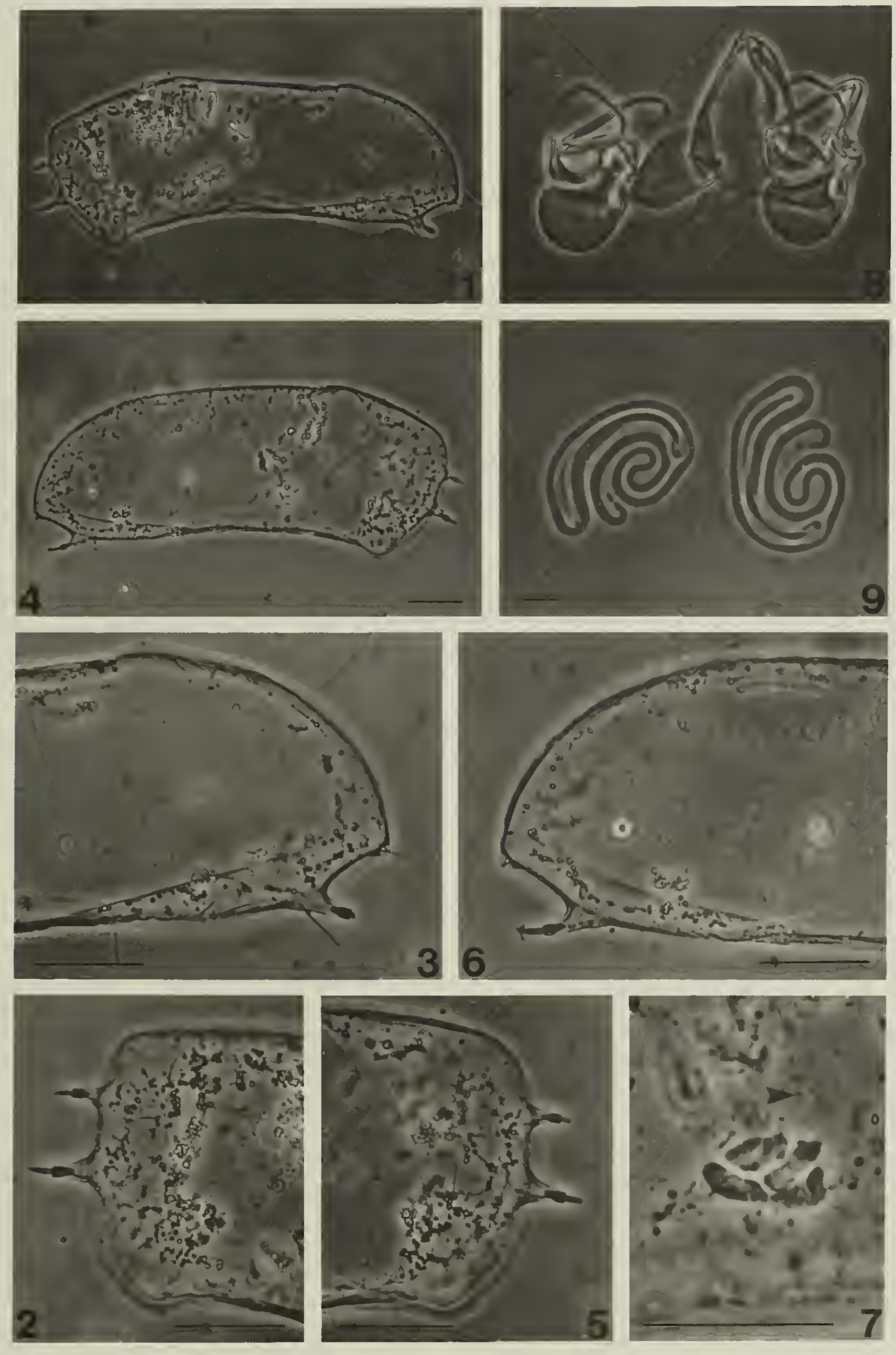

Fig. 4. *Pussella fijiensis,* new species. Male (holotype: NSMT-Cr11413). 1. internal view of right valve; 2. idem, anterior part; 3. idem, posterior part; 4. internal view of left valve; 5. idem, anterior part; 6. idem, posterior part; 7. adductor muscle scar (left); 8. furca and copulatory appendage; 9. testes. Each bar represents 0.05 mm.

short teeth. Two long mouthward directed setae present. Respiratory plate with about ten setae.

First walking leg (Fig. 3-7) four-segmented; first segment with two long ventral setae of equal length, arising from a process on the middle of the ventral margin, and a long dorsodistal seta; third segment with a short subterminal seta on the anterior margin; distal claw strong; length ratio of first to fourth segments and distal claw 8.75:10: 8.75:1:10.75. Second walking leg (Fig. 3-8) more slender than first leg; first segment with a long ventral seta; second segment with a thin seta on the anterodistal edge; third segment with a short seta on the anterodistal edge; length ratio of first to fourth segments and distal claw 12.3:10:10.7:1:19.3. Third walking leg (Fig. 3-9) similar to second walking leg; length ratio of first to fourth segments and distal claw 11.7:10:10.3:1:25.

Copulatory appendage (Fig. 3-10; Fig. 4-8). Each hemipenis consisting of a round basal lobe, clasping apparatus (hook-like process with beak-like tip and a long curved claw-like process), and long copulatory tube bending acutely at proximal third and coiling along distal third. Testis (Fig. 4-9) coiled, as shown in figure.

Furca (Fig. 3-10; Fig. 4-8) composed of two juxtaposed claw-like processes (shafts), terminating in a sharp point. A bristle is present between the two shafts.

Brush-shaped organ (Fig. 3-11) consisting of a pair of lobes, whose length is about twice as long as wide; each lobe with long filaments.

Lip (Fig. 3-4) with hairs along anterior margin. Oesophagal chewing apparatus (Fig. 3-12) present.

Remarks.—The genus *Pussella* has one fossil species: *P. infraturonica* Pokorny, 1989 from Lower Turonian (90 million years B.P.) of Bohemia, Czechoslovakia, and three living ones including the present new species: *P. botosaneanui* Danielopol, 1973 from Cuba, *P. danielopoli* Maddocks, 1976 from Bermuda, and *P. fijiensis* sp. nov. Danielopol & Wouters (1992) discussed the evolution of the interstitial ostracods based upon these fossil and recent pussellids and other interstitial species.

The present new species is discernible from *P. botosaneanui* and *P. danielopoli* in the shape of its carapace. As described above, *P. fijiensis* has two anterior and two posterior processes on both valves, but the latter two species have one anterior and one posterior processes and three anterior and three posterior processes. In this respect, the new species resembles *P. infraturonica,* but it is larger and more elongate than Turonian species (Pokorny 1989).

In the male of *P. botosaneanui,* the third endopodite segment of the first walking leg is fused with the distal claw, while that of *P. fijiensis* clearly separated from it. The copulatory appendage of *P. fijiensis* is much different from that of *P. botosaneanui* in the shape of the clasping apparatus and copulatory tube. The male of *P. danielopoli* is unknown.

As Maddocks (1976) pointed out, further research is needed in the tropical interstitial environments, since our knowledge of the members of the genus *Pussella* is still poor.

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ARCTODIAPTOMUS NOVOSIBIRICUS KIEFER, 1971 IN ALASKA AND NORTHWEST TERRITORIES, WITH NOTES ON *A. ARAPAHOENSIS* (DODDS, 1915) AND A KEY TO NEW WORLD SPECIES OF *ARCTODIAPTOMUS* (COPEPODA: CALANOIDA)

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Abstract.—Diaptomid copepods identified in North American literature as *Diaptomus bacillifer* Koelbel, 1885 lack the prominent process on the posterior surface of the second article of the exopodite of the male right fifth leg, which is recognized as a hallmark of *A. bacillifer* and its immediate allies. Of the currently recognized species of *Arctodiaptomus,* the so-called *bacillifer* most clearly resembles *A. novosibiricus* Kiefer, 1971 and may be that species. If so then *A. novosibiricus* is known from the New Siberian Islands, St. Paul Island, St. Matthew Island and the northern coast of Alaska; Victoria Island, Bernard Harbour and Adelaide Peninsula, N.W.T. Ecological circumstances suggest that future collecting may fill in gaps in the present discontinuous distribution. *A. arapahoensis* (Dodds, 1915) bears a great morphological similarity to *A. acutilobatus* (G. O. Sars, 1903). Presently *A. acutilobatus* is known from the Altai mountains, Caucasus and Kurdistan mountains. *A. arapahoensis* is known in the Rocky Mountains of Colorado, Montana, British Columbia and Alberta. Future collecting seems unlikely to erase the present discontinuous distribution; therefore it seems advisable to retain both names.

The best-conceived, best-illustrated and most complete keys for the identification of North American freshwater copepods are contained in the 2nd Edition of Ward & Whipple's Freshwater Biology (Edmondson 1959) (Reid 1990).

Keys become dated not only through the discovery of "new" species but through studies of "old" species that lead to new insights and corrections in nomenclature, presumed affiliations and distribution. Not infrequently the identity of the species remains fairly constant, while its presumed affiliation at the genus level undergoes one or more revisions.

Ideally keys would fulfill two functions: identification in a systematic manner and express phylogenetic relationships (Gurney 1931). For reasons discussed by Gurney, methodical routes to identification rarely satisfy the second function. One approach to methodical treatment is to reduce large and seemingly intractable groups to smaller, more manageable subgroups.

The genus *Diaptomus* Westwood, 1836 in the broad sense surely qualifies as a large group; Dussart & Defaye (1983) listed 406 species plus 15 incertae sedis and several subspecies. Kiefer (1932a, 1932b) attempted to find morphological groupings among the many named species of *Diaptomus*; in the latter paper he established a new subfamily, Diaptominae, in the family Diaptomidae G. O. Sars, 1903. In the Diaptominae, Kiefer place the genera *Diaptomus* Westwood, 1836, *Hemidiaptomus* G. O. Sars, 1903 and 10 new genera. In general non-North American copepodologists have accepted Kiefer's genera. Students of North American diaptomids, especially those making comprehensive or intensive regional investigations, have been inclined to view Kiefer's genera as subgenera of *Diaptomus* Westwood, 1836; for example, Light (1939), Wilson (1959), Smith & Fernando (1978a) and Williamson (1991). However many others including Torke (1979) and Boileau & Hebert (1988) have accepted Kiefer's genera. Light (1939) noted that while many species possessed definite specific characters, the range of morphological variation within the genus was not great.

Wilson (1959) noted that the genera proposed by Kiefer lack the morphological gaps characteristic of other calanoid genera and added that more precise diagnoses, evaluation and interpretation of variation and distribution of North American species are required before formally defining genera.

Sadly we are no nearer today to a comprehensive taxonomic treatment of North American diaptomids than we were in 1959. Part of the difficulty may be in deciding on what constitutes a genus gap; a second less obvious difficulty may be in attempting to assess ecological niches in anthropocentric rather than copepodocentric terms.

Fewer additions and corrections have occurred among the North American Calanoida since 1959 than among the Cyclopoida or Harpacticoida (Reid 1990). However there are reasons to reexamine the status of two diaptomids appearing in Wilson's 1959 key: *Diaptomus bacillifer* Koelbel, 1885 and *D. arapahoensis* Dodds, 1915.

I use Kiefer's *Arctodiaptomus* genus because the arctodiaptomids possess a set of morphological characters none of which alone is sufficient to constitute a gap but in concert they produce a fairly coherent morphological, if confusing ecological grouping.

Specimens were dissected and examined in glycerin or lactic acid. Insofar as possible, examinations and drawings were made without cover slips. Details were verified with oil immersion lenses.

Marsh (1920) identified as *Diaptomus bacillifer* Koelbel, 1885 some copepods collected 6 October 1915 from a pond one foot in depth on a ridge 100 feet above sea level at Bernard Harbour, N.W.T. (68°45'N, 114°44'W). Concerning these animals Marsh wrote (1920 p. 6j): "Up to the present time no species of *Diaptomus* found on the American continent has been considered identical with those of Europe or Asia. Therefore a good deal of care was used to make certain that the identification of this species was correct. The determination is based on the original description of Koelbel, 1884 (sic), supplanted by the later descriptions, especially those of Sars and Schmeil."

In the same paper, Marsh said that he had examined specimens of *D. bacillifer* from Saint Paul Island, Alaska (57°07'N, 170°17'W).

Marsh (1924) synonymized *Diaptomus arapahoensis* Dodds, 1915 with *D. bacillifer* Koelbel, 1885. Marsh (1929) reaffirmed this synonymy with the words "an examination of the description reveals that *D. arapahoensis* is *D. bacillifer.*"

Wilson (1953) stated that she had examined Marsh's specimens of *D. bacillifer* and found his identification to be correct. She, however, believed *D. arapahoensis* not to be conspecific with *D. bacillifer,* and treated them as two species (Wilson 1959).

Reed (1962, 1963) followed the lead of Marsh and Wilson and identified arctodiaptomids from Alaska and N.W.T. as *Diaptomus bacillifer.*

In 1956 while the late Mrs. Wilson was gathering specimens for a long-planned monograph on North American diaptomids (Damkaer 1988), I had the good fortune to work with her at the University of Saskatchewan for a short time. Wilson was completely aware that some European copepodologists were questioning Marsh's (1920) records of *Diaptomus bacillifer.* First, the press of larger, more demanding taxonomic problems, then ill health which cut short the proposed monograph (Damkaer 1988) prevented Wilson from fully dealing with questions surrounding the identity of North American *D. bacillifer.*

Kiefer (1971) provided a complete review of taxonomy of the Arctodiaptomi; it is necessary here to recount only the portions which impinge directly on North American forms.

In 1885 Koelbel described and named *Diaptomus bacillifer* from specimens collected in Plattensee, Hungary. Also in that year Imhoff named *Diaptomus alpinus* from an alpine lake in Berner Oberland (Kiefer 1971).

Schmeil (1893) noted only one absolute difference between *bacillifer* and *alpinus,* the presence of a "Cuticularvorsprung am zweiten Aussenastsegments des richten mannlichen Greiffusses" of *D. bacillifer* (Kiefer 1971 p. 127). Schmeil did not believe that the "Cuticularvorsprung" was sufficient to differentiate *alpinus* and *bacillifer* as species and synonymized *alpinus* with *bacillifer,* thus placing his not inconsiderable prestige behind Koelbel's species.

Schmeil's decision had far-reaching effects. For more than the next half century the works of many prominent copepodologists would show the influence of Schmeil, including Giesbrecht and Schmeil (1898), Sars (1898, 1903b), Marsh in several papers, Damian-Georgescu (1966) and Dussart (1967) among others.

Kiefer (1932b) placed *D. bacillifer* in one of his new genera, *Arctodiaptomus,* and perhaps under the influence of Schmeil and others, omitted mention of *D. alpinus.* By the late 1960's the nomenclature of *Arctodiaptomus* had become so confused, particularly in regard to *bacillifer* and *alpinus,* that Kiefer (1971) undertook a revision of the genus.

Arctodiaptomus novosibiricus Kiefer, 1971
Fig. 1

Specimens examined.—Northwest Territories.—Victoria Island: Lady Franklin Point, 22 Aug 1957, Cambridge Bay (69°03′N 104°05′W) 3 tundra ponds, 16 & 17 Sep 1957; Bernard Harbour: (68°44′N 114°27′W) little tundra pond, 20 Aug 1957; Adelaide Peninsula: shallow lake, 3 Sep 1957 (68°09′N 97°45′W). Alaska.—Near junction of Kikiakrorak and Colville rivers: (70°01′N 151°36′W), small tundra pond, 4 Aug 1955; Oliktok Point: (70°32′N 150°30′W), 3 tundra ponds, 24 & 25 Aug 1955; Point Barrow: (71°33′N 156°30′W), 3 tundra ponds, several dates 1963–64; Saint Matthews Island: (60°30′N 172°45′W), tundra ponds.

Description.—Most of the following description is based on Point Barrow specimens and checked against specimens from other localities.

Length without caudal setae: Most females ranged between 1.4 and 1.6 mm, one female from Adelaide Peninsula measured 1.8 mm. Males ranged between 1.2 and 1.45 mm.

Female: Body widest at mid-prosome (Fig. 1a). Pedigers 4 and 5 not divided dorsally, laterally a small furrow marks their joining (Fig. 1b). Posterior lateral margins pediger 5 moderately produced with lateral and dorsal sensilla. Genital segment little widened anteriorly, nearly symmetrical, lateral processes small, left with oblique postero-laterally directed sensillum, that of right projecting laterally (Fig. 1a), genital segment nearly as long as 2 succeeding segments and ramus combined. Urosome 2-segmented. Caudal rami about twice as long as wide, hairs on medial and lateral margins. Antennule extending to mid-genital segment (Fig. 1a); with 2 setae on articles 11 and 13, 1 on articles 14–19, seta on article 1 long, reaching beyond distal margin of article 5 (Fig. 1c). Rostrum small, pointed (ca. 25 μm) (Fig. 1d). Lappet (Schmeil's organ) present on posterior surface of second article of endopodite leg 2 (Fig. 1e). Leg 5: posteriorly basipodite 1 extending over proximal end of basipodite 2; basipodite 2 with lateral seta near distal margin (Fig. 1f); exopodite 1 about 2.5 to 3 times longer than wide; exopodite 2 seta well developed, claw with spinules on outer margin; exopodite 3, separated, setae strong, inner about twice as long as outer, endopodite of 2 articles, but dividing suture not always distinct, terminating in truncate margin, no setae, subapical row of hairs (Fig. 1f).

Male: Smaller, body shape similar to female. Rostral points short (ca. 25 μm), rounded, usual protrusion on right margin (Fig. 1g). Antennule: left similar to female in setation, except seta on article 1 short. Right antennule short spine on article 8, moderately long slender spines on articles 10 and 11, very small spine on article 12, short heavy spine on article 13 (Fig. 1h), seta on article 12 occasionally spine-like (Fig. 1i). Process of antepenultimate article long, straight, tip often slightly thickened (Fig. 1j), extending at least to mid-length of ultimate article. Lappet of leg 2 similar to that of female but smaller. Leg 5 left; basipodite 1 lacks process but may overhang proximal margin of basipodite 2 (Fig. 1k); basipodite 2 inner margin with thin, flexible, cuticular process (Fig. 1k) extending from mid-segment to mid-exopodite 1; exopodite terminal article with long, blunt fingerform outer process and curved, sharply pointed spine-like inner seta with spinules; proximal pad relatively small, hairy (Fig. 1l), endopodite 1- or 2-segmented, rounded, blunt tip, about equal to exopodite 1 in length, few small hairs. Leg 5 right: basipodite 1 with prominent process and sensillum (Fig. 1k, 1m) basipodite 2 with prominent semicircular or elongate oval process on posterior surface (Fig. 1m), rounded process on proximal inner margin; flap-like cuticular membrane extending along middle ⅓ to ½ of inner margin; exopodite 1 projecting distally over exopodite 2 at outer margin, small prominences on posterior distal margin; exopodite 2 about twice as long as wide; lateral spine straight, about 1.3 times article width, inserted at distal ¼ of article, usually small cuticular process near base of spine; claw long, slender, recurved near tip. Endopodite 1- or 2-segmented, widened and rounded on outer proximal margin, terminating in rounded and slanted tip bearing a sharp point on inner margin (Fig. 1n).

The Point Barrow specimens belong to the genus *Arctodiaptomus* as characterized in the key of Kiefer (1978) on the basis of these morphological features: 1) configuration of the terminal processes of the exopodite of male left fifth leg, 2) endopodite of female leg 5 armed only with a row of hairs, 3) two setae on article 11 of female and male left antennules and 4) spine of article 13 male right antennule not enlarged, spines of articles 10 and 11 strong, process of antepenultimate article straight.

Comparison.—Inexplicably, Marsh (1920) overlooked the prominent process on the posterior surface of basipodite article 2 of the male right fifth leg exopodite. This process is clearly visible in lateral view of the intact specimen (Fig. 1m). Cover slip pressure on a dissected leg five may cause the protrusion of basipodite article 1 to flatten, obscuring the process of article 2.

Marsh's (1920) description and drawings do not mention or show a cuticular process on the second segment of the male right exopodite leg five. Notes in the Marsh Collection at the National Museum of Natural History, Smithsonian Institution reveal that Marsh compared descriptions and drawings of several authors in regard to this process. Perhaps the most telling is this note in respect to the Canadian Arctic Expedition specimens: "Differs from Giesbrecht's analysis only in 2nd seg rt exop having no [cuticular-vorsprung]." Since Schmeil had already accepted the presence or absence of the "Vorsprung" as less than specific value, Marsh did not think it worth mentioning in his account of North American *bacillifer.*

The Point Barrow males resemble males of *A. alpinus* in lacking a process on the posterior surface of the right second exopodite article, but differ in minor respects of the right antennule.

The Point Barrow females are similar to some other arctodiaptomid females in se-

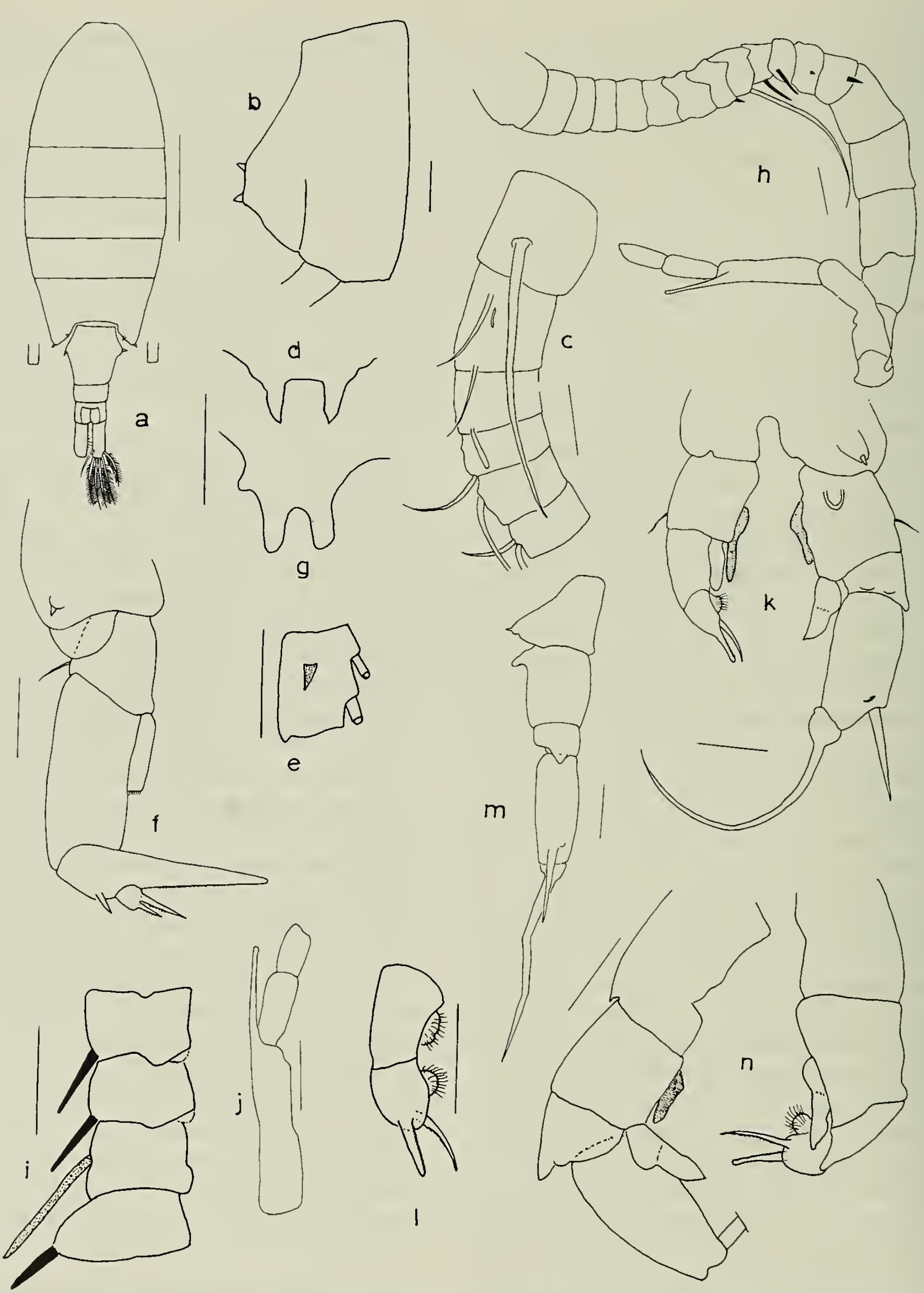

Fig. 1. *Arctodiaptomus novosibiricus.* Female: a, habitus; b, pedigers 4 and 5, lateral view; c, antennule articles 1–6; d, rostrum; e, Schmeil's organ; f, leg 5. Male: g, rostrum; h, right antennule; i, spines on right antennule articles 10–13; j, last three articles, right antennule; k, fifth legs, posterior view; l, exopodite left leg 5; m, right exopodite, lateral view; n, fifth legs, anterior view. Scale: a, 400 μm, all other bars 50 μm.

Table 1.—Subgeneric classification (A, H, R) number of setae ( ) on articles 11, 13, 15 of female and male left antennule and presence (+) or absence (−) of process on posterior surface of 2nd article, right exopodite, male leg 5 of some *Arctodiaptomus* species. Data from Kiefer (1971).

11 (1)	11 (2)	11 (2), 13 (2)	11 (2), 13 (2), 15 (2)
kurilensis Kiefer, 1937 H +	*byzantinus* (Mann, 1940) A −	*alpinus* (Imhoff, 1885) R −	*acutilobatus* (G. O.. Sars, 1903) R
parvispineus Kiefer, 1935 H ?	*burduricus* Kiefer, 1939 R −	*bacillifer* (Koelbel, 1885) R +	*centetes* (Brehm, 1938) R +
nepalensis Ueno, 1966 H ?	*dentifer* (Smirnov, 1928) A +	*laticeps* (G. O. Sars, 1863) A −	*similis* (Baird, 1859) A +
	dudichi (Kiefer, 1932) A −	*niethammeri* (Mann, 1940) R −	*arapahoensis* (Dodds, 1915) R
saltillinus (Brewer, 1898) (A) +	*kerkyrensis* (Pesta, 1935) A +	*novosibericus* Kiefer, 1971 R −	
floridanus (Marsh, 1926) (A) +	*pectinicornis* (Wierzejski, 1887) A −	*piliger* (Brehm, 1955) A −	
dorsalis (Marsh, 1907) (A) +	*salinus* (Daday, 1885) R −	*osmanus* Kiefer, 1974 A ?	
asymmetricus (Marsh, 1907) (A) +	*spinosus* (Daday, 1891) R −		
	steindachneri (Richard, 1897) A +		
	stephanidesi (Pesta, 1935) A −		
	wierzejski (Richard, 1885) A −		
	arapahoensis (Dodds, 1915) R +		
	acutilobatus (G. O. Sars, 1903) R +		

Subgenera: A, *Arctodiaptomus* s. str.; H, *Haplodiaptomus*; R, *Rhabdodiaptomus*.

tation of articles 11 and 13 (Table 1) and in possessing a lateral furrow between the fourth and fifth thoracic segments. The rostrum of female *bacillifer* is long (40–50 μm); whereas those of *alpinus, laticeps* and *novosibiricus* are short (20–25 μm).

Sars (1898) identified the New Siberian diaptomids as *D. bacillifer* Koelbel. Sars' description of the New Siberian specimens is sketchy but his figures clearly show no process on the posterior surface of the second article of the male right fifth leg. Sars (1898:332) stated: "This (*D. bacillifer*) is one of the most characteristic Copepoda of the territory, occurring in great abundance as far north as the Expedition has reached." Sars also stated (1898:333): "This species is also recorded by Prof. Lilljeborg from Nordenskjolds Expedition, as occurring at Inserowa on the Siberian continent." In the synonymy of *D. bacillifer,* Sars listed "*D. retusus,* Lilljeb. Ms." Perhaps Lilljeborg's *D. retusus* name was never published; neither Kiefer (1971, 1978) nor Dussart and Defaye (1983) mention a *D. retusus.*

The lack of the process on the posterior surface of article 2, male right exopodite fifth leg led Kiefer (1971) to reject Sars' identification as *D. bacillifer* for the New Siberian specimens. He placed them in the *A. alpinus* group and named them *A. novosibiricus.* Apparently no specimens of *novosibiricus* from Siberia have come to hand since Sars' (1898) collections. Borutskyi et al. (1991) in their review of freshwater calanoids of U.S.S.R. and discussion of *A. no-*

vosibiricus list only the island of Lachovski, one of the New Siberian Islands from whence Sars' specimens came.

The couplet which distinguishes male *novosibiricus* from male *alpinus* in Kiefer's (1971) key reads:

> Seitendorn des 2 Aussenastgliedes rechts insertiert nahe der Basis der Endklaue (Abb. 41); Fortsatz des drittletzten Gliedes des Greifantenne sehr lang und zugespitzt (Abb. 41) .... *novosibiricus*
> Seitendorn sitzt etwa im 2 Drittel des Aussenrandes (Abb. 28–30); Fortsatz des drittletzten Gliedes der Greifantenne wie (Abb. 16a, 22, 25, 26, 28–30, 37–39) .... *alpinus*

The females of *A. alpinus* and *A. novosibiricus* fall out together in Kiefer's (1971) key.

In Kiefer's (1978) key males of *A. novosibiricus* are separated from males of *A. alpinus* by the length of the process on the antepenultimate article of the right antennule: that of *alpinus* being at most as long as the following segment or usually shorter and that of *novosibiricus* at least as long as the following segment or much longer.

Again in the key to females, *alpinus* and *novosibiricus* fall out together along with *A. laticeps.* Male *A. laticeps* are quite different from males of *novosibiricus* and *alpinus* in several characters.

If one accepts Kiefer's (1971) revision of the Arctodiaptomi, then the lack of a process on the posterior surface of the second article of the male fifth right exopodite is a strong argument to reject Marsh's designation of *D. bacillifer* for the Canadian Arctic Expedition specimens and by extension for the present animals. The morphological differences between *alpinus* and *novosibiricus* are not great and ultimately they may be shown to be conspecific. For the time being the least objectionable course is to designate the North American form as *A. novosibiricus* Kiefer, 1971, partly on morphological evidence and partly on distributional and ecological considerations.

Sars (1898) provided no ecological data for *A. novosibiricus* collected on the New Siberian Islands. In North America, *A. novosibiricus* is an inhabitant of small and shallow ponds. The Point Barrow specimens came from tundra ponds less than 250 m^2 in area, that varied in depth through the summer from 15 to 51 cm (Kalff 1967). The Adelaide Peninsula pond was about 6 ha, but less than 1 m deep. A polygon pond containing *A. novosibiricus* at Kikiakroarak was about 40 m^2 in area and 10 cm in depth.

Arctodiaptomus arapahoensis
(Dodds, 1915)
Fig. 2

Specimens examined.—Colorado.—Larimer County: East (3295 m) and West Rainbow lakes, Rawah Wilderness Area; Jackson County: Lower Slide Lake; Hinsdale County: Emerald Lake (3112 m); San Juan County: Silverking, Ice (3752 m), Fuller (3843 m) lakes; Pitkin-Lake counties: alpine tundra ponds, Independence Pass (3689 m).

Description.—Most of the following description and drawings are based on East Rainbow and Silverking specimens and checked against specimens from other localities.

Female: Dodds (1915) gave the lengths of females that he examined as from 1.6 to 2.1 mm and lengths of males between 1.35 and 1.7 mm. Sixteen females from East Rainbow Lake ranged between 1.46 and 1.75 mm, mean 1.53; 28 males ranged between 1.32 and 1.48, mean 1.41 mm.

Wings of last prosome segment produced posteriorly past level of sensilla on genital segment (Fig. 2a). Reflexed antennules extend to midlength of genital segment, which is essentially symmetrical, about 1.1 times longer than greatest width, sensilla directed postero-laterally. Urosome segments 2 & 3 combined about equal to length of genital segment. Rami haired on inner margins.

Rostrum well developed, about 100 μm

Fig. 2. *Arctodiaptomus arapahoensis.* Female: a, pediger 5 and urosome; b, rostrum; c, antennule segments 1–8; d, Schmeil's organ; e, leg 5. Male: f, rostrum; g, right antennule, spines on articles 8–13; h, last three articles, right antennule; i, right exopodite leg 5, lateral view; j, fifth legs, posterior view; k, fifth legs, anterior view; l, terminal articles, left exopodite; m, right endopodite. Scale: a, 400 μm, all other bars 50 ≫.

in length (Fig. 2b). Seta of first segment of antennule about 260 μm long, extending to midlength of article 7 (Fig. 2c). Antennule articles 9, 11, 13 and 15 with 2 setae each.

Second article of endopodite leg 2 bearing hyaline lappet (Schmeil's organ) (Fig. 2d).

Leg 5. Basipodite 2 with small process bearing a short, moderately strong spine (Fig. 2e). Inner margin basipodite 2 much longer than outer margin. First article of exopodite long, slender, about 2 times as long as wide; claw of second article sinuous on inner margin, finely denticulate on outer. Article 3 of exopodite well developed, distinct from article 2, outer seta about twice the length of inner, both well developed and slightly spinulose. Endopodite of one article, end square bearing few hairs, with spine on inner corner.

Male: Rostrum smaller than that of female, tips 40 to 50 μm, right side with usual protuberance on margin (Fig. 2f). Left antennule articles 9 and 11 with 2 setae, one seta on articles 12–17. Right antennule, article 8 with short spine, spines of articles 10 and 11, moderately long, slender; spine of article 12 short, spine of article 13 moderate (Fig. 2g); antepenultimate article with long slender process extending nearly to distal end of last article (Fig. 2h).

Schmeil's organ smaller than that of female.

Right leg 5, basipodite article 1 with prominent posterior process; basipodite 2 with posteriorly directed process on posterior margin (Fig. 2i, k), flap of hyaline membrane mid-inner margin; exopodite article 1 produced into point on outer margin (Fig. 2i, k) exopodite article 2 with process on posterior face at midlength (Fig. 2i, k) small hyaline process near base of lateral spine; lateral spine stout, inserted at distal ⅓ of article and about equalling or exceeding article length. Claw long, curved, slender, finely denticulate, with recurved tip. Endopodite long, nearly reaching midlength of exopodite 2, apex oblique, acute.

Left leg (Fig. 2j, k), basipodite 2 with long, hyaline process on inner margin; digital process of terminal article of exopodite elongate, somewhat broadened, with roughened inner border (Fig. 2l); inner process a stout, spinulose spine (Fig. 2l). Endopodite 1 article, terminating in sharp tip.

Curiously Dodds (1915) failed to either mention or figure the prominent process on the posterior surface of the second basipodite of the exopodite of the right male fifth leg. *A. arapahoensis* bears an unmistakably clear morphological resemblance to *A. acutilobatus,* (G. O. Sars, 1903) (Sars 1903b). In 1953 when Wilson called attention to this resemblance, the setation of the antennules of *acutilobatus* was not known, and she believed more information was needed to decide conspecificity. Kiefer (1971) found the setation of *acutilobatus* to be exactly the same as that reported for *arapahoensis,* but perhaps for want of further information, took no stand on the conspecificity of *arapahoensis* and *acutilobatus.*

Arctodiaptomus arapahoensis is known from the Rocky Mountains of Colorado (Dodds 1915, Reed & Olive 1958, Wilson 1959), Montana (Wilson 1959) and British Columbia and Alberta (Anderson 1974). *Arctodiaptomus arapahoensis* has been most frequently found in lakes ranging from 1.4 to 150 ha and 2.5 to 34 m deep; however the Independence Pass record shows that it is capable of inhabiting smaller and shallower waters.

Kiefer (1971) listed *A. acutilobatus* from the Altai mountains, lakes and ponds in the Caucasus mountains from 1800 to 3200 m and the mountains of Kurdistan (Turkey). To these locations Kiefer (1978) added Mongolia and "Mundungsgebiet der Samara."

In spite of the morphological congruity of Colorado specimens with Kiefer's figures and descriptions of *A. acutilobatus,* it is my opinion that Dodd's name *arapahoensis* should be retained for the North American form on distributional considerations.

Discussion

The morphological similarity of *A. novosibiricus* to an arctodiaptomid occurring along the northern coast of North America and that of *A. acutilobatus* and *A. arapahoensis,* at least in the characters used, is unquestioned. In the understanding of present day biological species, morphological similarity or lack thereof is not a sure guide to conspecificity or species distinctness. In addition to external morphology, ecological, physiological, behavioral, and most of all, information on reproductive compatibility must be evaluated in answering questions concerning conspecificity. Breeding experiments, chromosomal studies, allozyme analyses, electrophoresis and other biochemical techniques have supported distinctness of species initially based on minor morphological differences (Boileau & Hebert 1988). In some instances of morphological differences, conspecificity has been established by chromosomal techniques (Einsle 1963). In still other instances reproductive isolation has been shown in species that could not be differentiated morphologically (Price 1958, Boileau 1991).

A decision regarding the designation of North American arctodiaptomids requires a presently unverifiable assumption regarding reproductive status. The data which would shed light on their standings as biological species are not available, nor are they likely to be available soon. A comparative study requiring live specimens would be useful. However, for practical reasons, the probability of such a study actually happening must be vanishingly small.

The North American populations of *A. arapahoensis* and Eastern Hemisphere populations of *A. acutilobatus* if reproductively isolated could represent two or more sibling species; if not reproductively isolated, then one species and possibly several subspecies.

We are still learning about gene flow between widely separated and nearby populations. *A. acutilobatus* and *A. arapahoensis* seem to occur in mountainous areas that are separated from each other by broad steppes, prairies, deserts and a broad expanse of ocean. Future collecting will almost certainly increase the number of waters known to contain these species in their respective mountainous areas but seems unlikely to produce populations in the vast areas separating the mountainous regions. Allopatry on the scale shown by *acutilobatus* and *arapahoensis* generally hints at different species rather than discontinuous distribution of one species. Hence my opinion that both be retained as species pending information on reproductive compatibility.

It is not known if *A. novosibiricus* from the new Siberian Islands would in fact produce viable offspring with Point Barrow or Bernard Harbour copepods. The few ecological data available suggest that they may occupy similar habitats.

The Siberian coastal regions north of the tree line contain very numerous bodies of water which range greatly in extent and depth (Zhadin & Gerd 1961). Black & Barksdale (1949) estimated that areas on the Alaskan Coastal Plain are 20 to 90 percent covered by water. Holmquist (1975) emphasized not only the number of ponds and lakes along the North American northwestern coast, but also the diversity of ecological conditions in them. Because of the similarity of terrain along the Arctic coasts of Siberia and North America, future collecting of copepods seems likely to fill in spaces between the presently known populations, thus reducing the discontinuity of distribution, and the likelihood of reproductive isolation.

Kiefer's 1971 study clearly illustrated the overall great similarity of many *Arctodiaptomus* species and simultaneously illustrated variation in morphological characters and combinations of characters. His study also underlines the importance of examining both sexes before reaching conclusions about identity. Females that are virtually specifically indistinguishable may belong with males that are clearly separable and *vice versa.*

In establishing subgenera of *Arctodiaptomus* Kiefer relied heavily on the form of the process of the third from last article of the male right antennule and on the 14th article of the antennule, as well as characters of the 5th pair of legs.

Which of the morphological characters are chosen for emphasis will greatly influence the species groupings within the Arctodiaptomi. Kiefer's emphasis on male right antennules led to grouping together forms which have quite different patterns of antennular setation. Grouping by antennular setation leads to mixing together species with other different morphological characters. At least four patterns of setation on the female antennules and male left antennule are known in the genus *Arctodiaptomus* (Table 1). The presence or absence of a process on the posterior surface of the second exopodite article of the male right leg 5 does not seem to bear a consistent relationship to antennular setation.

Key to New World species of *Arctodiaptomus*

1a. One seta on article 11 of ♂ left and both ♀ antennules 4

1b. Two setae on article 11 2

2a. Two setae on article 11, one seta 13–17 .... ♂ *A. arapahoensis* (Dodds, 1915)

2b. Two setae on article 13, one or two on articles 13–17 3

3a. Two setae on 13, one on article 15 .... *A. novosibiricus* Kiefer, 1971

– New Siberian Islands, Alaska, Northwest Territories

3b. Two setae on articles 13 and 15 . .... ♀ *A. arapahoensis* (Dodds, 1915)

– Colorado, Montana, British Columbia, Alberta

4a. Genital segment: ♀, right side produced into a large lateral lobe distal to usual process bearing sensillum. Leg 5 ♂ right exopodite 2, lateral spine thick, less than length of article .... *A. symmetricus* (Marsh, 1907)

– Cuba Marsh (1907)

4b. Genital segment ♀, large distal lobe lacking. Leg 5 ♂ exopodite 2, length of lateral spine about equal to or greater than that of article 5

5a. Leg 5 ♀, endopodite as long or nearly as long as exopodite 1, ♀ pediger 4, usually with single, double or triple medial dorsal process. Leg 5 ♂, right exopodite 2, lateral spine inserted proximal to mid-length of article, longer than article; left basipodite 2, width and length about equal .... *A. dorsalis* (Marsh, 1907)

– Arizona (Cole 1961), Louisiana (Marsh 1907), Mississippi (Harris 1978), Oklahoma (Robertson 1970), Cuba (Smith & Fernando 1978b), Haiti (Kiefer 1936) as *D. proximus,* Costa Rica (Collado et al. 1984), Mexico (Suárez 1991), Colombia (unpub. Suárez & Reid 1992), Nicaragua (Herbst 1960) as *D. alter,* Venezuela (González 1968) as *D. proximus.*

5b. Leg 5 ♀, endopodite ½ to ¾ length of inner margin exopodite 1; ♀ pediger 4, with or without dorsal medial process. Leg 5 ♂, right exopodite 2 lateral spine inserted at mid-length or distally, spine length about equal to article length; left basipodite 2 longer than wide ... 6

6a. Right metasomal wing ♀ produced outward beyond lateral margin of body (dorsal view). Leg 5 ♂, right exopodite greatly exceeding length of inner margin exopodite 1, lateral spine exopodite 2 inserted at mid-length of article. Right antennule ♂, antepenultimate article without process .... *A. kurilensis* Kiefer, 1937

– Kurile Islands (Kiefer 1937), Aleutian Islands (Wilson 1959)

6b. Right metasomal wing ♀ not protruding beyond lateral margin of body. Leg 5 ♂ right exopodite, lateral spine inserted near distal end of article; right endopodite little if any longer than inner margin of exopodite 1. Right antennule ♂, antepenultimate article with curved distal process 7

7a. Caudal ramus ♀, usually with hairs on inner margin only, pediger 4 with or without dorsal medial process. Leg 5 ♀, claw of exopodite 2 about as long as exopodite 1. Leg 5 ♂, basipodite 2 with small hyaline process on inner margin .... *A. saltillinus* (Brewer, 1898)

– Nebraska (Brewer 1898), Oklahoma (Robertson 1970), Texas (Wilson 1953).

7b. Caudal ramus ♀, Usually with hairs on inner and outer margins. ♀ pediger 4 with or without dorsal medial process. Leg 5 ♀, claw of exopodite 2 much shorter than exopodite 1. Leg 5 ♂, basipodite 2 lacking inner hyaline process ... .*A. floridanus* (Marsh, 1926)

– Florida (Marsh 1926), Georgia (Humes 1950) as *D. albuquerquensis* det. by Wilson (1953), Oklahoma (questionable record by Keeton 1959); discussed by Robertson (1970).

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OBSERVATIONS ON THE GENUS *MYSIDOPSIS* SARS, 1864 WITH THE DESIGNATION OF A NEW GENUS, *AMERICAMYSIS*, AND THE DESCRIPTIONS OF *AMERICAMYSIS ALLENI* AND *A. STUCKI* (PERACARIDA: MYSIDACEA: MYSIDAE), FROM THE GULF OF MEXICO

W. Wayne Price, Richard W. Heard, and Lidia Stuck

Abstract.—Americamysis, a new genus, is proposed to receive six American species: *Mysidopsis bigelowi* Tattersall, 1926; *M. almyra* Bowman, 1964; *M. bahia* Molenock, 1969; *M. taironana* Brattegard, 1973; and two new species, *Americamysis alleni* and *A. stucki. Mysidopsis bigelowi* is designated as the type species of the new genus. *Americamysis* is defined by a combination of characters, most notably: the presence of two articles in the carpo-propodus of thoracic endopods 3–8; the absence of a terminal article on antennal scale; and the presence of less than eight ventrolateral spines on uropodal endopod, all of which are confined to the region of the statocyst. *Americamysis, Mysidopsis,* and its subgenera are distinguished from each other by a variety of characters, including the morphology of the mandibular palp, antennal scale, and telson. A complete systematic review may indicate that the genus *Mysidopsis sensu lato* is polyphyletic and represents three or more distinct genera. The new species, *Americamysis alleni* and *A. stucki,* which are both only known from the Gulf of Mexico, are most similar and apparently most closely related to *A. bigelowi.* They can be separated from each other, *A. bigelowi* and the other species of *Americamysis* by the setation of their telsons and second thoracic endopods. A diagnostic table and key for separating the species of *Americamysis* and related species of *Mysidopsis* is presented. The distribution of the species within *Americamysis* extends along the Atlantic coasts of the Americas from the northeastern United States to Colombia.

The genus *Mysidopsis* Sars, 1864 presently contains a heterogeneous group of 49 nominal species, demonstrating a wide size range and a variety of morphological characters (Băcescu 1968b, Brattegard 1969, Tattersall 1969, Băcescu & Gleye 1979, Mauchline 1980). Brattegard (1969) discussed the similarity of *Mysidopsis almyra, M. bahia,* and *M. bigelowi* and designated these three northwestern Atlantic species as the "*almyra* group." Later (1973), he described *M. taironana* from the Caribbean coast of Colombia and noted its affinities with this group.

Tattersall (1951), Clarke (1956), Stuck et al. (1979a, 1979b), Modlin (1982), Price (1982) and Price et al. (1986) reported *M. bigelowi* from the coastal and shelf waters of the northern Gulf of Mexico. Reexamination of the material used in these studies indicates the specimens identified as "*M. bigelowi*" actually represent two undescribed species within the "*almyra* group" and that *M. bigelowi sensu* Tattersall (1926) does not occur in the Gulf of Mexico. Based on Brattegard's observations and our examination of specimens of *M. almyra, M. bahia, M. bigelowi,* and the two undescribed species from the Gulf of Mexico, we now believe that the members of the "*almyra* group" represent a distinct genus, which is endemic to the Atlantic coastal regions of the Americas.

Americamysis, new genus

Diagnosis.—Thoracic endopod 1 composed of 4 articles, preischium and ischium fused; thoracic endopods 3–8 having carpopropodus with 2 articles; antennal scale lacking distal article and spinose tip; telson linguiform, midapical spine setae much (4 times) longer than lateral spine setae; uropodal endopod armed with 8 or fewer spines adjacent to statocyst or along inner margin.

Type species: *Americamysis bigelowi* (Tattersall, 1926), new combination.

Additional species: *A. almyra* (Bowman, 1964), new combination; *A. bahia* (Molenock, 1969), new combination; *A. taironana* (Brattegard, 1973), new combination; *A. alleni,* new species; and *A. stucki,* new species.

Remarks.—*Americamysis* appears to form a natural group containing six species, all of which seem to be confined to the northwestern Atlantic. The known species of this genus are endemic to estuarine and shallow shelf waters along the east coasts of the Americas from New England to Colombia.

The combination of a distally unarticulated antennal scale, a 2-articulate carpopropodus on the endopods of thoracic limbs 3–8, distinctly fewer articles in the exopod of the fourth male pleopod, and the presence of one or more mesial pairs of apical spine-setae on the telson distinguishes the genus *Americamysis* from the type species of *Mysidopsis, M. didelphys* (Norman, 1863).

Since Sars' (1885) generic diagnosis, the generic limits of *Mysidopsis* have been broadened, resulting in the inclusion of many apparently distantly related species. Among the characters given by Sars (1885) in his generic definition of *Mysidopsis* were (1) the presence of an apical or distal article on the antennal scale and (2) three articles in the carpo-propodus of thoracic endopods 3–8. The morphological limits were broadened by the description of *Mysidopsis acuta* Hansen, 1913, the first species assigned to the genus having an antennal scale terminating in an acute spinose process and lacking an apical suture. W. Tattersall (1926) further expanded the generic definition with the description of *M. bigelowi,* a species characterized by having two (instead of three) articles in the carpo-propodus of thoracic endopods 3–8. Like *M. acuta, M. bigelowi* has an antennal scale lacking a distal suture. Unlike *M. acuta,* however, the tip of *M. bigelowi*'s antennal scale is blunt with distal setae. Excluding *M. bigelowi* and the other species being assigned to *Americamysis,* there are now six nominal species of *Mysidopsis* that lack a distal article on the antennal scales (Hansen 1913, O. Tattersall 1962, Brattegard 1973, Brattegard 1974b, Gleye 1982, and Băcescu 1984).

In a synopsis of *Mysidopsis,* O. Tattersall (1969) erroneously stated in her rediagnosis of the genus that the carpo-propodus of thoracic endopods 3–8 "is divided by a transverse suture into two subsegments . . . ," which would exclude the type species and most of the other described species of the genus. She also considered the 4-articulate endopod of first thoracic appendages which was due to the fusion of the preischium and ischium, a unique character of the genus *Mysidopsis.* At present, however, there appear to be at least two other genera, *Metamysidopsis* W. Tattersall, 1951 and *Taphromysis* Banner, 1953 that have their first thoracic endopods composed of four articles as in *Mysidopsis,* instead of the five normally found in other genera of the family Mysidae (see Mauchline 1980). Based on the illustrations of Brattegard (1969, p. 62, fig. 18E) and Gleye (1982, fig. 1f), respectively, the genera *Brasilomysis* Băcescu, 1968 and *Cubanomysis* Băcescu, 1968 also may have 4-articulate first thoracic endopods. Brattegard's (1969) illustrations of *Brasilomysis castroi* Băcescu, 1968 were based on specimens from the Bahamas, while those for *Cubanomysis mysteriosa* Gleye, 1982 accompanied the original description based on specimens from California waters. Though not described in the text, the illustration (fig. 4C) for the only other nominal species of *Brasilomysis, B.* (=*Mysidopsis*) *inermis* Coifmann, 1937) indicates four articles in the first thoracic endopod. The generic status of *B. inermis* is still unsettled. Its original and only description was quite incomplete and the type material, which came from Pacific waters off Ecuador, appears to be no longer extant. The number of articles in the first limb of the type and remaining species of *Cubanomysis, C. jimenesi* Băcescu, 1968b, has not been reported or illustrated.

O. Tattersall (1969) treated 21 species of *Mysidopsis.* Since her work the number of described species has more than doubled to 49 (including the four species being placed in *Americamysis*). Of the 28 species added to the genus since O. Tattersall's synopsis, the majority (21) are from the western Atlantic (Băcescu 1968b, 1984; Brattegard 1969, 1973, 1974a, 1974b; Modlin 1987, Moleneck 1969, da Silva 1979, Hoffmeyer 1993, Ortiz & Lalana 1993). One of these, *M. cojimarensis* Ortiz & Lalana, 1993, may be synonymous with *Antromysis* (*Parvimysis*) *bahamensis* (Brattegard 1970); however, it is tentatively retained in the genus *Mysidopsis* pending a comparison of the types of these two species. The remaining seven species are from the coastal waters of East and West Africa, the Pacific coast of North America, and Japan (Murano 1970, Băcescu & Vasilescu 1973, Băcescu 1975, Băcescu & Gleye 1979, Gleye 1982, Wooldridge 1988).

The combination of a 2-articulate carpopropodus in thoracic endopods 3–8 and an antennal scale lacking a distal article distinguishes *Americamysis* from the heterogenous group of species tentatively retained within the genus *Mysidopsis.* Eight of these species, like the members of the genus *Americamysis,* have thoracic endopods 3–8 with a 2-articulate carpo-propodus, but their antennal scales have a terminal article. Five of these, *M. californica* W. Tattersall, 1932; *M. intii* Holmquist, 1957; *M. tortonesi* Băcescu, 1968b; *M. robustispina* Brattegard, 1969 and *M. ankeli* Brattegard, 1973, differ strikingly from both the type species (*M. didelphys*) and the species being referred to the genus *Americamysis* by the presence of numerous spine-setae or true spines (*M. ankeli, M. intii*) along the inner margin of the uropodal endopod. These species, which are known only from the Atlantic and Pacific waters of the Americas, appear to be more closely related to the genus *Americamysis* than to the genus *Mysidopsis.* We have temporarily retained them within *Mysidopsis* pending further systematic revision of the genus *sensu* O. Tattersall (1969). Because of the spiniform tip of their antennal scales, three of these species (*M. californica, M. robustispina, M. tortonesi*), along with *M. acuta* and *M. coelhoi* Băcescu, 1968b, were included in Brattegard's (1969) "*coelhoi* group."

Three other species of *Mysidopsis,* two from South Africa (*M. camelina* O. Tattersall, 1955 and *M. suedafricana* O. Tattersall, 1969) and one from the tropical northwestern Atlantic (*M. bispinulata* Brattegard, 1974a), also have thoracic endopods 3–8 with a 2-articulate carpo-propodus. However, in other respects these species are quite distinct from each other and are not apparently closely related to other species with similarly articulated thoracic endopods.

Based largely on the presence of highly modified mandibular palps and telson setation, Băcescu & Gleye (1979) created the two monotypic subgenera, *Mysidopsoides* and *Pseudomysidopsis,* to receive *Mysidopsis bispinosa* O. Tattersall, 1969 and *Mysidopsis camelina* O. Tattersall, 1955, respectively. Both of these subgenera are endemic to South Africa and may represent distinct genera.

In conclusion, based on our own observations and a review of the literature, we consider that the genus *Mysidopsis sensu lato* represents a polyphyletic melange of taxa. We believe that in addition to the "almyra" group (*Americamysis*), the other subgeneric groupings proposed by Brattegard (1969), the subgenera described by Băcescu & Gleye (1979), and other distinctive, "atypical" species or species groups (i.e., *M. angusta, M. acuta, M. ankeli-intii*) may be unrelated and may represent distinct genera. Except for members of the "almyra group", we have been unable to critically examine many of the other nominal species of *Mysidopsis,* especially those from European and African waters, belonging to these other subgeneric groupings or "atypical" species. Systematic studies of the heterogenous species or species complexes still accommodated within the genus *Mysidopsis* is needed. Such studies using the systematic tools of cladistics and molecular genetics will likely result in the removal of additional species from the genus.

Table 1 presents a listing of the nominal species currently retained within the genus *Mysidopsis* with information on their general distribution and distinctive characters for some of the atypical species or species groups. *Mysidopsis incisa* Sars, 1885, which has only been tentatively reported once (Thompson 1894) since its original description, is included. Its taxonomic status, however, remains uncertain. Eight species originally assigned to the genus, including four in this report, have been transferred to other genera. These are listed in Table 2 with their current generic designations.

Americamysis alleni, new species
Figs. 1–2

Mysidopsis bigelowi.—Tattersall 1951:139 (in part).—Price 1982:16 (in part), figs. 17, 20.—Price et al. 1986:49 (in part).

Type material.—Holotype: adult male (USNM 253072), length 5.1 mm, Biloxi Beach, Mississippi; Mississippi Sound (30°23.3′N, 88°58.5′W): depth 1 m, sand substratum, dredge net, David Hard (coll.), 27 Oct 1991.—Paratypes: 5 ♂, 5 ♀ (USNM 253073), 5♂, 5♀ (GCRL 1317), same collection data as for holotype.

Additional material examined.—Texas coast: 4 ♂ (6.3–7.3 mm), 4 ♀ (7.3–7.4), Lavaca Bay, station 1 (28°35.3′N, 96°31.7′W), depth 2.1 m, otter trawl, 4 Mar 1971.—6 ♂ (6.6–7.3 mm), 2 ♀ (6.9–7.4 mm), Lavaca Bay, station 7 (28°33.3′N, 96°28.5′W), depth 2.7 m, otter trawl, 5 Dec 1970, 2 Feb 1971.—6 ♂ (4.4–5.3), 2 ♀ (5.0–5.1 mm), West Bay, station WB6 (94°58.5′N, 29°15.8′W), depth 1.2 m, Oct 1973.—15 ♂ (5.3–6.0 mm) 15 ♀ (5.3–5.6 mm), West Bay, station WB2 (94°57.2′N, 29°14.5W), depth 1.5 m, Oct 1973.—15 ♂ (3.8–5.2), 15 ♀ (3.8–5.4 mm), West Bay, station WB4 (94°57.8′N, 29°15.0′W) depth 1.5 m, June 1973. West Bay specimens collected with epibenthic sled and all Texas material in collection of WWP.

Diagnosis.—Apex of antennal scale not pointed; endopod of thoracic leg 2 normally developed in both sexes, merus with 2–3 simple setae on inner proximal margin and 4 simple setae along outer margin; inner margin of carpo-propodus armed with 5–10, occasionally 4, spiniform setae; carpo-propodus of thoracic endopods 3–8 2-segmented; exopod of pleopod 4 of male 7-segmented; endopod of uropods armed with 3–4 (rarely 2 or 5) spine-setae near statocyst; apex of telson with 3 pairs of strong spine-setae, outermost pair ½–¾ length of inner pairs, innermost pair ⅓ or less length of telson and shorter than, or equal in length to, adjacent pair.

Description.—General body form (Fig. 1A): moderately slender, adult males to 7.3 mm and females to 7.4 mm; anterior margin of carapace produced between eyes into short, triangular rostrum; posterior dorsal margin emarginate, exposing thoracic segment 8; anterolateral corners rounded.

Antennular peduncle (Fig. 1B): more robust in males than females; segment 1 about as long as segments 2 and 3 combined, distomedial margin armed with 4–5 long and

Table 1.—Species presently included in the genus *Mysidopsis* by region. Distinctive characters of some species groups are presented.

	General location	Character*
Eastern Atlantic		
M. angusta Sars, 1864	North Europe, Western Mediterranean	(3)
M. (*Mysidopsoides*) *bispinosa* O. Tattersall, 1969	South Africa	(1, 5)
M. (*Pseudomysidopsis*) *camelina* W. Tattersall, 1955	South Africa	
M. didelphys (Norman, 1863): Type species	North Europe, Iceland, Western Mediterranean	
M. eremita W. Tattersall, 1962	South Africa	
M. gibbosa Sars, 1864	North Europe, Western Mediterranean	
M. major Zimmer, 1912	South Africa	
M. schultzei (Zimmer, 1912)	South Africa	
M. similis (Zimmer, 1912)	South Africa	
M. suedafrikana O. Tattersall, 1969	South Africa	(1)
Western Atlantic		
M. acuta Hansen, 1913	Argentina	(4)
M. ankeli Brattegard, 1973	Colombia	(1, 2)
M. arenosa Brattegard, 1974	Panama	
M. badius Modlin, 1987	Belize, Mexico	
M. bispinulata Brattegard, 1974	Colombia, Panama	(1, 5)
M. brattstroemi Brattegard, 1969	Bahamas, South Florida, Panama	
M. coelhoi Băcescu, 1968	Brazil	(4)
M. cojimarensis Ortiz & Lalana, 1993**	Cuba	
M. cultrata Brattegard, 1973	Colombia	
M. eclipis Brattegard, 1969	South Florida	
M. furca Bowman, 1957	Southeastern United States	
M. juniae da Silva, 1979	Brazil	
M. mathewsoni Brattegard, 1969	Bahamas	
M. mauchlinei Brattegard, 1974	Panama	
M. mortenseni W. Tattersall, 1951	Bahamas, South Florida, Caribbean	
M. rionegrensis Hoffmeyer, 1993	Argentina	
M. robusta Brattegard, 1974	Colombia	
M. robustispina Brattegard, 1969	Bahamas, Colombia	(1, 4)
M. sankarenkuttkyi Băcescu, 1984	Brazil	
M. tortonesei Băcescu, 1968	Brazil, Colombia	(1, 4)
M. velifera Brattegard, 1973	Caribbean	
M. virgulata Brattegard, 1974	Colombia	
Eastern Pacific		
M. acuta Hansen, 1913 sensu Holmquist (1957)	Chile	(4)
M. brattegardi Băcescu & Gleye, 1979	California	
M. californica W. Tattersall, 1932	California	(1, 4)
M. cathengelae Gleye, 1982	California	
M. intii Holmquist, 1957	Chile	(1, 2)
M. onofrensis Băcescu & Gleye, 1979	California	
Western Pacific		
M. japonica Ii, 1964	Japan	
M. surugae Murano, 1970	Japan	
M. incisa Sars, 1884 incertae sedis	Southern Australia	(3)
Indian Ocean		
M. buffaloensis Wooldredge, 1988	South Africa	
M. coralicola Băcescu, 1975	Tanzania	

Table 1.—Continued.

	General location	Character*
M. helvillensis Nouvel, 1964	Mozambique	
M. indica W. Tattersall, 1922	India	
M. kempi W. Tattersall, 1922	India	
M. kenyana Băcescu & Vasilesco, 1973	Kenya	

* Character codes: (1) 2-articulate carpo-propodus on thoracic endopods 3–8; (2) margin of uropodal endopod with serrate spines; (3) telson distinctly cleft; (4) antennal scale with acute, spinose tip; (5) lateral margins of telson lacking spine-setae.

** This species may be synonymous with *Antromysis* (*Parvimysis*) *bahamensis* (Brattegard, 1970).

2–3 shorter plumose setae, distolateral margin with 1 short and 4 long plumose setae; medial margin of segment 2 with strong simple spine and 5 plumose setae; segment 3 with 2 plumose setae along medial margin and 5–6 plumose setae distally, distal margin with dorsomedial lobe bearing 2 tooth-like processes and 2 plumose and 2–3 simple setae, 1 plumose and 1 simple seta grouped proximal to dorsomedial lobe, males with densely setose lobe on outer ventral surface.

Antenna (Fig. 1C): scale lanceolate, reaching beyond distal end of antennular peduncle, 5.5–6 times as long as maximum width, inner margin slightly convex, outer margin slightly concave, setose all around, lacking distal article; antennal peduncle extending about 0.6 length of scale, article 2 about 1⅔ times as long as 3, with 2–3 plumose setae on inner distal margin and 1 plumose seta on outer distal margin; article 3 with 2 plumose and 3 simple setae on inner distal margin and 2 plumose setae along outer margin; distolateral corner of sympod with prominent tooth.

Eyes (Fig. 1A): large, cornea wider than distal end of eyestalk, lacking ocular papilla.

Labrum (Fig. 1D): rounded anteriorly; posterior margin with medial emargination, middle ⅔ with fine setae.

Mandible (Fig. 1E): cutting edges typical of genus. Palp (Fig. 1F) 3-articulate, articles 2 and 3 more robust in males than females; article 2 armed with 10–14 submarginal simple setae along outer margin and 10–15 simple setae on inner margin, distal margin with 3–5 simple setae; article 3 about ½ as long as 2, inner surface with 3–4 marginal and 3–4 submarginal simple setae, distal portion armed with 1 long simple seta, 1 long curved spine-seta with medial barbs and 9 thick blunt densely barbed spine-setae, outer margin with 2 simple setae.

Maxillule (Fig. 1G): outer lobe with 9 stout, sparsely serrate apical spine-setae; in-

Table 2.—Nominal species of *Mysidopsis* transferred to other genera.

Original designation	Present generic designation	Reference
M. bigelowi W. Tattersall, 1927	*Americamysis*	Present study
M. almyra Bowman, 1964	*Americamysis*	Present study
M. bahia Molenock, 1969	*Americamysis*	Present study
M. taironana Brattegard, 1974	*Americamysis*	Present study
M. inermis Coifman, 1937	*Brasiliomysis*	Băcescu (1968)
M. elongata Holmes, 1900	*Metamysidopsis*	W. Tattersall (1951)
M. munda Zimmer, 1918	*Metamysidopsis*	W. Tattersall (1951)
M. pacifica Zimmer, 1918	*Metamysidopsis*	W. Tattersall (1951)

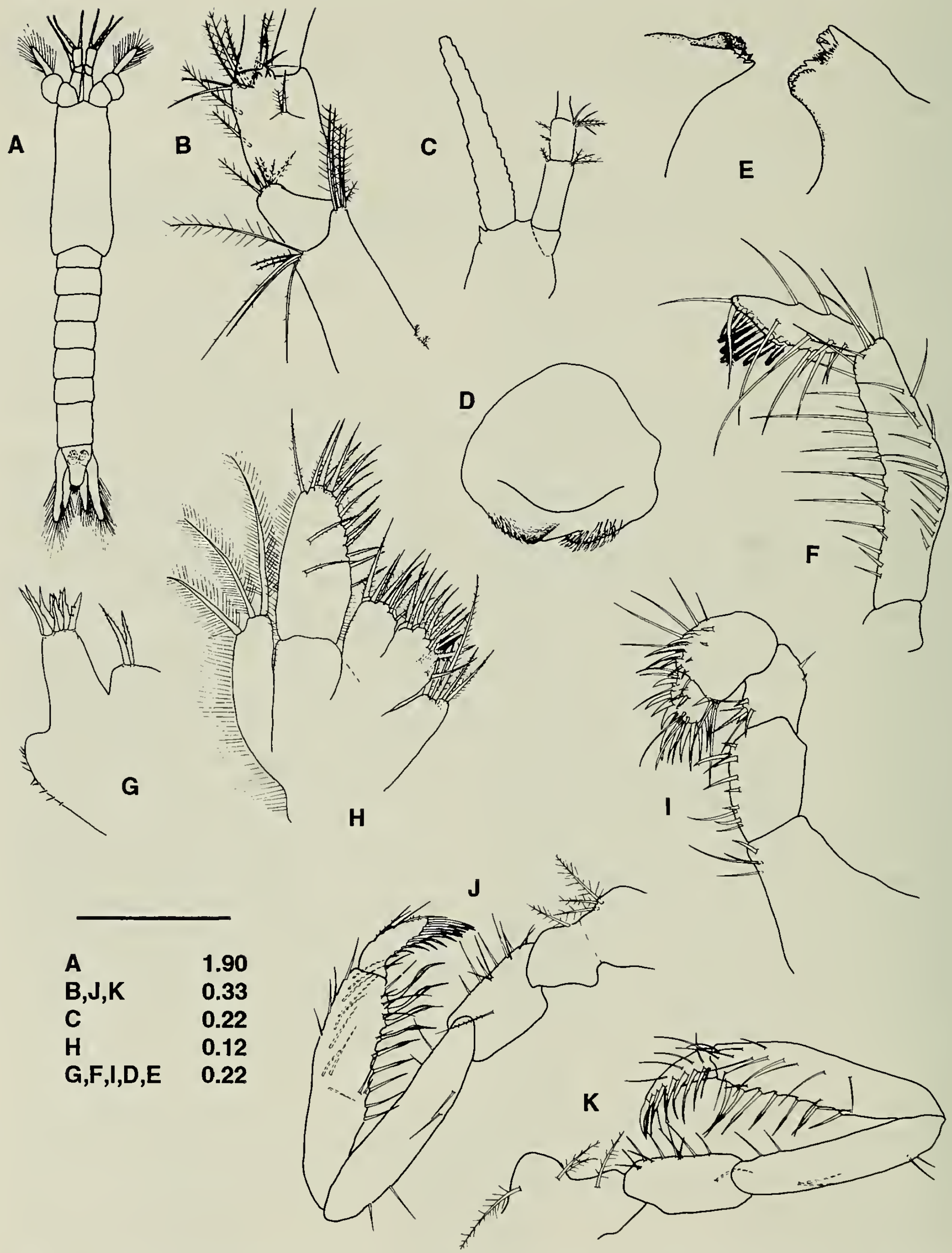

Fig. 1. *Americamysis alleni,* new species. A, adult female, dorsal view; B, antennular peduncle; C, antennal peduncle and scale; D, labrum; E, mandibles; F, mandibular palp; G, maxillule; H, maxilla; I, endopod, thoracic limb 1; J, K, endopod, thoracic limb 2, female, male, respectively. Scales in mm.

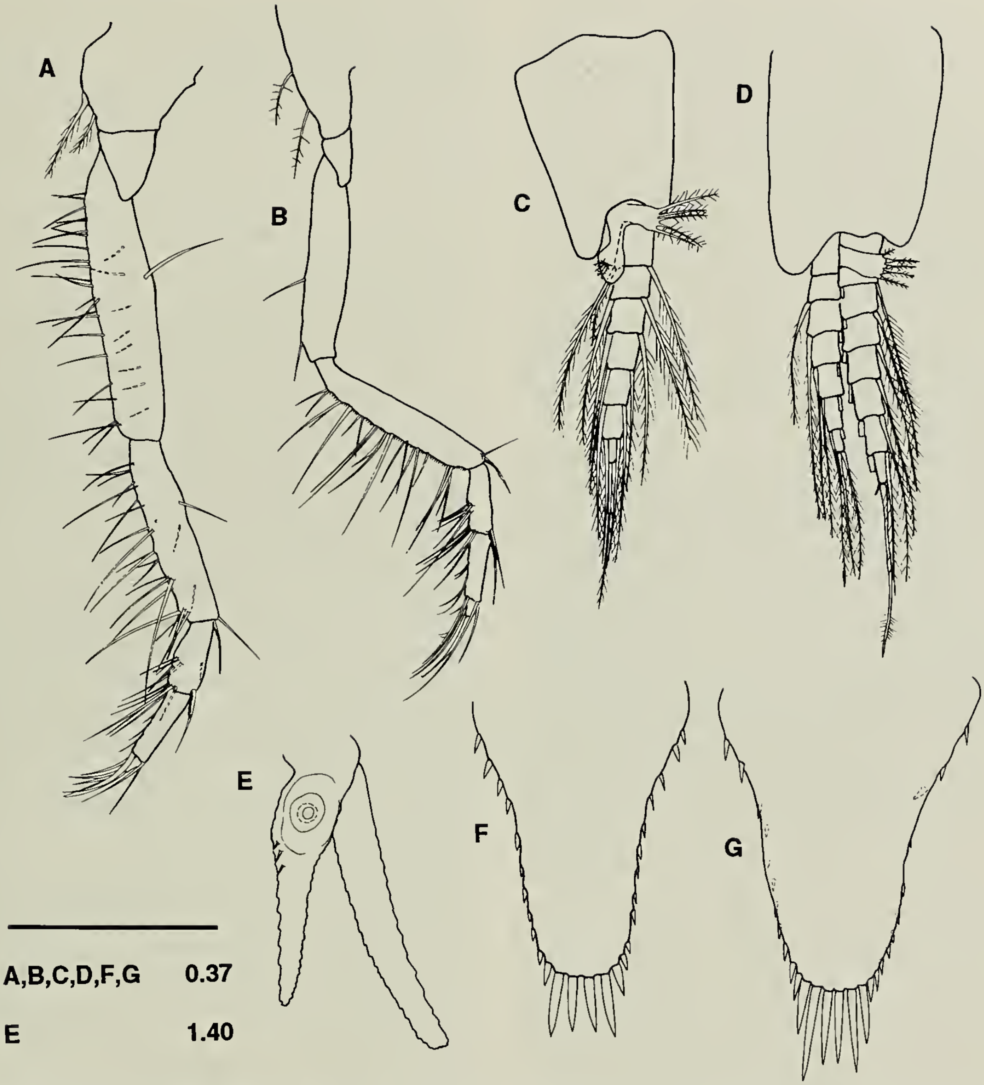

Fig. 2. *Americamysis alleni,* new species. A, endopod, thoracic limb 3; B, endopod, thoracic limb 8; C, male pleopod 1; D, male pleopod 4; E, uropod; F, G, telsons. Scales in mm.

ner lobe with 2 large serrate apical setae subequal in length.

Maxilla (Fig. 1H): typical of genus; exopod with 3–6 plumose setae; endopod 2-articulate, distal article armed with 2–3 submarginal and 16–24 plumose setae on apex and inner margin; lobe of sympodal article 2 with 5 plumose setae; sympodal article 3 bilobed, inner lobe with 10–15 plumose setae, outer lobe with 8–10 plumose setae.

Endopod of thoracic limb 1 (Fig. 1I): robust typical of genus; carpo-propodus twice length of dactyl, distal part with numerous simple setae and serrate spine-setae; dactyl wider than long with numerous simple setae, serrate spine-setae and a single large claw, slightly longer than dactyl.

Endopod of thoracic limb 2: (Fig. 1J, K): large and robust, more developed in females than in males; ischium about ½ length of merus with several simple setae on inner margin; merus subequal in length with carpo-propodus, with 2–3 simple setae on inner proximal margin, 4 simple setae along outer margin; carpo-propodus with 5–10, occasionally 4, flared spiniform setae and numerous simple setae on distal ½ to ⅔ of inner margin; dactyl ⅓ length of carpo-propodus armed with numerous curved, serrate spine-setae, simple setae and a serrate distal claw.

Endopod of thoracic limb 3 (Fig. 2A): basis with 2 plumose setae; ischium 1.5 times as long as merus, setose along inner margin; merus setose along inner margin with serrate seta and simple seta on outer distal margin; 2-segmented carpo-propodus slightly shorter than merus with segments subequal in length, proximal segment with 1 small submarginal serrate seta and 1 large serrate seta on outer distal margin; dactyl small with long, slightly curved claw on distal tip surrounded by several simple setae extending from distal margin of the carpo-propodus.

Endopod of thoracic limb 8 (Fig. 2B): basis with 2 plumose setae; ischium slightly longer than merus with 2 simple setae on distal part of inner margin; merus with many simple setae along inner margin and 1 serrate seta and 1 simple seta on outer distal margin; 2-articulated carpo-propodus 0.7 times length of merus with articles subequal in length, proximal article with 2 serrate setae on outer distal margin; dactyl with slender claw surrounded by several long, simple setae, extending from distal article of carpo-propodus.

Female pleopods reduced to setose uniramus plates.

Male pleopod 1 (Fig 2C): 1-articulated endopod with 1 plumose seta distally, 5 plumose setae proximally and pseudobranchial lobe furnished with 5 terminal plumose setae; 7-articulated exopod.

Male pleopods 2, 3, 5: exopods and endopods 7-segmented.

Male pleopod 4 (Fig. 2D): 7-articulated endopod with pseudobranchial lobe similar to first pleopod; 7-articulated exopod, slightly longer than endopod, setule on outer distal margin of article 7, with long barbed apical spine-setae as long as the 5 distal articles combined.

Uropods (Fig. 2E): exopod 1.3–1.4 times as long as endopod and 1.8–1.9 times as long as telson, outer margin concave, inner margin convex; endopod 1.3–1.4 times as long as telson, inner margin almost straight, outer margin concave, armed with 3–4, occasionally 2 or 5 spine-setae near statocyst; exopod and endopod setose along both inner and outer margins.

Telson (Fig. 2F, G): entire, linguiform, shorter than 6th abdominal segment, 1.4–1.5 times as long as maximum width, lateral margins concave and armed with 10–15 short, stout spine-setae; apex with 3 pairs of strong spine-setae, outermost pair ½–¾ length of inner pairs, innermost pair ⅓ or less length of telson and shorter than, or equal in length to, adjacent pair.

Coloration.—The following description is of preserved specimens collected in Mississippi Sound, Mississippi. Pairs of black chromatophore located dorsally at base of telson and ventrally at base of mandibles and thoracic legs 3 and 7. Posterior ventral margin of abdominal segments 1–5 with a single black chromatophore. Antennular peduncles mottled brown; male lobe with brown along distal and medial margins. Brown along distal margin of sympod of antenna and on distomedial margin of scale. Females with one chromatophore at base of each posterior oostegite.

Distribution.—Inshore and continental shelf waters in the northern Gulf of Mexico from Lavaca Bay, Texas to Mississippi Sound, Mississippi.

Habitat.—Hypoplanktonic in meso or polyhaline waters of bays and shallow continental shelf waters to a depth of 15 m.

Etymology.—This species is named for Dennis Allen in recognition of his contributions to our knowledge of the biology of mysids along the east coast of North America.

Americamysis stucki, new species
Figs. 3–4

Mysidopsis bigelowi, Brattegard 1969:53, fig. 15.—Farrell 1979:32, figs. 1, 2, 11e, f, g.—Stuck et al. 1979:235, figs. 2j, 3j, 4j, 5j.—Price 1982:16 (in part), figs. 18, 21.

Type material.—Holotype: adult ♂ (USNM 253074), length 5.2 mm, SEAMAP station 35056 (30°11.6′N, 88°11.2′W), continental shelf waters off Mississippi, 16 Oct 1981.—Paratypes: 3 ♂, 4 ♀ (USNM 253075), 5 ♂, 5 ♀ (GCRL 1316), same collection data as for holotype.

Additional material examined.—Continental shelf waters off Texas: 3 ♂ (4.4–5.2 mm), 4 ♀ (5.7–6.0 mm), NMFS St. 1 (29°22.5′N, 94°34.0′W), depth 8.2 m, 13 Jan 1969.—14 ♂ (4.3–6.4 mm) 18 ♀ (4.5–5.0 mm), NMFS St. 17 (28°42.4′N, 94°58.0′W), depth 19.2 m, 14 Jan 1969. West coast of Florida: 10 ♂ (3.8–4.6 mm), 10 ♀ (3.9–5.0 mm), Anclote Key St. 15 (28°11.1′N, 82°52.4′W), depth 3.2 m, 23 Jul 1982.—25 ♂ (3.5–5.1 mm), 25 ♀ (3.9–5.0 mm), Tampa Bay St. 9 (27°37.3′N, 82°35.3′W), depth 3.5 m, 15 Jun 1983.—10 ♂ (4.1–4.6 mm), 10 ♀ (4.0–5.2 mm), offshore St. 5 (27°38.8′N, 82°49.7′W), depth 7.6 m, 3 Oct 1981.—8 ♂ (3.6–4.8 mm), 8 ♀ (3.7–4.8 mm), Sarasota Bay St. 8 (27°20.2′N, 82°33.7′W), depth 3.7 m, 7 Jun 1982.—15 ♂ (3.7–4.1 mm) 15 ♀ (3.5–4.9 mm), Charlotte Harbor St. 34 (26°43.5′N, 82°15.4′W), depth 3.7 m, 8 Aug 1982.—7 ♂ (4.8–5.0 mm), 5 ♀ (4.6–5.5 mm), San Carlos Bay St. 55 (26°27.2′N, 82°0.2′W), depth 5.5 m, 11 Jul 1982.—1 ♂ (3.8 mm), 1 ♀ (4.3 mm), Bear Point, Big Marco River St. 63 (25°58.0′N, 81°42.2′W), depth 3.7 m, 12 Jul 1982. All Texas and Florida material collected with epibenthic sled and in collection of WWP.

Diagnosis.—Apex of antennal scale not pointed; endopod of thoracic limb 2 exhibiting sexual dimorphism, in males proximal portion of merus very slender, bearing 4–8 setae along inner margin and 4–6 setae along outer margin, proximal part of merus not as slender in females as in males, inner margin bearing 4–7 setae and outer margin with 3–5 setae; inner margin of carpo-propodus armed with 5–9 spiniform setae; carpopropodus of thoracic endopods 3–8 2-articulated; exopod of pleopod 4 of male 7-articulated; endopod of uropods armed with 4–5 (rarely 3) spine-setae near statocyst; apex of telson armed with 3 pairs of strong, widely spaced spine-setae, outermost pair ¼ to ⅓ length of inner pairs, innermost pair greater than ⅓ length of telson and slightly longer to subequal in length with adjacent pair.

Description.—General body form (Fig. 3A): moderately slender, adult males to 6.4 mm, females to 6.0 mm; anterior margin of the carapace produced into a short, triangular, rostrum reaching to the bases of the eye-stalks; posterior dorsal margin broadly emarginate exposing thoracic segment 8; anterolateral corners rounded.

Antennular peduncle (Fig. 3B): more robust in males than females; article 1 about as long as articles 2 and 3 combined, distomedial margin armed with 3–4 long sparsely plumose setae and 3–4 shorter plumose setae; distolateral margin with 1 short and 3–4 long plumose setae; medial margin of article 2 with strong simple spine-seta and 5 plumose setae; article 3 with 2 plumose setae along medial margin and group of 6 plumose setae distally, distal margin with dorsomedial lobe bearing 2 tooth-like processes and 4 plumose setae, lateral margin with 1 long and 1 short submarginal plumose seta; males with densely setose lobe on outer ventral surface.

Antenna (Fig. 3C): scale lanceolate, 5.0–5.5 times as long as maximum width, inner margin slightly convex, outer margin slightly concave, all margins setose; lacking distal

Fig. 3. *Americamysis stucki,* new species. A, adult female, dorsal view; B, antennular peduncle; C, antennal peduncle and scale; D, labrum; E, mandibles; F, mandibular palp; G, maxillule; H, maxilla; I, endopod, thoracic limb 1; J, K, endopod, thoracic limb 2, female, male, respectively. Scales in mm.

article; antennal peduncle extending about ⅔ length of scale, article 2 about 1.5 times as long as 3, having 3 plumose setae on inner distal margin and 1 plumose seta on outer distal margin, article 3 with 4 simple and 2 plumose setae on inner distal margin and 2–3 short plumose setae along outer margin; distolateral corner of sympod with prominent tooth.

Eyes (Fig. 3A): large, cornea wider than distal end of eyestalk, lacking ocular papilla.

Labrum (Fig. 3D): rounded anteriorly; posterior margin with medial emargination, middle ⅔ with fine setae.

Mandible (Fig. 3E): with cutting edges typical of the genus. Palp (Fig. 3F) 3-articulated; article 2 more robust in males than females, armed with 11–12 submarginal setae on mesial surface and 17–19 simple setae on inner surface, distal margin with 4–6 strong simple setae; article 3 ⅔ as long as 2, inner surface with 5–9 marginal and 3–5 submarginal simple setae, distal portion armed with 1 long simple seta, 1 long curved spine barbed along its middle part, and 9 thick, blunt densely barbed spines.

Maxillule (Fig. 3G): outer lobe with 9 stout serrate apical spine-setae; inner lobe with 2 serrate setae subequal in length.

Maxilla (Fig. 3H): typical of genus; exopod with 4 to 7 plumose setae; endopod 2-articulated, distal article armed with 2–4 submarginal and 20–22 plumose setae on apex and inner margin. Lobe of sympodal segment 2 with 4 long plumose setae; sympodal segment 3 bilobed, inner lobe with 12–14 plumose setae, outer lobe with 11 plumose setae.

Endopod of thoracic limb 1 (Fig. 3I): robust, typical of the genus; carpo-propodus twice length of dactyl, distal part with numerous simple setae and strong serrate spine-setae; dactyl as long as wide with numerous simple setae, serrate spine-setae and single large claw, slightly longer than dactyl.

Endopod of thoracic limb 2 (Fig. 3J, K): exhibiting sexual dimorphism; in males (Fig. 3K) merus subequal in length with carpo-propodus, proximal portion very slender, bearing 4–8 simple setae along inner margin, 4 to 6 setae along outer margin and 1 seta on outer distal margin; inner margin of carpo-propodus armed with 5–9 flared spiniform setae gradually increasing in length distally, and a short submarginal seta at the base of each spiniform seta. In females (Fig. 3J) merus ⅔ as long as carpo-propodus, proximal part not as slender as in male, inner margin bearing 4–7 setae, outer proximal margin with 3–5 setae and distal margin with 1 seta; inner margin of carpo-propodus armed with 5–9 flared spiniform setae as in male; dactyl ⅓ length of carpo-propodus, armed with numerous curved serrate spine-setae and serrate distal claw.

Endopod of thoracic limb 3 (Fig. 4A): basis with 3 plumose setae, ischum 1.5 times as long as merus, setose along inner margin; merus setose along inner margin with serrate seta on outer distal margin; 2-articulated carpo-propodus slightly shorter than merus with segments subequal in length, proximal segment with 1 large serrate seta on outer distal margin; dactyl small with long slightly curved claw on distal tip surrounded by several simple setae extending from distal margin of the carpo-propodus.

Endopod of thoracic limb 8 (Fig. 4B): basis with 2 plumose setae; ischium slightly longer than merus with simple setae scattered along entire inner margin; merus with many simple setae along inner margin and 1 serrate and 1 simple seta on outer distal margin; length of 2-articulated carpo-propodus slightly shorter than merus, articles subequal in length, proximal article with 1 submarginal serrate seta and 2 serrate setae on outer distal margin; dactyl with slender terminal claw and minute setule surrounded by several long simple setae extending from distal margin of carpo-propodus.

Female pleopods reduced to setose uniramous plates.

Male pleopod 1 (Fig. 4C): endopod 1-articulate with 1 plumose seta distally, 4–5 plumose setae proximally and pseudo-

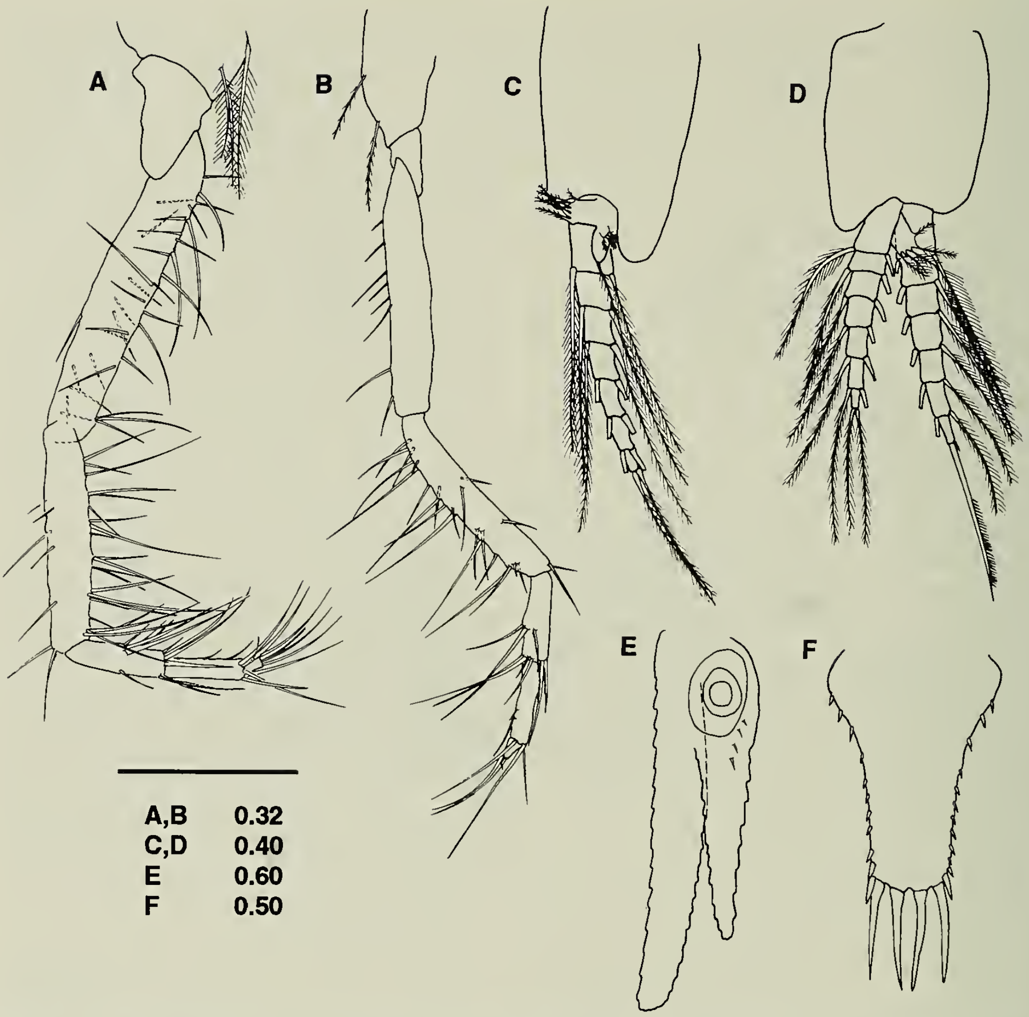

Fig. 4. *Americamysis stucki,* new species. A, endopod, thoracic limb 3; B, endopod, thoracic limb 8; C, male pleopod 1; D, male pleopod 4; E, uropod; F, telson. Scales in mm.

branchial lobe furnished with 1 subterminal and 4–5 terminal plumose setae; exopod 7-articulated.

Male pleopods 2, 3, 5: exopods and endopods 7-articulated.

Male pleopod 4 (Fig. 2D): endopod 7-articulated with pseudobranchial lobe similar to first pleopod; exopod 7-articulated, slightly longer than endopod, setule on outer distal margin of article 7, with long barbed apical spine-seta as long as the 5 distal articles combined.

Uropods (Fig. 4E): exopods 1.2–1.3 times as long as endopod and 2.0 times as long as telson, outer margin concave, inner margin convex; endopod 1.5–1.6 times as long as telson, inner margin almost straight, outer margin concave, armed with 4–5 (rarely 3) spine-setae near statocyst; exopod and endopod setose along both inner and outer margins.

Telson (Fig. 4F): entire, linguiform, shorter than 6th abdominal segment, 1.3–1.5 times as long as maximum width, lateral margins concave and armed with 9–11 short stout spine-setae; apex armed with 3 pairs of strong widely spaced spine-setae, outermost pair ¼–⅓ length of inner pairs, innermost pair greater than ⅓ length of telson, slightly longer or subequal in length to adjacent pair.

Coloration.—The following description is of a population from Tampa Bay, Florida. In living specimens, pairs of black chromatophore located dorsally at base of telson, and ventrally at base of mandibles and thoracic legs 3 and 7. Posterior ventral margin of abdominal segments 1–5 with a single median black chromatophore; when dispersed, abdominal chromatophore extend laterally and dorsally giving abdomen a mottled brownish appearance; pigmentation from chromatophore of adjacent segments never merges. Abdomen often yellowish, ventral half with pink-purple cast. Eyestalks with brown pigmentation dorsally; cornea black. Antennular peduncles usually mottled light brown; inner flagella pigmented on 10 or fewer proximal segments; male lobe partly brown. Brown along the distal margin of sympod of antenna and on distomedial margin of scale. Carpo-propodus and dactyl of thoracic leg 1 partially or totally brown. Proximal ¼ of inner margins of merus of thoracic legs 3–6 brown. Longitudinal brown line extending length of proximal segment of thoracic exopods 2–7. Females with one chromatophore at base of each posterior oostegite. Sympods of male pleopods 1–5 partially brown. Exopod of uropod with ⅓ or less of distomedial margin lined with brown. Endopod of uropod with ½–⅔ of distomedial margin lined with brown.

In preserved specimens the following coloration persists. Pairs of chromatophore at bases of telson, mandibles, thoracic legs 3 and 7. Single chromatophore on abdominal segments 1–5, posterior oostegites. Partial pigmentation on male lobe and distomedial margins of uropods.

Distribution.—Continental shelf waters in northern Gulf of Mexico between Texas and Alabama. Continental shelf waters to 20 m and inshore waters of west coast of Florida from Anclote Key to Marco Island.

Habitat.—Bottom plankton in deeper waters of bays and bottom, mid and surface water plankton in continental shelf waters to a depth of 200 m.

Etymology.—This species is named for Kenneth Stuck in recognition of his excellent work on malacostracan Crustacea of the Gulf of Mexico.

Remarks.—*Americamysis alleni,* n. sp. and *A. stucki,* n. sp. are morphologically most similar and apparently most closely related to *A. bigelowi.* They can be distinguished from *A. bigelowi* and each other by the setation of the second thoracic endopod and the telson. Table 3 presents characters that may be used to distinguish the six species of *Americamysis.*

The following key separates the species of *Americamysis* and the seven species of *Mysidopsis* (excluding *M. cojimarensis*) that have a 2-articulate carpo-propodus on thoracic endopods 3–8 and a normally developed mandibular palp. As mentioned earlier *M. cojimarensis* may not belong to *Mysidopsis.*

Key to the Species of *Americamysis* and the Species of *Mysidopsis* having a 2-articulate Carpo-propodus on Thoracic Endopods 3–8

1. Lateral margin of telson lacking spine-setae (only terminal spine setae present) 2
– Lateral margin of telson with spine-setae 3
2. Telson entire with 3 pairs of terminal spine-setae; uropodal endopod with 2 ventral spine-setae adjacent to statocyst near inner margin ....
.. *Mysidopsis suedafricana* O. Tattersall, 1969
– Telson weakly cleft with single spine seta on each apical lobe; uro-

Table 3.—Common and specific adult characters of *Americamysis* species.

Characters	Species					
	almyra	*bahia*	*bigelowi*	*stucki,* new species	*alleni,* new species	*taironana*
Anterior dorsal margin of carapace	broadly rounded	short, triangular rostrum	short, triangular rostrum	short, triangular rostrum	short, triangular rostrum	well developed rostrum
Distal article on antennal scale	absent	absent	absent	absent	absent	absent
Length/width ratio of antennal scale	6.0–6.5	6.0–6.5	6.0	5.0–5.5	5.5–6.0	5.0
No. articles in carpo-propodus of thoracic endopods 3–8	2	2	2	2	2	2
Thoracic endopod 2 of ♂, ♀	normally developed	normally developed	normally developed	merus more slender in ♂♂ than ♀♀	normally developed	normally developed
No. seta on inner margin of merus of thoracic endopod 2	7–18	7–18	2	4–8	2–3	4
No. setae on inner margin of carpo-propodus of thoracic endopod 2	2–3	2–3	6–12, spiniform	5–9, spiniform, flared	4–10, spiniform, flared	3
No. articles no exopod of male pleopod 4	7	7	7–8	7	7	6
No. spine-setae on uropodal endopod	1	1–5, usually 2–3	5, rarely 3–4	4–5, rarely 3	3–4, rarely 2 or 5	2–4, usually 3
No. pairs of apical telson spine-setae	4–8	3–6	3	3	3	2
Length of apical telson spine-setae in relation to lateral spine-setae	gradually increasing	abruptly increasing	abruptly increasing	abruptly increasing	abruptly increasing	abruptly increasing
Length of inner most apical spine-setae of telson/length of adjacent pair	1.1–1.3	1.1–1.2	1.0–1.1	1.0–1.1	0.9–1.0	1.4–1.6

podal endopod with 10–20 ventral spine-setae along inner margin .. ... *Mysidopsis bispinulata* Brattegard, 1974

3\. Antennal scale with distal article 4
Antennal scale lacking distal article 8

4\. Tip of antennal scale with setae, not spiniform; uropodal endopod with inner margin wavy, armed with groups of spines inserted between setae 5

– Tip of antennal scale without setae, acute, spiniform; uropodal endopod inner margin not wavy, lacking armed processes along inner margin; 18–50 ventral spine-setae extending distally from statocyst near inner margin 6

5\. Area adjacent to statocyst with single spine-seta; uropodal endopod with inner margin having 6–7 wavy shallow processes each armed with 2–4 spines .... *Mysidopsis ankeli* Brattegard, 1973

– Area adjacent to statocyst lacking spine-seta; uropodal endopod with inner margin with 8 wavy processes each armed with 5–7 spines .... *Mysidopsis intii* Holmquist, 1957

6\. Uropodal endopod with more than 45 spine-setae along inner ventral margin .... *M. californica* W. Tattersall, 1932

– Uropodal endopod with 15–25 spine-setae along inner ventral margin 7

7\. Uropodal endopod having inner ventral surface near posterior margin of statocyst with stout rounded spine-setae producing pad-like appearance; telson with marginal spine-setae gradually becoming larger and longer toward apex ... .. *Mysidopsis tortonesi* Băcescu, 1968

– Uropodal endopod lacking stout rounded spine-setae on inner surface near statocyst; telson with apical 2 pairs of spine-setae much more robust and distinctly longer than anterolateral pair .... *Mysidopsis robustispina* Brattegard, 1969

8\. Rostrum well-developed, extending to distal ⅓ of first peduncular article of antennule; telson with innermost apical pair of spine-setae over ⅓ longer than adjacent pair *Americamysis taironana* (Brattegard, 1973)

– Rostrum not well-developed, not extending past proximal ½ of first peduncle article of antennule; telson with innermost apical pair of spine-setae subequal, equal, or only slightly longer than adjacent pair 9

9\. Carpo-propodus of second thoracic endopod with 2–3 setae on distal part of inner margin, merus with 7–18 setae on proximal ⅔ of inner margin 10

– Carpo-propodus of second thoracic endopod with series of 4–12 spiniform setae on distal ½ to ⅔ of inner margin, merus with 2–8 spine-setae on inner margin 11

10\. Anterior margin of carapace (rostral shield) broadly rounded; uropodal endopod with 1 spine near statocyst; apex of telson of adults usually with 4–8 pairs long slender spine-setae .... *Americamysis almyra* (Bowman, 1964)

– Anterior margin of carapace produced to form short triangular rostrum; uropodal endopod with 1–5 (normally 2–3) spine-setae near statocyst; apex of telson of adults usually with 3–6 pairs of long slender spine-setae .... *Americamysis bahia* (Molenock, 1969)

11\. Telson with innermost spine or pair of spines on apex shorter than, or equal in length to adjacent pair, never longer; uropodal endopod usually with 3–4, occasionally 2–5, spine-setae near statocyst . . . . *Americamysis alleni,* new species

– Telson with innermost spines slightly longer, never shorter than adjacent pair; uropodal endopod usually with 5 (occasionally 4, rarely 3) spine-setae near statocyst . . . 12

12. Endopod of second thoracic limb normally developed in both sexes, merus (article 5) with 2 setae on proximal inner margin; carpo-propodus with inner margin armed with an irregularly alternating row of short and long spiniform setae . . . *Americamysis bigelowi* (Tattersall, 1951)

– Endopod of second thoracic limb with merus in male very slender, merus in both sexes with 4–8 setae spaced along entire inner margin, carpo-propodus with inner margin armed with spiniform setae gradually increasing in length distally *Americamysis stucki,* new species

The genus *Americamysis* is presently known only from the Northwest Atlantic. Its species occur in estuarine and shelf waters along the coasts of the Americas from the northeastern United States to Colombia. The type species, *A. bigelowi* has been reported from off Massachusetts (Georges Bank) southward to Florida and westward along the Gulf coast to Aransas Bay, Texas (Tattersall 1951; Clark 1956; Bowman 1964; Brattegard 1969; Wigley & Burns 1971; Stuck et al. 1979a, 1979b; Stuck & Heard 1981, Modlin 1982, Price et al. 1986). Based on our present studies *A. bigelowi* appears to be restricted to the east coast of the United States. All the Gulf of Mexico records for this species are now referable to either *A. alleni* or *A. stucki,* which both appear to be endemic to this region. *Americamysis alleni,* an inshore bay species, is currently known from the northwestern and northern central Gulf, whereas, *A. stucki,* commonly found in higher salinity, near shore waters, is known from southeastern Gulf westward to Texas.

Americamysis almyra and *A. bahia* are closely related species with similar distributions, however, the former is generally found in lower salinities than the latter species. Both are reported from inshore waters along the entire coast of the Gulf of Mexico from Terminos Lagoon, Mexico to the southwestern Everglades in South Florida (Bowman 1964; Brattegard 1969, 1970; Molenock 1969; Price 1978, 1982; Stuck et al. 1979a, 1979b; Escobar-Briones and Soto 1988). The ranges of both species extend northward along the Atlantic east to Patapsco River, Maryland (Grabe 1981) for *A. almyra* and to Narragansett, Rhode Island (Lussier et al. 1988) for *A. bahia.*

Americamysis taironana, the only member of the genus not found in North American waters, occurs along the Caribbean coasts of Colombia and Panama (Brattegard 1973, 1974a, 1974b).

Acknowledgments

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ARMADILLIDIUM TABACARUI (ISOPODA: ONISCIDEA: ARMADILLIDIIDAE), A NEW TROGLOBITIC SPECIES FROM A SULFUROUS CAVE IN ROMANIA

Magdalena Gruia, Vasilica Iavorschi, and Serban M. Sarbu

Abstract.—Four species of terrestrial isopods belonging to *Caucasonethes, Haplophthalmus, Trachelipus* and *Armadillidium* were collected in Movile Cave, Romania. *Trachelipus troglobius* was described recently and *Armadillidium tabacarui,* a new species, is described here. It was collected in the lower level of the cave where it is present in large numbers on the walls of the cave's air-bells. It feeds on the rich chemoautotrophic microbiota covering the walls.

A diverse troglobitic community was recently discovered in Movile Cave in southern Dobrogea, Romania (Sarbu & Popa 1992). Thirty-one previously unknown terrestrial and aquatic species have been identified so far and further discoveries are expected. Most are characterized by an advanced degree of troglomorphy suggesting that they have been isolated from the surface for a long time. Four species of terrestrial isopods (Oniscidea) inhabit Movile Cave: *Trachelipus troglobius* Tabacaru & Boghean, 1989 (Trachelipidae), *Haplophthalmus* sp. and *Caucasonethes* sp. (Trichoniscidae). A new species of *Armadillidium* Latreille, 1804 (Armadillidiidae) is described here.

Armadillidium tabacarui, new species

Fig. 1

Derivation of name.—This new species is named in honor of our colleague, Dr. Ionel Tabacaru, a well-known specialist in terrestrial isopod taxonomy.

Holotype.—Adult male, "Emil Racoviţă" Speleological Institute (ERSI), Bucharest, Romania, from Movile Cave, leg. Viorel Boghean, 28 Dec 1990.

Paratypes.—Three males; two females, ERSI, from Movile Cave, leg. Serban M. Sarbu and Dumitru Pegulescu, 28 Dec 1990.

Distribution.—The lower level of Movile Cave, southern Dobrogea, Romania.

Diagnosis.—The new species of *Armadillidium* is typified by the following characters: volvation of mesospheric type; smooth white tegument; pleotelson triangular with rounded posterior margin; armadillidiid type cephalon; frontal plate projects slightly above vertex and is slightly prismatic; frontal fossa hidden by posterior margin of plate; male ischium of pereiopod VII elongate, thickened distally with slightly concave ventral margin with zone of piliform scales; merus of pereiopod VII strongly widened distally; internal lobe of exopodit of male pleopod 1, pointed and slightly curved laterally; dorsal valvula of stomach, rectangular shaped.

Description.—Body length—6.7 mm in males, 6.45 mm in females; Body width—3.35 mm in males, 3.05 mm in females; Color—white, white-pinkish; Eye—16–18 small ommatidia, with slight traces of pigment (Fig. 1).

Tegument: smooth, lacks granulation, with small hyaline semicircular scales (Fig. 2A). Triangular scale-spines with large base and rounded tip on posterior margin (Fig. 2B) and on surface of pereionites. Triangular scale-spines, with narrow base and pointed tip (Fig. 2C), on anterolateral sur-

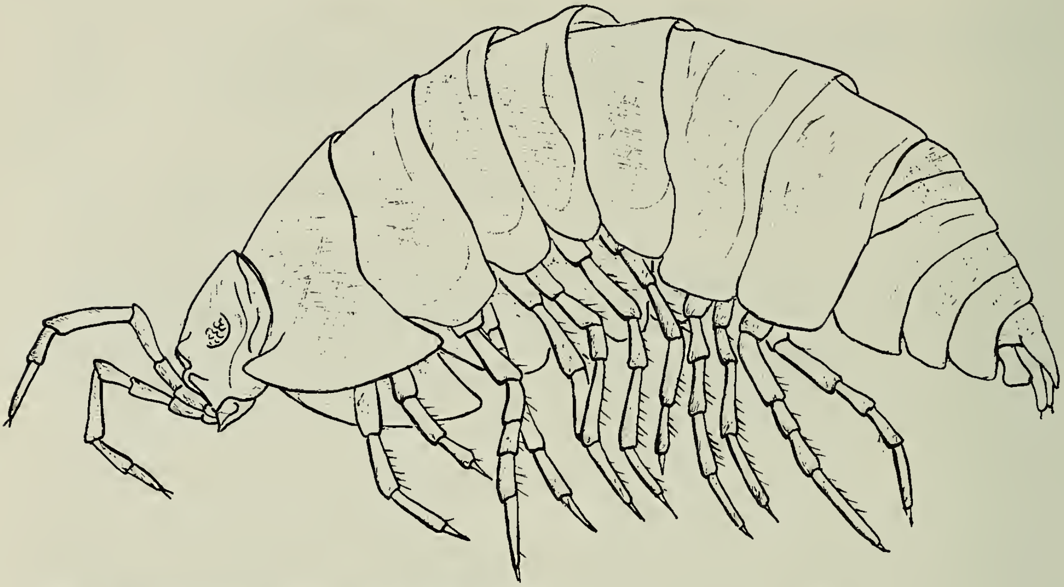

Fig. 1. *Armadillidium tabacarui*, new species: lateral view.

face of pereionites II–VII and especially on uropods. Simple short spines on surfaces of all pereionites (Fig. 2D). Long acutely pointed spines along interior margin of pereionites (Fig. 2E) and on anterolateral surface of pereionites II–VII, along with simple hairs. Long triangulate flexible hyaline scales forming bundles on anterolateral margin of pereionites II–VII (Fig. 2F). Lateral nodes small and inconspicuous (Fig. 2G), located posterolaterally, close to posterior margin; in reference to lateral margin, lateral nodes situated on line extending past posterior angle of pereionites; no major differences regarding position of nodes on all pereionites. Glandular fields of *Armadillidium* type.

Cephalon: rectangular in dorsal view. Scutellum convex, slightly prismatic; anterior margins of scutellum forming wide angle in dorsal view (Fig. 2H), posterior margin straight. Scutellum triangulate in frontal view (Fig. 2I). Subscutellar fossa slightly deepened and widened, hidden by posterior margin of scutellum, bent posteriorly (Fig. 2J). Posterior margin extending very slightly above vertex (Fig. 2K). Postscutellar line continuing toward eyes, bordered by 2 lateral prominent rectangular lobes. Antennal lobes with thick upper margin in frontal view; lobes protrude laterally in dorsal view (Fig. 2L). Frontal line short.

Pereion: anterior angle of pereionite I frontally directed, slightly lifted (mesospheric type). Acute posterior angle, posterior margin only slightly concave (Fig. 1). Pereionites II–VII, of different shapes: pereionites II–IV decrease progressively in length. Epimeron of tergite IV smallest, with rounded edge. Tergite VII with largest epimeron, posterior angle 90° (Fig. 1).

Pleon: size of epimera decreases from pleonites 3 to 5 (Figs. 1, 3A), posterior angle changing from acute (3) to obtusely rounded (5).

Telson: width–length ratio 1.5:1. Telson triangular, rounded tip extending only slightly beyond posterior most part of enveloping pereionite 5. Telson limited ventrally by clearly visible carina (Fig. 3A).

Antennule: articles of unequal length, basal article longest. Short spine present distally on dorsal convex edge of article 1. Ar-

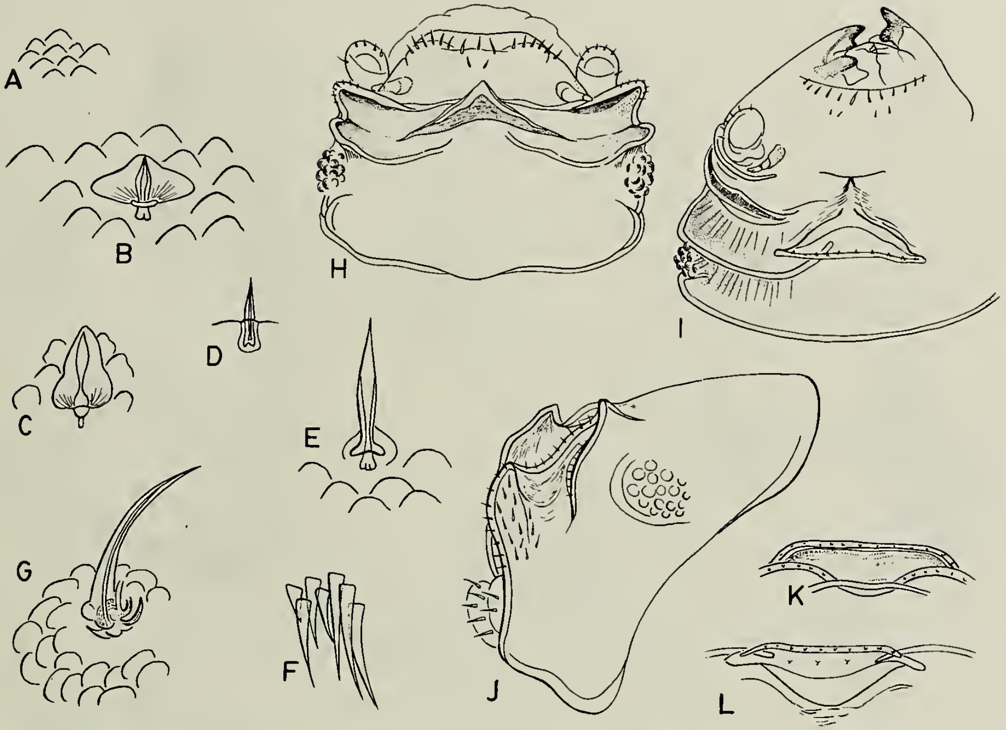

Fig. 2. *Armadillidium tabacarui,* new species: holotype. A, semicircular scales; B, triangulate scale-spines on surface of pereionites; C, triangulate scale-spines on surface of uropods; D, spine on anterolateral surface of pereionites; E, spine on anterolateral surface of pereionites; F, scales on anterolateral margin of pereionites; G, lateral nodes; H, cephalon, dorsal view; I, same, frontal view; J, same, lateral view; K, scutellum, posterior view; L, scutellum, anterior view.

ticle 2 shortest. Apical article bearing 3 rows of aesthetascs (10–12), tip pointed, with 1 aesthetasc (Fig. 3B).

Antenna: long (Fig. 3C), reaching posterior edge of pereionite I. Flagellum with article 2 1.25–1.30 × longer than article 1; 5–6 aesthetascs on article 1 (Fig. 3C, b).

Mandible: molar compound; 4 setae in setal row on both mandibles; seta and hair-like setae on lacinia mobilis (Fig. 3D).

Maxillule: outer ramus with 10 apical teeth, outer 4 plain, inner 6 thin with bi- or tri-lobed tip (Fig. 3E). Inner ramus tipped with 2 subequal penicillate setae.

Maxilliped: endite longer than wide, with 3 short spines on upper edge; especially stout spine on endite surface; palp with 2 large spines on basal article; one on edge and complex of spines (one large) on article 2; apex with scale-like spined tip with several spines (Fig. 3F).

Pereiopods: robust (Fig. 4A–C), tegument uniformly covered by semicircular hyaline scales; rod-shaped spines of various sizes and shapes variously placed on pereiopods (Fig. 4B–C, a).

Pereiopod I (Fig. 4A): inner surface with 2 regions covered by long, flexible, hyaline hairs (14–15 rows) on carpus, and short hairs with 4 rows of spines on propodus, both regions bordered on both sides by rows of moderately long setae (Fig. 4A, a). Sternal edge with different shaped rods (Fig. 4A, b–c), forming two rows on carpus and one row of four rods on propodus.

Uropods: length–width ratio of basis 1:2;

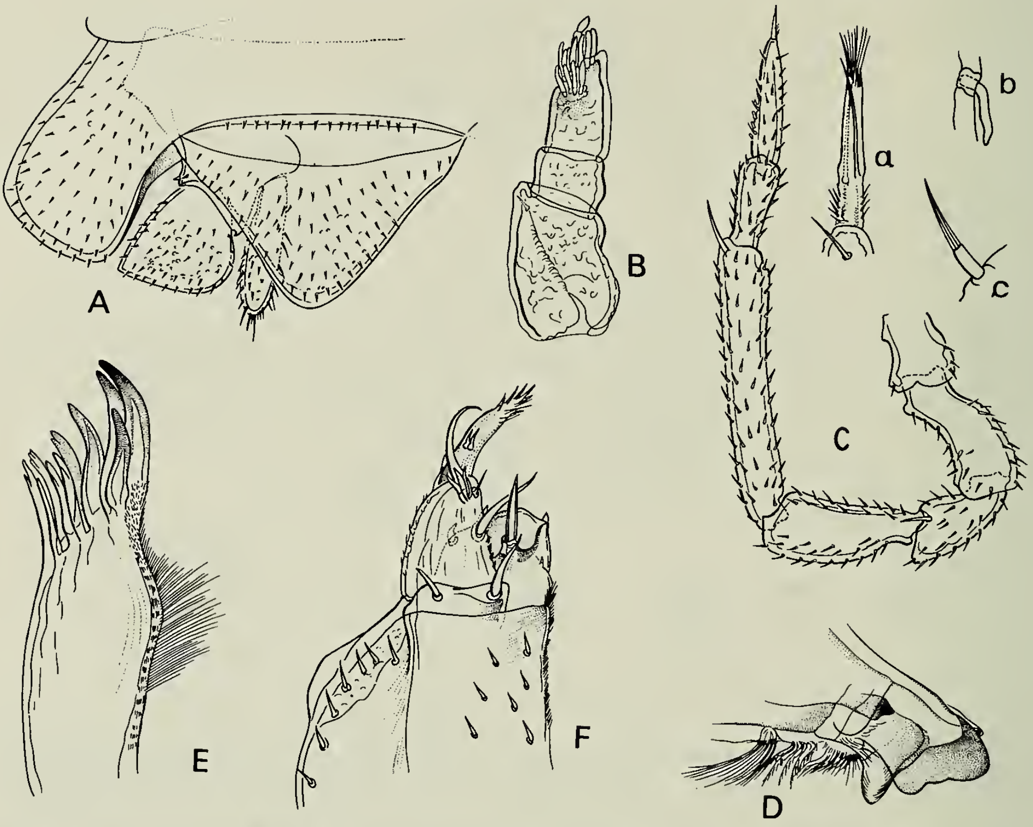

Fig. 3. *Armadillidium tabacarui,* new species: holotype. A, telson; B, antennule; C, antenna: a, apex of antennal flagellum; b, aesthetasc on flagellar article 1; c, terminal spine of peduncular segment 5; D, left mandible; E, outer ramus of maxillule; F, maxilliped.

exit region from basis of flattened wide exopod oblique; exopod with medial margin rounded and lateral corner pointed (Fig. 4D); endopod long and narrow, extending slightly past tip of telson (Fig. 3A).

Stomach (Fig. 4E, F): dorsal lamella of stomach in *A. tabacarui* n.sp. rectangular. Dorsal lamella short and wide, with lateral margins about half as long as posterior and basal margins. Posterior margin sinuous, with central excavation (Fig. 4F). Dorsal lamella covering only ⅓ of stomach length. Lateralium exhibiting complex three dimensional structure: triangulate in dorsal view, and anteriorly covered by dorsal valvula. Upper anterior margin covered by spines. Internal interior surface hyaline and covered by short thin hairs (Fig. 4E, a). Upper plate with well developed tritulating part; anterior zone with abundant hairs (Fig. 4E, b). Trituration zone of lower plate with rows of long curved, laterally oriented hairs (Fig. 4E, c).

Male sexual characters.—Pereiopod VII (Fig. 4B, C): longest; basis very narrow with few tegumentary formations; ischium elongate, wider distally with slightly concave external edge and elongate area covered by long hyaline hairs next to inner surface (Fig. 4C); merus narrow proximally, very wide distally especially toward external edge, being 1.5 × longer than wide; last 3 segments with characteristic rods (Fig. 4C, a) on outer edge of both surfaces.

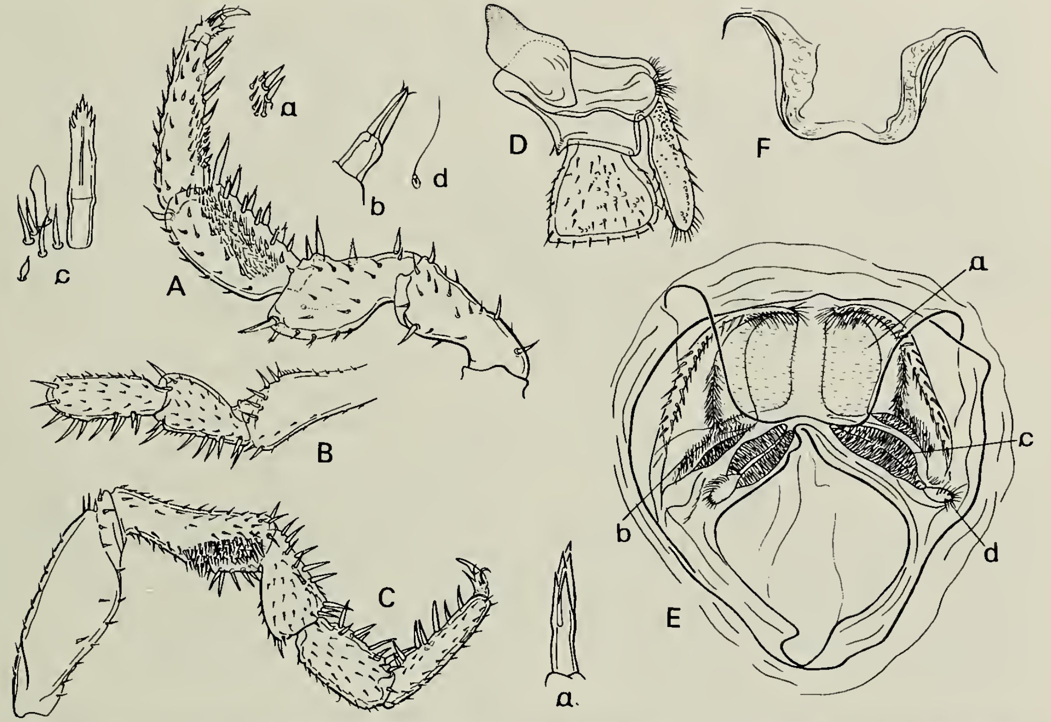

Fig. 4. *Armadillidium tabacarui,* new species: holotype. A, pereiopod I, inner surface: a, short spines on surface of pereiopod I; b, rod on outer surface of pereiopod I; c, rod on rostral surface of pereiopod I; d, sensory hair on pereiopod I; B, pereiopod VII, inner surface; C, same, outer surface: a, rod on sternal edge of pereiopod VII; D, uropod; E, stomach: a, lateralium, interior hyaline surface; b, upper plate; c, trituration zone of lower plate; d, filtration zone of lower plate; F, same, dorsal valvula.

Pleopod 1 (Fig. 5A): triangular exopodit with convex posterolateral margin, pseudotrachea obvious, tip pointed, fringing setae on medial and posterolateral margins of point; endopodit elongate and straight, distal extremity slightly curved with 2 unequally long, curved tips: internal tip longer, with row of foliaceous spines increasing in size distally, extending for short distance along endopod; external tip tiny, curved laterally and plain (Fig. 5B).

Pleopod 2–5 (Fig. 5C–F): exopodits pointed with rows of short hairs; endopodit 2 (Fig. 5C) only slightly longer than exopod.

Discussion

Eight species of *Armadillidium* have been recorded from Romania. Three are found in Dobrogea: *A. jaqueti* Dollfus, 1897 (banks of the Danube at Isaccea, in western Dobrogea), *A. traiani* Demianowics, 1932 (abundant in Bessarabia, also in Dobrogea—Radu 1985), and *A. vulgare* (Latreille) 1804, cosmopolitan (Radu 1985).

Armadillidium tabacarui can be included in the *vulgare-maculatum* group (Strouhal 1927), but a perfect attribution of this species to any of these groups is difficult to make. Compared to *A. vulgare* and *A. traiani* which belong to the *vulgare* group and are surface species present in Dobrogea, the subterranean *A. tabacarui* differs mainly through: the shape of the head (mesospheric type) and through the presence of a piliferous area on the ischium of the pereiopod VII in males. Resemblance with other species of the *vulgare* group consists mainly in

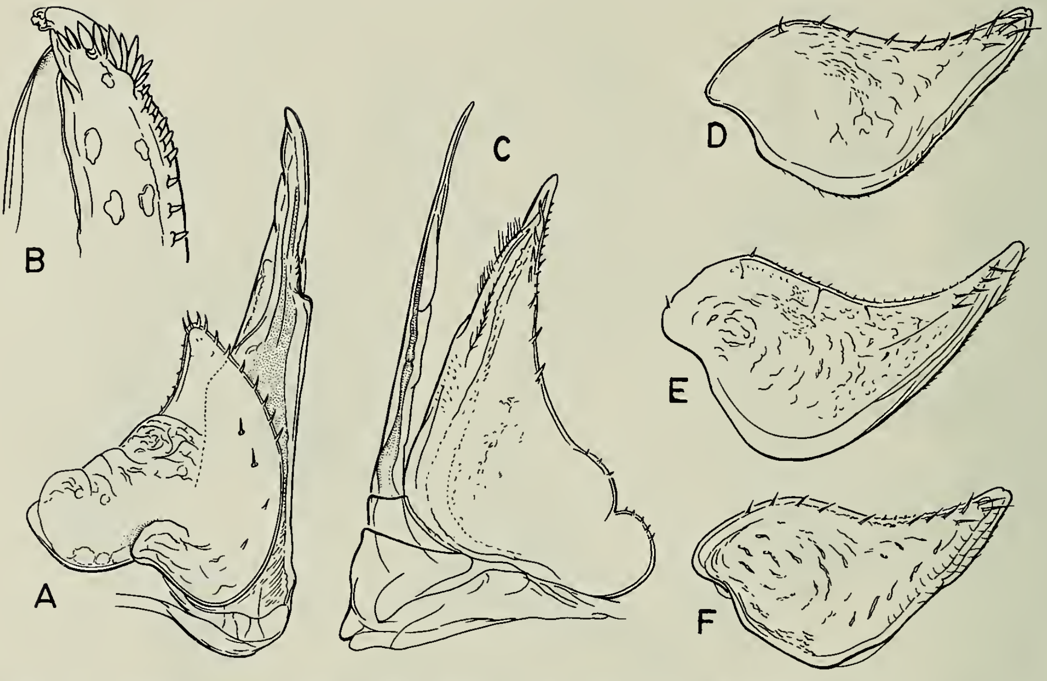

Fig. 5. *Armadillidium tabacarui*, new species: holotype. A, pleopod 1; B, same, distal extremity of endopod; C, pleopod 2; D, exopod of pleopod 3; E, exopod of pleopod 4; F, exopod of pleopod 5.

the shape of the frontal plate of the cephalon which is slightly prominent close to the level of the vertex (Vandel 1962). The presence of the piliferous area in *A. tabacarui* suggests a close resemblance to *A. delattini* Verhoeff, 1943 which inhabits the Marmarean region. The broad telson of *A. tabacarui* resembles that of *A. traiani* and especially *A. absoloni* Stroughal, 1939 (present in caves in Bosnia and Herzegovina), as well as *A. azerbaidzhanum* Schmalfuss, 1990 from Azerbaijan and the northern Caucasus (Schmolzer 1965, Schmalfuss 1990).

The presence of several characters suggests that *A. tabacarui* may belong to the *maculatum* group. These characters are: the mesospheric type of the shape of the body; the triangulate shape of the telson; the shape of the ischium of the pereiopod VII in males. The later character is present in *A. banaticum* Verhoeff, 1907, an endemic species for western Romania (Radu 1985). The comparison of *A. tabacarui* with species of the *maculatum* group present in the Balkan region such as *A. klugi* Brandt, 1883 and *A. bulgaricum* Frankenberger, 1941, reveals additional affinities with this group such as the shape of the pleopod I in males, as well as differences such the shape of the merus of the pereipod VII in males (Frankenberger 1941). The shape of the frontal plate is the main character that determines the imperfect fit of *A. tabacarui* into the *maculatum* group as described by Vandel (1962).

The anatomical analysis of the stomach in our new species reveals differences in the shape of the dorsal lamella and the lateralium compared to *A. vulgare.* In the latter the dorsal lamella has a deeper central excavation on the posterior margin and the interior hyaline surface has a rounded median margin as opposed to *A. tabacarui* where this margin is straight.

The comparative analysis of the characters shows that *A. tabacarui* presents a mixture of characters which makes its precise attribution to a certain group of species difficult.

The additional comparison of *A. tabacarui* with taxa from Greece and Turkey, such as those described by Schmalfuss (1981, 1982, 1985), Strouhal (1937, 1956), and Vandel (1980), shows affinities of our new species with eastern mediterranean forms.

Ecological Observations

In the lower level of the cave, the surfaces of the water and the cave walls are covered by microbial mats consisting of heterotrophic and chemoautotrophic sulfur-oxidizing microbes (Sarbu & Popa 1992). All four oniscids were found exclusively in the vicinity of the sulfurous pools, especially in the air-bells of the lower level of the cave (Tabacaru & Boghean 1989). They feed on the microbial mats that cover the walls. Chemoautotrophically produced food (Sarbu & Popa 1992) is in such abundance that *A. tabacarui* reaches densities of several hundred specimens per square meter in the air-bells. On several occasions *A. tabacarui* was seen being eaten by the clubionid spider *Lascona cristiani* and by the large centipede *Cryptops anomalans.*

The physico-chemical parameters of the cave's atmosphere are highly stable without marked diurnal or annual fluctuation. The air temperature is 20.9°C (±0.3) and the relative humidity 100%. The atmosphere of the air-bells is low in oxygen (7–10%) and rich in carbon dioxide (2.5–3%). It contains up to 1 ppm hydrogen sulfide and 1% methane.

Acknowledgments

The authors are grateful to Viorel Boghean and Dumitru Pegulescu for their help with collecting the material and to all those who made the collecting trips possible. We would like to express special thanks to Dr. G. Schultz, Dr. S. Taiti, and Dr. H. Schmalfuss for their suggestions regarding the final preparation of the manuscript. This research was supported by the "Emil Racoviţă" Speological Institute in Bucharest, Romania, the Dept. Biological Sciences of the Univ. of Cincinnati, the National Geographic Society (4639-91), the Cave Research Foundation, the Explorers Club, the National Speleological Society, and the Sigma Xi Scientific Research Society.

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TWO NEW SPECIES OF *PODOCERUS* LEACH (CRUSTACEA: AMPHIPODA: PODOCERIDAE) FROM BERMUDA

Adam J. Baldinger and Michael F. Gable

Abstract.—Two new species, *Podocerus tachyrheo* and *Podocerus lazowasemi,* are described from Bermuda. *Podocerus tachyrheo* is a non-carinate, highly pigmented species lacking uropodal interramal spines; *P. lazowasemi* possesses distinct uropodal interramal spines and dorsal carinations, but usually lacks pigmentation.

In Kunkel's (1910) monograph on the amphipods of Bermuda no specimens of the genus *Podocerus* were recorded. Johnson (1986) and Gable et al. (1988), however, both refer to the existence of a single species of *Podocerus* in Bermuda. Examination of collections at the Yale Peabody Museum (YPM) and at the National Museum of Natural History (USNM) clearly documents the presence of two species of *Podocerus* in Bermuda, both of which are newly described in this paper.

In the figures, body parts are marked by abbreviations as follows: A, antenna; Gn, gnathopod; LL, lower lip; Md, mandible; Mx, maxilla; Mxpd, maxilliped; P, pereopod; T, telson; U, uropod; UR, urosome.

Podocerus tachyrheo, new species
Figs. 1–5

Podocerus sp.—Johnson, 1986:378, fig. 125.—Gable et al., 1988:148–149.

Etymology.—Named for the ability of individuals of this species to live in areas of extremely swift (G. tachy-) currents (G. rheo), such as those at The Flatts, Bermuda, where all tidal flow from Harrington Sound moves through one narrow channel.

Diagnosis.—Pereon without dorsal carinations. Pereon segments 5–7 with dorsal and lateral spine groups, pleon segments 1–2 with dorsal spine groups only. Adult males and females with varying degrees of pigmentation. Coxal plates 1–5 with a strong distal spine. Male antennae 1–2, gnathopods 1–2, maxillae 1–2, mandibular palp, and maxilliped with plumose setae. Male antenna 2, flagellum 3-articulate and ornamented with submarginal spines. Female antennae 1–2, gnathopod 1, maxillae 1–2, mandibular palp, and maxilliped with plumose setae. Male gnathopod 2, article 5 masked by articles 4 and 6, palm with irregular margin bearing a proximal conical tooth and a distal rectangular process. Article 6 of all pereopods with strong bifurcate spines. Uropods 1–2 with bifurcate spines but lacking peduncular interramal spines.

Description.—Male: Body and appendages with pigmentation, body lacking dorsal carinae, pereon segments 5–7 and pleon segments 1–2 with dorsal distoposterior spine groups, pereon segments 5–7 also with lateral distoposterior spine groups. Coxae reduced with serial discontiguity, coxae 1–5 each with a large marginal spine, located anteriorly on coxae 1–4. Head less than pereonites 1 and 2 in length, cuboidal with ocular bulges. Eyes pigmented.

Antenna 1, 33% of total body length, peduncular ratio 1:3:2.7, flagellum 5-articulate; accessory flagellum 1-articulate and prominent. Antenna 2 greater than antenna 1 in

Fig. 1. *Podocerus tachyrheo,* male, 4.0 mm, YPM No. 9239.

length, articles 4 and 5 subequal, flagellum 3-articulate with distinct submarginal spines.

Mandible with 3-segmented palp, penultimate article triangular with marginal setae, terminal article clavate with facial and apical setae; incisor and lacinia both with 4 teeth; spine row of 3 short, broad spines; molar normal. Maxilla 1, inner plate vestigial; outer plate with 9 strong apical spines; palp 2-articulate, terminal article with 3 apical, medially bulging spines and 1 apical seta, 4 submarginal setae, and 4 facial spines. Maxilla 2, outer plate with 10 long apical setae; inner plate with 10 apical setae, inner margin with fine setae distally. Maxilliped, inner plate with marginal and submarginal setae and a single outer marginal spine; outer plate reaching 50% length of palp, with an inner marginal spine row and submarginal setae; palp 4-articulate, terminal article triangular. Lower lip, normal.

Gnathopod 1, coxal plate rhomboidal with a distinct distoanterior spine; article 6, palmar margin longer than hind margin; dactyl with 3 marginal setae. Gnathopod 2 heavily pigmented, robust, and much larger than gnathopod 1; article 5 hidden behind articles 4 and 6; palm of article 6 with irregular margin, bearing a proximal conical tooth and a distal rectangular process, margin heavily setose with 2 proximal spines. Bases of pereopods 3–7 with posterior plate-like extensions; article 6 of all pereopods with distally bifurcate spines.

Uropods 1 and 2 elongate, biramous,

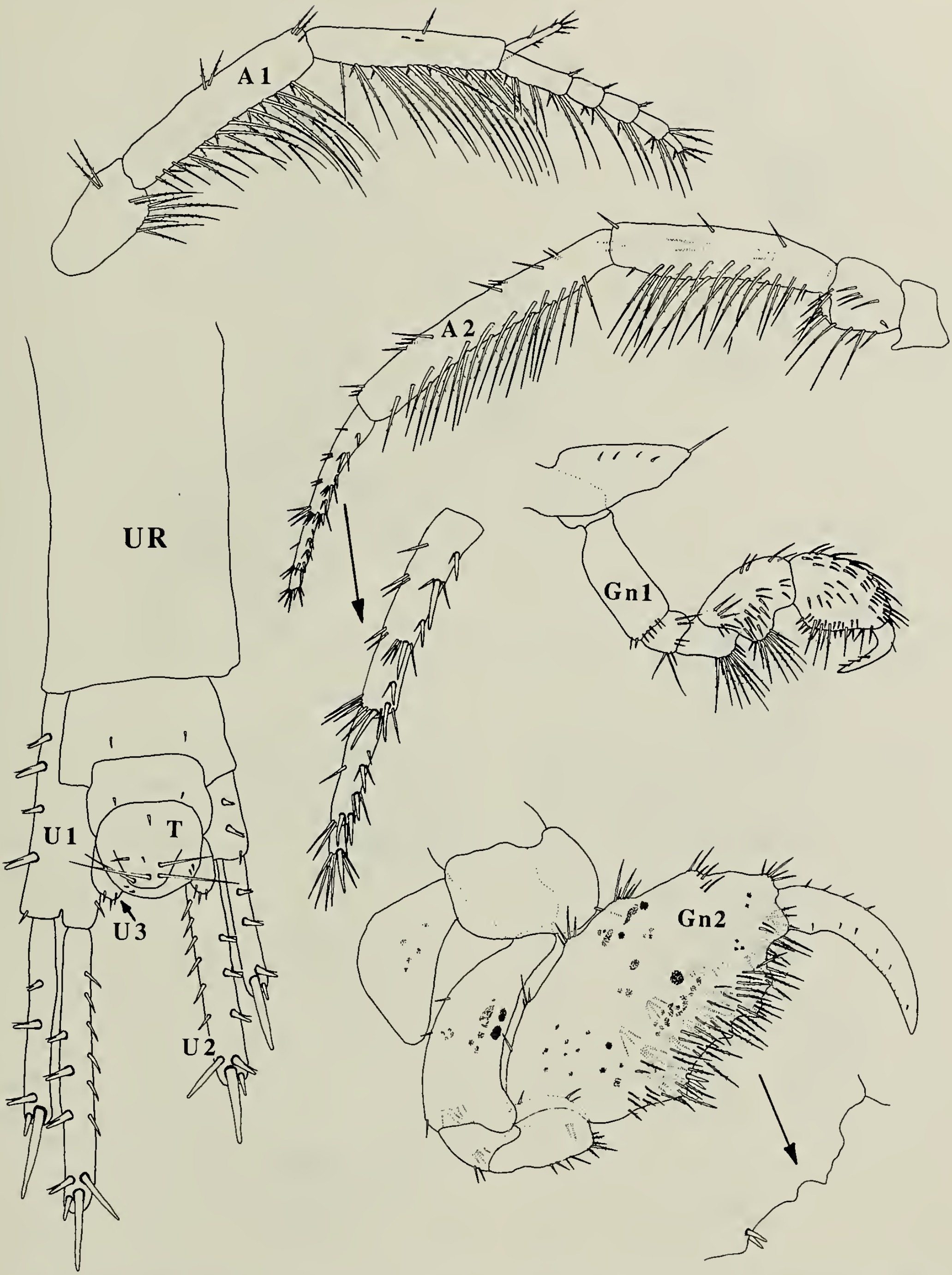

Fig. 2. *Podocerus tachyrheo,* male, 4.0 mm, YPM No. 9239: A1, Gn1, Gn2, UR (with left U1, right U2, right and left U3, T). Male, 2.9 mm, YPM No. 9242: A2.

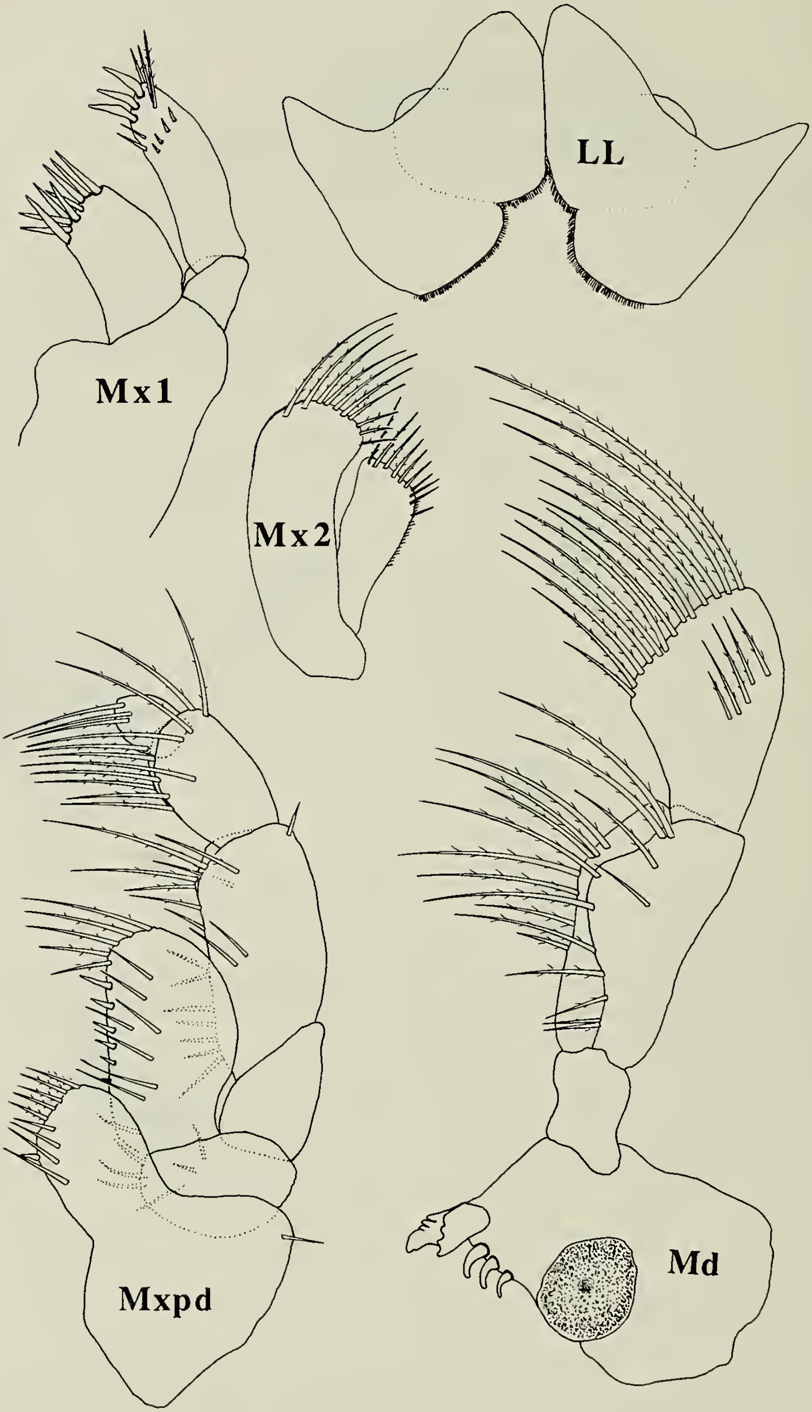

Fig. 3. *Podocerus tachyrheo,* male, 4.1 mm, YPM No. 9241.

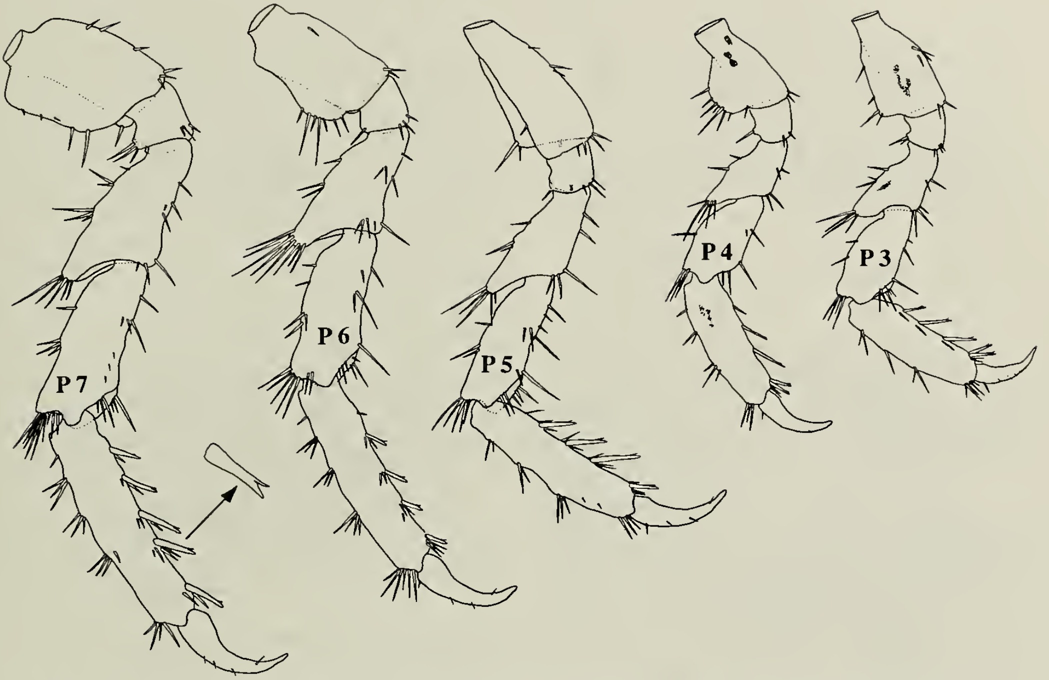

Fig. 4. *Podocerus tachyrheo*, male, 2.9 mm, YPM No. 9242: P3–P4. Male, 4.0 mm, YPM No. 9239: P5–7.

lacking interramal spines; peduncles and rami with marginal bifurcate spines, rami with distinct apical spines. Uropod 3 leaf-like with 3 apical setules. Telson dorsally produced and armed with 4 long setae and 6 short setules.

Female: All features same as those for male except as noted. Body lacking dorsal spine groups. Antenna 1, 40% of total body length; flagellum 4-articulate. Flagellum of antenna 2 lacking distinct submarginal spines. Gnathopod 1, article 6, proximal corner of palm demarcated by a spine. Gnathopod 2 resembling gnathopod 1 but twice the size and less ornamented.

Remarks.—The degree and patterns of pigmentation are variable among individuals of *P. tachyrheo*; juveniles, smaller males, and females may completely lack pigment. Larger males appear to have a uniform pigment band along the musculature of the pereon segments. Pigment has also been observed in males on almost every body segment, even on the most distal antennal segment. In females, however, pigmentation appears to become much denser on the ventral margin of the pereon, and may extend to the basal portions of the oostegites. Male/female differences in body spination, in the flagella of both antennae, in both gnathopods, and in pigmentation obviously make *P. tachyrheo* sexually dimorphic.

Podocerus tachyrheo is morphologically most closely related to *Podocerus multispinis* K. H. Barnard, 1925 and *Podocerus multispinis* var. *levis* K. H. Barnard, 1925. The only major difference between *P. multispinis* and *P. multispinis* var. *levis* is the almost complete absence of the dorsal spiniform tubercles in the variety (Barnard 1925). Based upon the description and one illustration of gnathopod 2 by both Barnard (1925) and Griffiths (1976), the most significant differences between *P. tachyrheo* and *P. multispinis* are: the number of flagellar

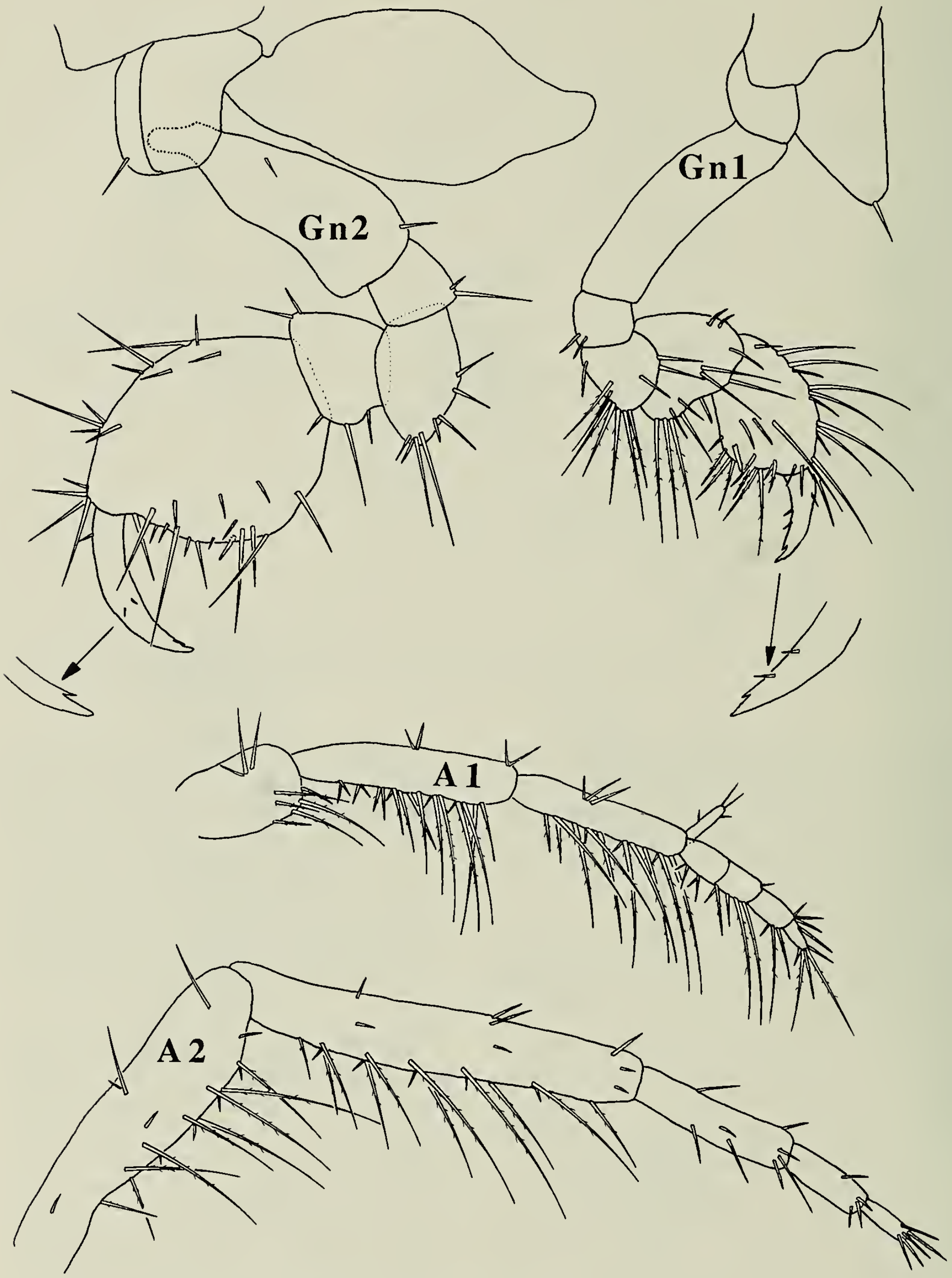

Fig. 5. *Podocerus tachyrheo,* female, 3.0 mm, YPM No. 9240.

articles of antenna 1, *P. tachyrheo* with five and *P. multispinis* with eight; the lateral spines on the pereon, present in *P. tachyrheo* and absent in *P. multispinis*; the number of setae present on the telson, four on *P. tachyrheo* and two on *P. multispinis*; the irregular margin of the palm of article 6 of gnathopod 2, *P. tachyrheo* with one tooth and one rectangular process and *P. multispinis,* as described by Barnard (1925), with two teeth and one rectangular process. In addition, Barnard (1925) does not mention *P. multispinis* or the variety as having pigmentation. Finally, although close morphologically to *P. tachyrheo, P. multispinis* is endemic from Natal to Saldanha Bay, South Africa (Griffith's 1975). *Podocerus tachyrheo,* therefore, may be considered a species endemic to Bermuda.

Other than its morphology, little is known about *P. tachyrheo.* In Bermuda most specimens collected were associated with hydroids; one collection yielded several hundred specimens taken from a small portion of a large colonial hydroid, *Halocordyle disticha* (Goldfuss), found attached in an area of very strong current.

Material examined.—Male holotype, YPM 9254, The Flatts, Harrington Sound, Bermuda, M. F. Gable, 23 May 1989, 5.0 mm, on *Halocordyle disticha* (Goldfuss) attached to a subtidal pipe. Female allotype, YPM 9245, The Flatts, Harrington Sound, Bermuda, M. F. Gable, 23 May 1989, 2.9 mm, mature, on *Halocordyle disticha* (Goldfuss) attached to a subtidal pipe. 1 male paratype, YPM 9239, Harrington Sound, behind Bermuda Aquarium, Bermuda, M. F. Gable, 2 Jun 1987, 4.0 mm, within hydroids and algae. 1 female paratype, YPM 9240, (same data as YPM 9239), 3.0 mm. 20 paratypes, males, females and juveniles, YPM 9243, Long Bird Causeway, Bermuda, S side and under causeway, E. A. Lazo-Wasem, 20 Jun 1988, washing of rocks. 1 male paratype, YPM 9241, The Flatts, Bermuda, M. F. Gable, 23 May 1989, 4.1 mm. 1 male paratype, YPM 9242 (same data as YPM 9241), 2.9 mm. 1 female paratype, ovigerous, YPM 9244 (same data as YPM 9243), 3.5 mm, highly pigmented. 5 paratypes, 2 males, 2 females, ovigerous, and 1 juvenile, deposited by YPM in Bermuda Museum of Natural History (same data as YPM 9243).

Podocerus lazowasemi, new species

Figs. 6–9

Etymology.—Named in appreciation for the technical assistance, sound advice, and encouragement received for this and many other projects from our colleague and good friend, E. A. Lazo-Wasem (YPM).

Diagnosis.—Pereon segments 6–7 and pleon segments 1–2 with dorsal carinations and spine groups. Coxal plates 1–7 each with 1 large marginal spine. Antennae 1–2, maxillae 1–2, maxilliped, and male gnathopods 1–2 with plumose setae. Maxilla 1, outer plate with 8 apical spines. Male gnathopod 1, article 6 with anterior marginal setae; gnathopod 2, palm at dactyl hinge with a pronounced rectangular process. Dactyls of all pereopods with a proximoanterior plumose seta. Peduncle of uropods 1–2 with interramal spine. Dorsal lobe of telson with 2 long and 2 short setae.

Description.—Male: Body unpigmented with conspicuous dorsal carinae and dorsal spine groups on pereon segments 6–7 and pleon segments 1–2. Coxae reduced with serial discontiguity, each with a large marginal spine. Head equal to pereonites 1–2 in length, cuboidal with lateral ocular bulges. Eyes pigmented.

Antenna 1, 40% of total body length, geniculate, article 2 slightly longer than article 3, flagellum 5-articulate; accessory flagellum, 1-articulate and prominent. Antenna 2, bigeniculate, article 5 nearly twice as long as article 4, flagellum 4-articulate and ornamented with spines and setal groups.

Mandible with 3-segmented palp, penultimate segment with submarginal and marginal setae, terminal article clavate with

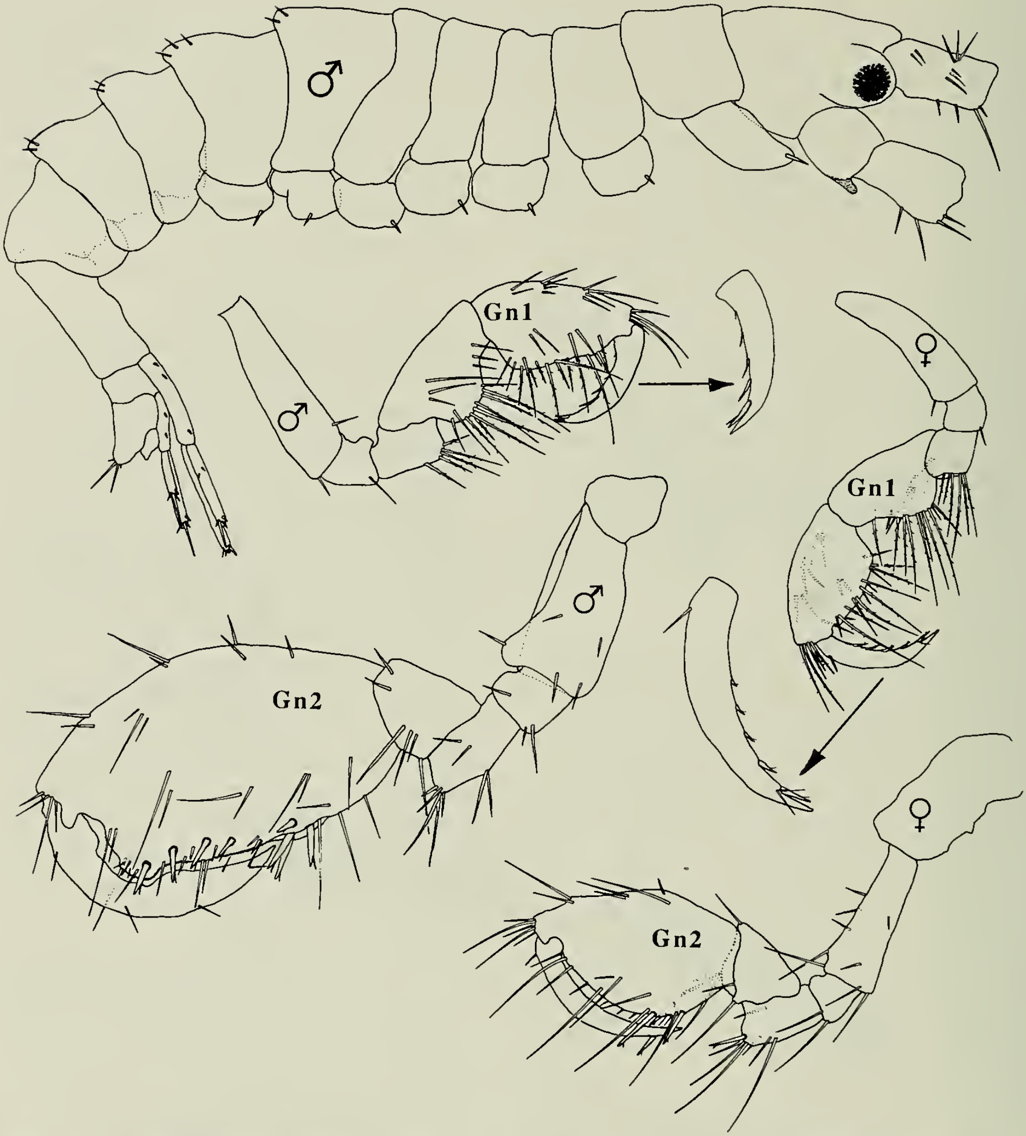

Fig. 6. *Podocerus lazowasemi,* male, 3.0 mm, YPM No. 9260: body, Gn1, Gn2. Female, 2.4 mm, YPM No. 9261: Gn1, Gn2.

facial and apical setae; incisor with 4 teeth; lacinia with 5 teeth; spine row of 3 short, broad spines; molar normal. Maxilla 1, inner plate vestigial; outer plate with 8 strong apical spines, 2 of them bifurcate; palp 2-articulate, terminal article with 4 strong apical spines and 3 apical setae. Maxilla 2, inner plate with 10 apical setae, inner margin lined with fine setae; outer plate with 9 apical setae. Maxilliped, inner plate clavate with apical and facial setae, distal inner corner with a large marginal spine; outer plate <50% length of palp, with 4 inner marginal spines and with submarginal and marginal setae; palp 4-articulate with submarginal and marginal setae. Lower lip, normal.

Gnathopod 1, coxal plate rhomboidal

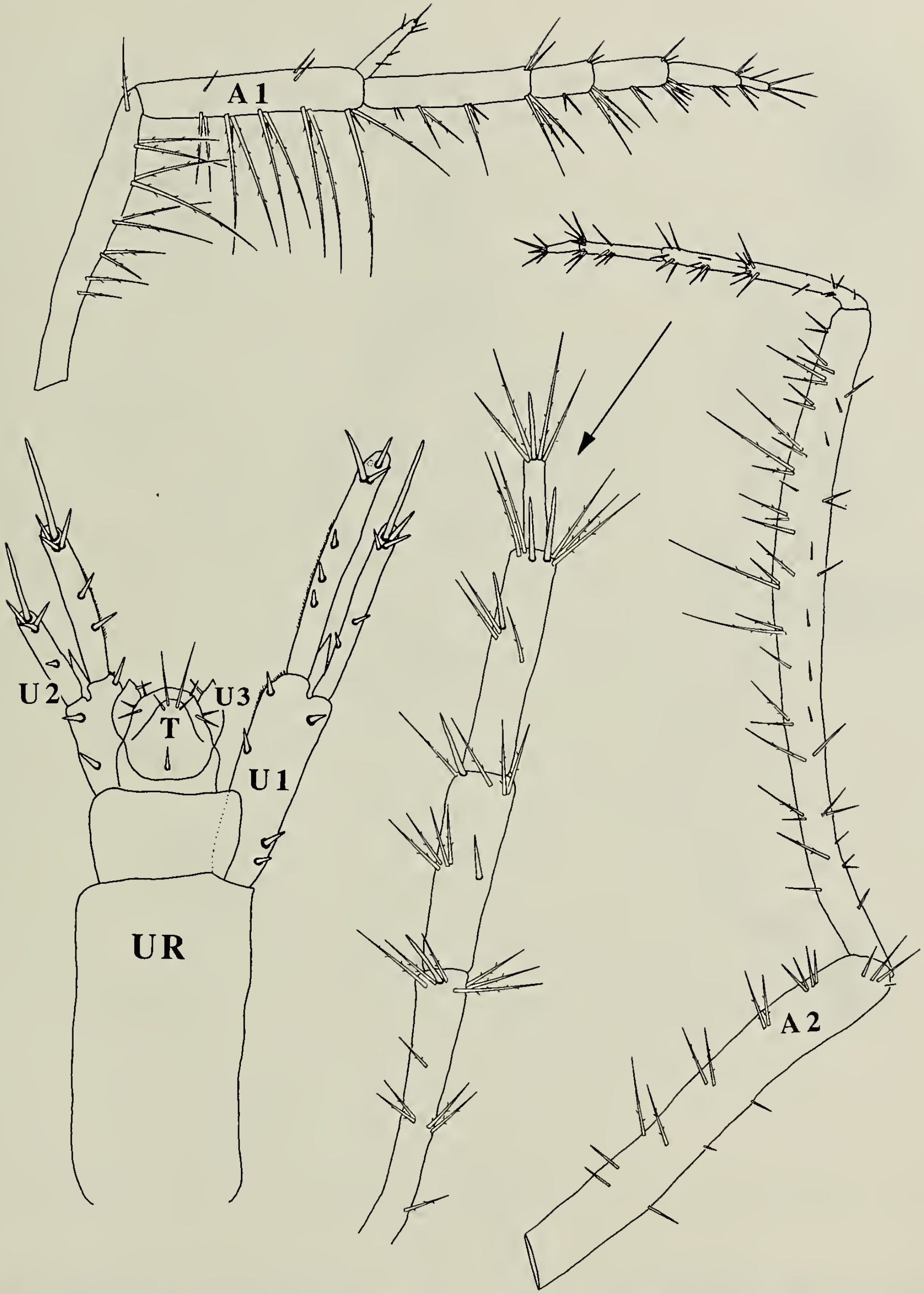

Fig. 7. *Podocerus lazowasemi,* male, 3.3 mm, YPM No. 9262: A1, A2. Male, 3.1 mm, YPM No. 9259: UR (with right U1, left U2, right and left U3, T).

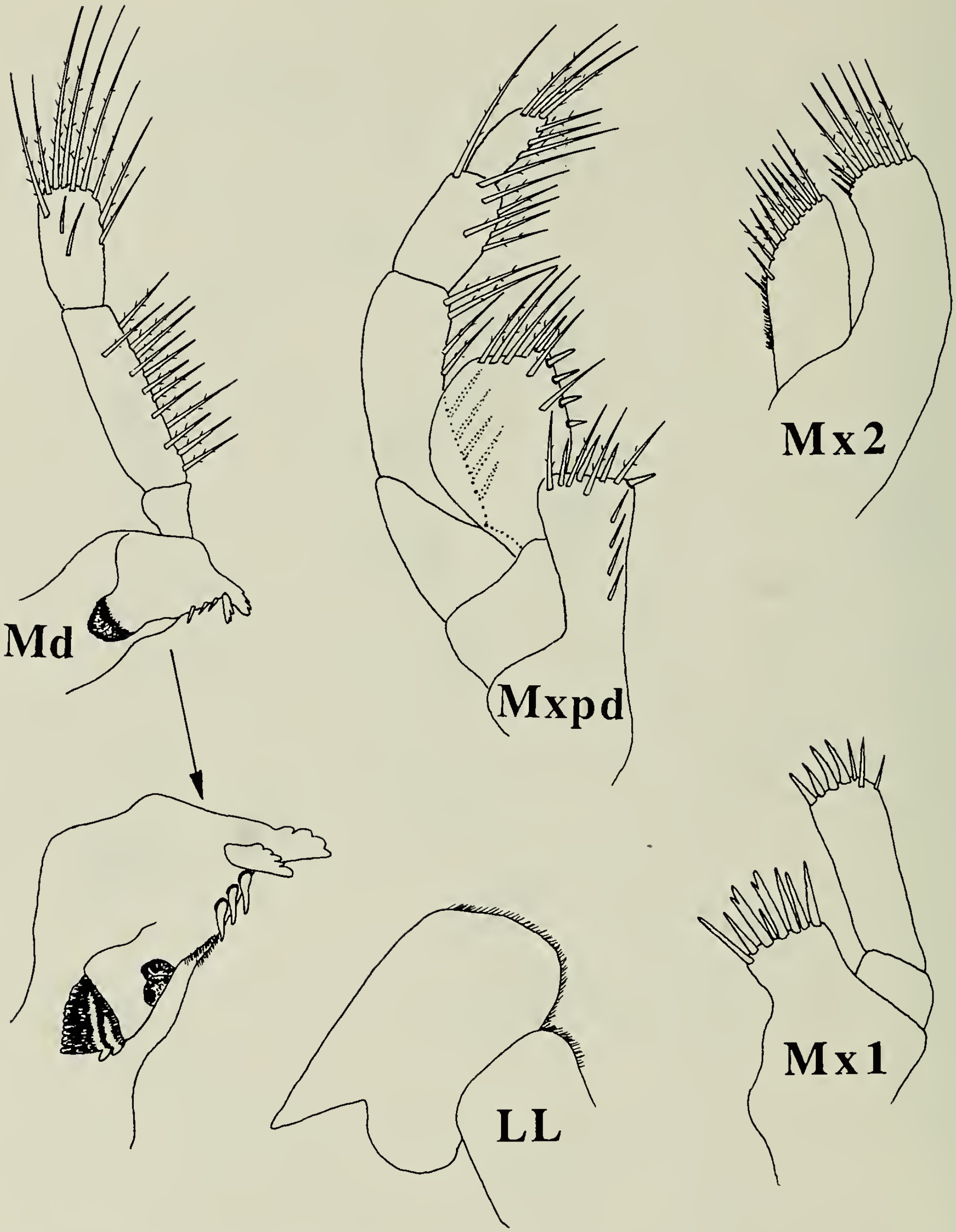

Fig. 8. *Podocerus lazowasemi,* male, 3.3 mm, YPM No. 8357.

with 1 large distoanterior spine; article 6, palm much longer than hind margin and with marginal setae, anterior margin with 4 setal groups; dactyl with 4 marginal setules and a subterminal bifurcate spine. Gnathopod 2 robust and much larger than gnathopod 1; basis triangulate, formed by a distoanterior lobed projection; article 6, palm setose with a pronounced distal rectangular process and 4 distinct submarginal bifurcate

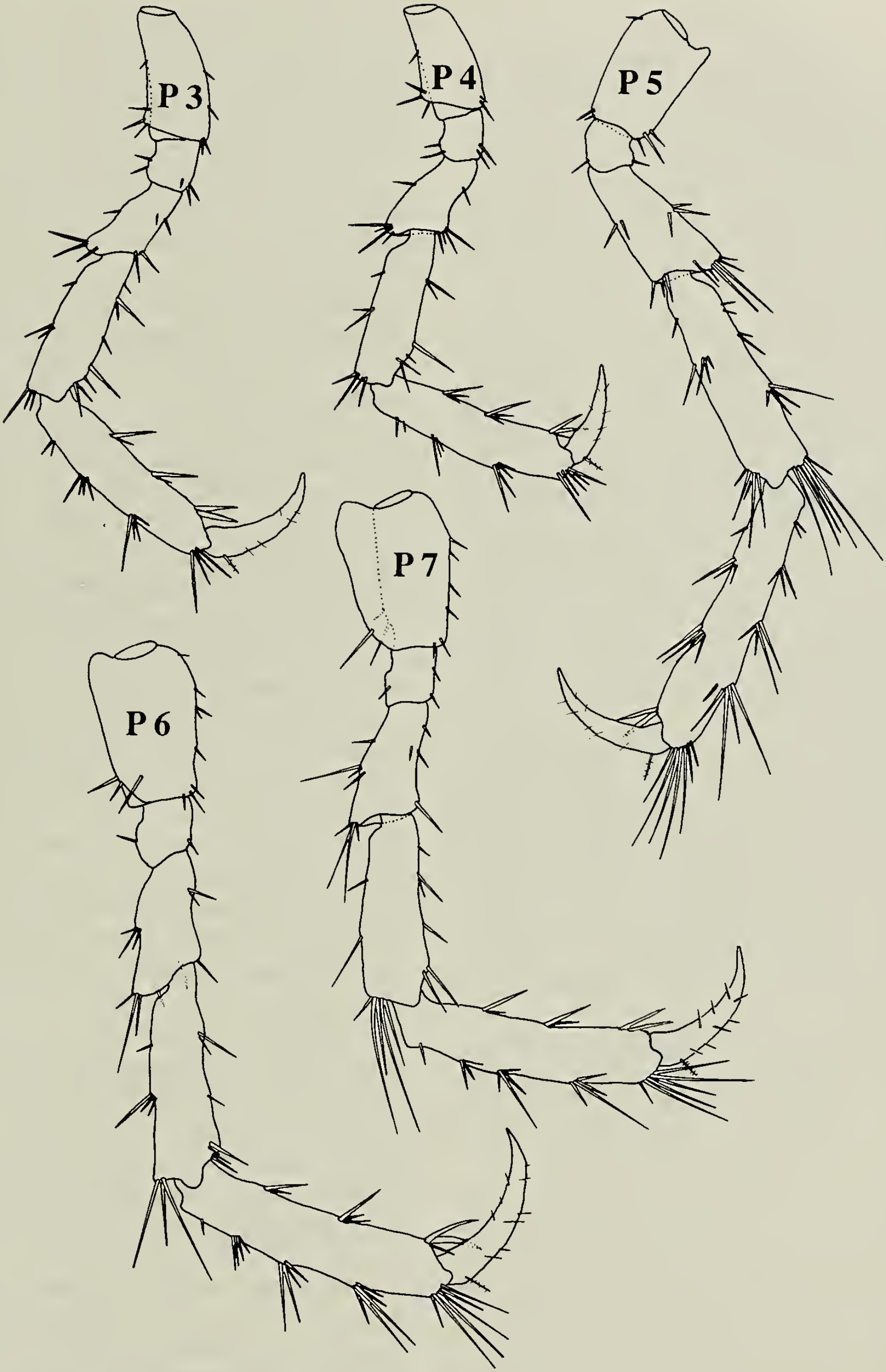

Fig. 9. *Podocerus lazowasemi,* male, 3.1 mm, YPM No. 9263.

spines, margin proximal to palm with 4 distinct bifurcate spines; dactyl with anterior marginal setae and a concavity fitting the rectangular process of article 6. Bases of pereopods 3–7 with posterior plate-like extensions becoming progressively more pronounced posteriorly, anterior and posterior margins of all articles variably spinose and setose. Dactyls each with a proximoanterior plumose seta.

Uropods 1 and 2 elongate, biramous; peduncles with a large interramal spine; rami with apical spines; peduncles and rami with marginal spines. Uropod 3 leaf-like with 1 marginal seta. Telson with 4 marginal and 2 submarginal posterior setae, 1 distinct anterior facial spine, and 4 setae; dorsally produced process with 2 long and 2 short setae.

Female: All features same as those for male except as noted. Gnathopod 2 resembling male, but less robust; basis lacking anterior lobed projection; palm lacking process and less spinose.

Remarks.—The marked differences in gnathopod 2 make *P. lazowasemi* sexually dimorphic. The dorsal carinations appear to become more pronounced as individual size increases. Although *P. lazowasemi* is typically non-pigmented, two specimens (YPM 9268 (juvenile) and 8371 (female)) possess pigment similar to females of *P. tachyrheo.*

Morphologically, *P. lazowasemi* most closely resembles *Podocerus fulanus* Barnard, 1962. Based on comparisons of specimens of both species, the most significant differences between *P. lazowasemi* and *P. fulanus* are: coxal plate ornamentation, *P. lazowasemi* with one distinct spine on each plate and *P. fulanus* with no spines or with one or more setae; number of flagellar articles on antenna 1, *P. lazowasemi* with five and *P. fulanus* with six; spination on posterior margin of article 6 of gnathopod 2, *P. lazowasemi* with four palmar bifurcate spines and four submarginal bifurcate spines proximal to the palm and *P. fulanus* with simple spines on the palm and no spines proximal to the palm; spination of inner ramus of uropod 1, *P. lazowasemi* with three marginal spines and *P. fulanus* with eight–nine marginal spines. Barnard (1979) also describes the pereon and pleon segments of *P. fulanus* as having lateral cusps, and "ordinary" specimens (3–4 mm) as having two telsonic spines, the number variable depending upon the size of an individual. Lateral cusps are not present in *P. lazowasemi* and the number of telsonic spines does not seem to be size-related.

Podocerus fulanus is a Pacific species widely distributed in the open sea of Mexico and is limited to warm, ponded embayments of southern California (Barnard 1979). The recently described *Podocerus kleidus* Thomas & Barnard, 1992a from the Florida Keys is also morphologically similar to *P. lazowasemi* but still quite distinct. *Podocerus kleidus* lacks spines on the flagellum of antenna 2 and has an excavate coxa 1. *Podocerus fulanus* differs most significantly from *P. kleidus* in the lack of an excavate coxa 1 and has fewer medial spines on the outer rami of uropods 1 and 2 (Thomas & Barnard 1992a). With the differences between *P. lazowasemi, P. kleidus* and *P. fulanus* having been delineated, and as *P. lazowasemi* does not have an excavate coxa 1, *P. lazowasemi* is considered another endemic Bermuda amphipod.

Precise microhabitat preferences for *P. lazowasemi* are, unfortunately, not known, as most specimens are from general rock and algal washings. Some specimens were taken from collections of turtle and manatee grasses, *Thalassia testudinum* Konig & Sims and *Syringodium filiforme* Kütz, but it is not known if the amphipods were holding onto the grasses or onto epifauna, e.g., hydroids. *Podocerus lazowasemi* has been found from very shallow sublittoral waters to a depth of approximately 8 m.

Material examined.—Male holotype, YPM 9256, Long Bird Causeway (¼ from S end), Bermuda, M. F. Gable, 31 May 1987, 3.2 mm, washings from shallow, subtidal rocks. Female allotype, YPM 9257, Long Bird Causeway (¼ from S end), Bermuda, M. F. Gable, 31 May 1987, 3.2 mm, ovigerous, washings from shallow, subtidal rocks. 2 paratypes, ovigerous female, juvenile, YPM 9258 (same data as YPM 9257), 3.3 mm (female), 1.5 mm (juvenile). 2 male paratypes, USNM 346847, S Ireland Island, Bermuda, M. L. Jones, 31 Aug 1981. 1 male paratype, YPM 9259, Long Bird Causeway (¼ from S end), Bermuda, A. J. Baldinger, 31 May 1987, 3.1 mm, washings from shallow, subtidal rocks. 1 male paratype, YPM 9260, Spanish Point, Bermuda, E. A. Lazo-Wasem, 17 Jun 1988, 3.0 mm. 1 female paratype, ovigerous, YPM 9261 (same data as YPM 9260), 2.4 mm. 2 paratypes, male, female, YPM 9262, Ferry Reach, St. George's, Bermuda, E. A. Lazo-Wasem, 29 May 1987, 3.3 mm (male) and 2.2 mm (female). 1 male paratype, YPM 9263, Whalebone Bay, St. George's, Bermuda, E. A. Lazo-Wasem, 31 May 1987, 3.3 mm. 3 paratypes, 1 male, 2 female (1 ovigerous), YPM 8371, Tobacco Bay, St. George's, Bermuda, M. F. Gable, 2 Jun 1985, 4.6 mm (male), 3.4 mm (ovigerous female), 2.3 mm (female). 1 male paratype, YPM 8359, Bailey's Bay, Bermuda, A. J. Baldinger, 22 May 1987, 3.4 mm, 25 ft, SCUBA, algae attached to sand. 1 female paratype, ovigerous, YPM 8360, Whalebone Bay, St. George's, Bermuda, E. A. Lazo-Wasem, 31 May 1987, within *Thalassia testudinum* Konig & Sims and *Syringodium filiforme* Kütz. 1 juvenile paratype, YPM 9268, Shelly Bay, off Promontory, Bermuda, M. F. Gable, 27 May 1987, 2.5 mm. 1 male paratype, YPM 8357, Bailey's Bay, Bermuda, A.J. Baldinger, 22 May 1987, 3.3 mm, 25 ft, SCUBA, washed from algae attached to coral heads. 1 male paratype, deposited by YPM in Bermuda Museum of Natural History, Bailey's Bay, Bermuda, E. A. Lazo-Wasem, 17 Jun 1988, from algal washings. 1 female paratype, ovigerous, deposited by YPM in Bermuda Museum of Natural History (same data as YPM 9259).

Conclusions

Both Barnard & Karaman (1991) and Thomas & Barnard (1992b) provide a useful generic diagnosis for *Podocerus* and a species list. Considerable confusion still remains, however, regarding the taxonomy of *Podocerus.* Several authors (Barnard 1962, Nath 1972, Laubitz 1983, Ledoyer 1986) review the taxonomic problems and strongly suggest the need for a complete revision of the genus. Podocerids tend to be very fragile; limbs are often missing or broken, and descriptions and illustrations are incomplete for many species. Morphologically, the known intraspecific variability of podocerids amplifies the confusion regarding the taxonomy of this genus (Nath 1972).

A practical approach to the *Podocerus* problem is to give specific names to each population separated by considerable geographical distances, rather than assuming local variation on the part of one and the same species (Ledoyer 1986). In addition, Ledoyer recommends that the armature of the pereon, the configuration of gnathopods 1–2, particularly the palm and dactyl, and the morphology of the uropods and telson should be taken as reliable criteria for the identification of species of *Podocerus.* Despite Ledoyer's suggestion that any new podocerid not seeming to fit an existing species should for now be described as a new species, the authors believe that these two podocerids from Bermuda are not just variations but are genuinely new species.

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SYSTEMATIC IMPLICATIONS OF COLOR PATTERN POLYMORPHISM IN *GONIOPSIS PULCHRA* (DECAPODA: BRACHYURA: GRAPSIDAE) FROM ECUADOR

Richard von Sternberg

Abstract.—Three species in the genus *Goniopsis* de Haan are currently recognized: *G. pelii* Herklots, *G. cruentata* Latreille, and *G. pulchra* Lockington, found respectively along the coasts of tropical west Africa, the Caribbean, and the tropical east Pacific. Color pattern is used to distinguish between these species, with only minor morphological differences separating them. Specimens of *G. pulchra* collected from the coast of southern Ecuador were found to be variable in color. The overlap in color pattern phenotypes between some *G. pulchra* populations and *G. cruentata* suggests that both are subspecies of one American polytypic species, although hybridization between the two species or a sibling species-complex remain as less likely possibilities. Notes on the ecology and distribution of the color morphs are also presented.

Increased attention has been given recently to the importance of color pattern in the systematics of decapod crustaceans. Knowlton & Mills (1992), for example, have demonstrated that color morphs of several morphological species of alpheid shrimp represent reproductively isolated and biochemically distinct taxa and recognize that "color pattern holds enormous potential for defining species boundaries in this systematically difficult genus." The use of color patterns to differentiate among cryptic and sibling species in decapods may be applicable to the Brachyura as well (e.g., Williams & Felder 1986).

The grapsid genus *Goniopsis* de Haan (1833) consists of three sister species, *G. pelii* Herklots (1851), *G. cruentata* Latreille (1803), and *G. pulchra* Lockington (1876), which are distributed along the coasts of tropical west Africa, the Caribbean, and Pacific coasts of the tropical Americas, respectively. The three recognized species are virtually identical in morphology (e.g., gonopod structure) and are believed to constitute a species-complex of which two (*G. cruentata* and *G. pulchra*) are geminate (twin) forms. Rathbun (1918) and Manning & Holthuis (1981) differentiated the three species primarily on the basis of color pattern as this appeared to be species specific. While minor morphological differences (width of carapace, relative length of the dactylus and propodus of the fifth pereiopod, configuration of the anterior margin of the carapace, etc.) are stated to exist between the three species, the color patterns which allow the species to be distinguished are treated as diagnostic characters (Manning & Holthuis 1981). A description of the species-specific color patterns is presented in Table 1.

A collection of *G. pulchra* from southern Ecuador revealed considerable variation in color patterns. While no morphological differences (gonopod structure, width relative to length of carapace, ratio of fifth pereiopod dactylus length to propodus length, etc.) were noted, polymorphism in the color pattern of these crabs is described below with a dis-

Table 1.—Putative species-specific carapace color patterns of the three species of the genus *Goniopsis*. Color pattern descriptions are from Chace & Hobbs (1969) for *G. cruentata*, Rathbun (1918) for *G. pulchra*, and Manning & Holthuis (1981) for *G. pelii*. The geographic distribution of each species is also presented.

Species	*G. pelii*	*G. cruentata*	*G. pulchra*
Range	Atlantic: Tropical coast of west Africa	Atlantic: Bermuda, Bahamas and the Caribbean coasts	Pacific: Magdelena Bay, Baja, California to Peru
Carapace color pattern	Dark purple carapace with minute white spots. A conspicuous white stripe is present on the lateral margin of the carapace. Carinae on carapace with dark edgings.	Golden carapace with small purple spots giving a reticulated appearance. Distinct white circles with a dark red border on the lateral margin of the carapace. Transverse carinae on the carapace faint and unpigmented.	Purple-red carapace with irregular yellow or white spots. Distinct white circles with a dark red border on the lateral margin of the carapace. Transverse carinae on the carapace with dark edgings.

cussion of the potential systematic implications. Notes on the ecology and distribution of the color morphs are also presented.

Methods

Specimens of *Goniopsis pulchra* were collected using a large hand net or by hand and the coordinated effort of at least three people. A total of 55 specimens were captured at six collecting sites along the coast of southern Ecuador. The sites of collection were Puerto Exclusas, Guayaquil (02°15.7′S, 79°52.0′W; *n* = 2), San Pablo (02°08.5′S, 80°46.7′W; *n* = 9), Palmar (02°01.0′S, 80°44.1′W; *n* = 5), MonteVerde (02°02.7′S, 80°44.05′W; *n*= 11), Valdivia (02°56′S, 80°44.1′W; *n* = 15), and Rio Mancay, Olón (1°47.5′S, 80°45.4′W; *n* = 8). All of the specimens collected were adults belonging to both sexes with carapace width (cw) measuring from 25 to 46 mm. The color patterns of these specimens have remained quite stable in the preservative. The specimens discussed here have been deposited in the Division of Genetics and Physiology, Centro Nacional de Acuicultura e Investigaciones Marinas, San Pedro de Manglaralto, Ecuador.

Results

During three collecting trips (September 1991, January 1993 and October 1993), specimens of *G. pulchra* were collected exhibiting color patterns that did not fit the description for this species. For example, at two localities (Puerto Exclusas, Guayaquil City and Olón), two different color pattern morphs were observed and collected (Fig. 1). Specimens closely fitting the color description of *G. pulchra* (Table 1) were collected from burrows alongside a brackish-water lagoon of the Río Mancay, Olón, Ecuador (Fig. 1A). The carapace color pattern was purplish-red with widely spaced yellow spots very similar to the description of *G. pulchra* given by Rathbun (1918). (Wilson 1992, presents and agrees with the color pattern of the Olón specimens very well.)

In contrast, *Goniopsis* specimens collected from Puerto Exclusas, Guayaquil, Ecuador, displayed a color pattern distinctly different from the Olón specimens (Fig. 1B). The carapace of these crabs was golden with small purple reticulations (Fig. 1B) and matched the color pattern description of the Atlantic *G. cruentata* provided by Rathbun (1901, 1918) and the drawing presented in Chace & Hobbs (1969).

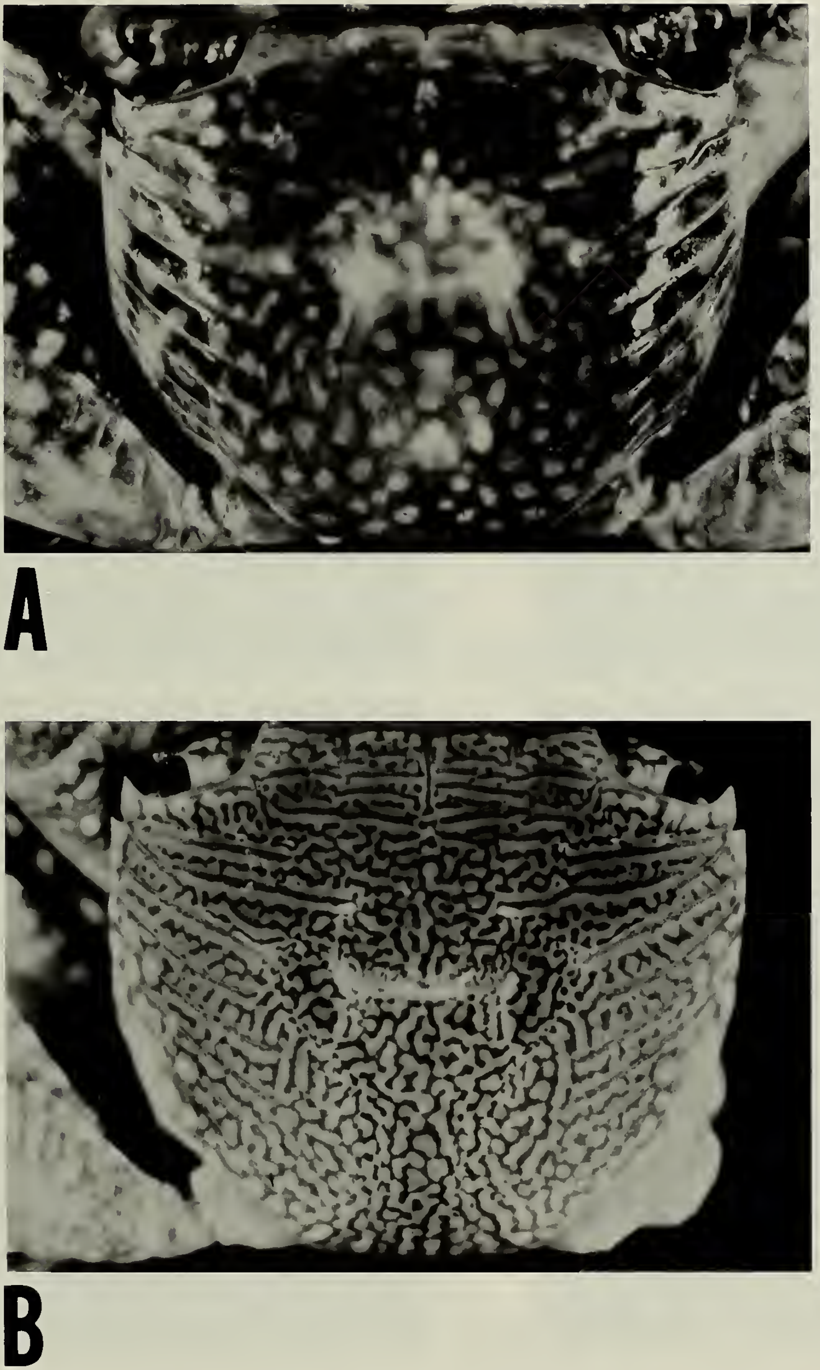

Fig. 1. Color pattern exhibited by two *Goniopsis pulchra* specimens collected from Olón, Ecuador (A), and Puerto Exclusas, Guayaquil, Ecuador (B). The specimen in A, a female (cw = 39 mm), displayed a dark purple-red carapace with widely spaced yellow spots. The front of the carapace in this specimen was bright red. The specimen in B, a male (cw = 32.5 mm), displayed a golden carapace with fine purple reticulations. The front of the carapace in this specimen was yellow.

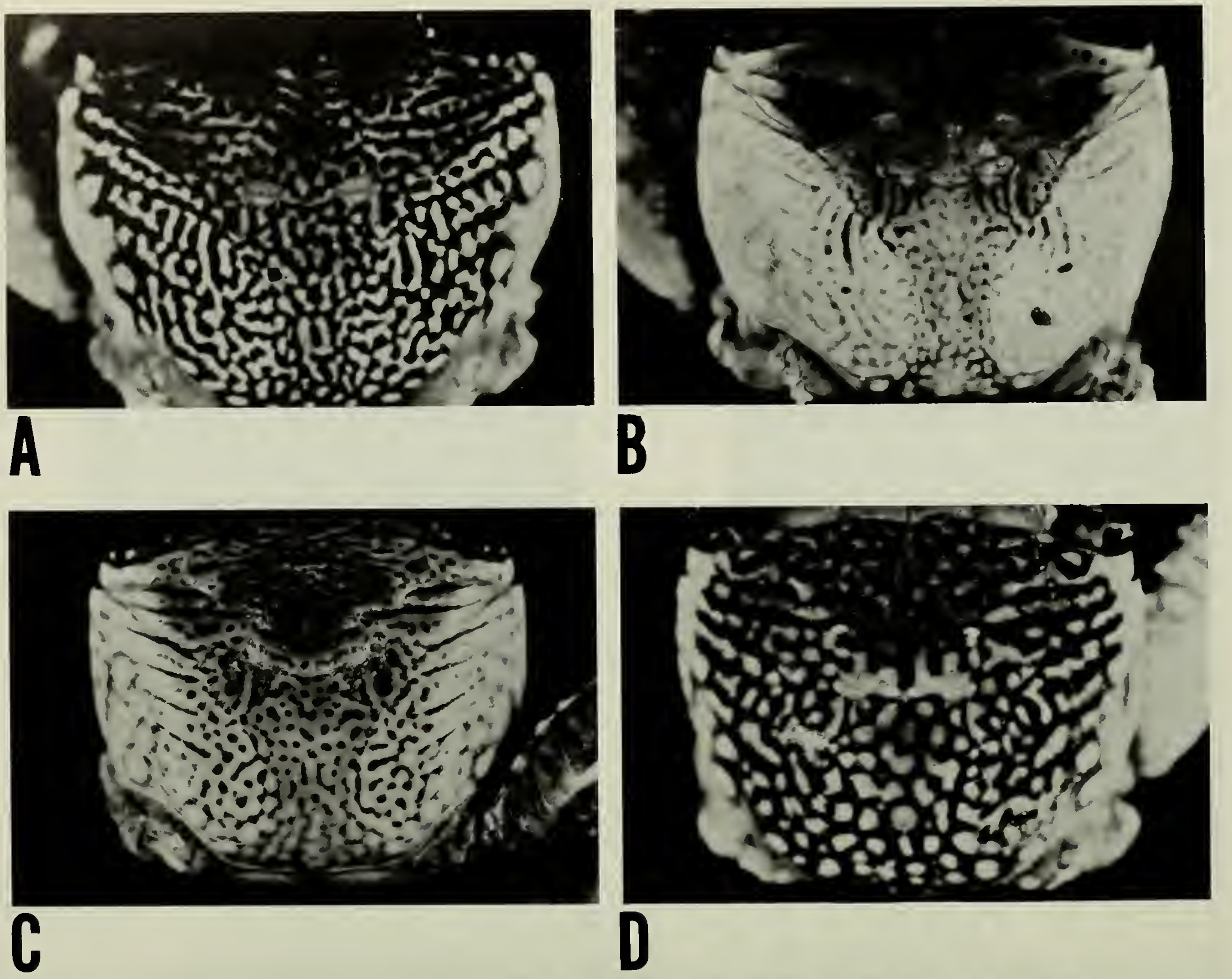

Fig. 2. Color pattern exhibited by *G. pulchra* specimens collected from a lagoon near MonteVerde, Ecuador. Coloration of the specimens are as follows: A, carapace color pattern intermediate between "*G. pulchra*" and "*G. cruentata*" specimens shown in Fig. 1 exhibited by a male (cw = 45 mm). The front of the carapace in this specimen was bright red. B, carapace color of a brilliant orange-yellow male (cw = 42 mm) with no carapace markings except for dark edgings on the transverse carinae. The front of the carapace in this specimen was a bright red. C, a female "*G. cruentata*" color morph (cw = 33 mm). The front of the carapace in this specimen was a bright red. D, a female (cw = 37 mm) "*G. pulchra*" color morph. The front of the carapace in this specimen was a bright red.

The "*G. pulchra*" and "*G. cruentata*" phenotypes were independent of the sex of the crabs.

A more complex array of color patterns was observed in the *G. pulchra* collected from an ecologically disturbed site near Monte Verde, Ecaudor. In an isolated saltwater lagoon fringed with mangroves, specimens were collected with color patterns intermediate between that of the "*G. pulchra*" and "*G. cruentata*" forms in addition to specimens with a different coloration (Fig. 2). One specimen had a color pattern intermediate between that of the specimens in Fig. 1 (Fig. 2A) and this specimen had a dark green-black carapace with large greenish-yellow blotches. Another specimen (Fig. 2B) was brilliant yellow-orange with very faint carapace markings. The color pattern of this individual was quite similar to that of brilliant red individuals also observed at this site. In addition, one specimen displayed a golden carapace with purple reticulations very similar to the "*G. cruentata*" specimen in Fig. 1B (Fig. 2C). A number of other specimens observed were more *G. pulchra*-like in appearance with the exception of the carapace ground color which was dark green-black and with the yellow spots less widely spaced (Fig. 2D).

The various morphs inhabiting the lagoon near Monte Verde were sympatric. Indeed, the four specimens in Fig. 2 were collected within ten meters of each other.

Morphological differences (e.g., gonopod structure) were not apparent between any of the *G. pulchra* specimens. However, one character used by Rathbun (1918) to differentiate *G. cruentata* from *G. pulchra* was carapace width. *Goniopsis cruentata* is described as having a carapace less broad than that of *G. pulchra.* In terms of this character almost all of the Eucadorian specimens can be established as *G. pulchra* with the exception of two individuals, which, while possessing a *G. pulchra*-like color pattern, have a square carapace (Fig. 2D).

Sampling of *G. pulchra* at six locations (see Materials and Methods) revealed geographic partitioning of color morphs which may be related to the ecology of the sampling sites. The *G. cruentata*-like morphs (Fig. 1B) comprise 100% of the population sampled in Guayaquil, San Pablo, Palmar, and Valdivia. The ecology of the sampling sites ranged from the mud banks and rubble of lagoons with little surrounding vegetation (Guayaquil, San Pablo and Valdivia) to the small mangrove forest of Palmar. The intermediate color morphs (Fig. 2A) predominated in Monte Verde (78% of the population) followed in number by the yellow-orange and red morphs (14%) and the "*G. cruentata*" morphs (7%). The MonteVerde site has approximately 20 mangrove trees fringing one region of a lagoon used for commercial salt production. Finally, the "*G. pulchra*" morphs have only been collected in the brackishwater marsh of the Río Mancay in Olón where they predominate and comprise 100% of the individuals collected. However, *Goniopsis cruentata*-like morphs have been observed in Olón. The "*G. pulchra*" morphs in Olón were found to be associated with the root complexes of trees and under logs whereas the *G. cruentata* morphs were observed to occupy burrows in the muddy shores of the lagoon.

Environmental factors which could possibly affect color and color pattern (e.g., food source, substrate, and time of mating) in the adults have been ruled out as laboratory populations from the six sampling sites have been maintained for up to six months with the specimen color patterns remaining constant throughout the moulting cycle.

Discussion

From a systematic point of view, the color pattern polymorphisms observed amongst *G. pulchra* collected from southern Ecuador raise serious questions about the status of *G. cruentata* and *G. pulchra* as distinct taxa. The most likely explanation for the color pattern variability observed is that *G.*

cruentata and *G. pulchra* are subspecies of one polytypic species (Mayr 1963). Gene complexes determining color pattern have been described in other crustacean species (reviewed in Hedgecock et al. 1982). It should be noted that approximately 95% of genes with visible effects in crustaceans involve polymorphisms in color or color pattern (Hedgecock et al. 1982). Extrapolating from the genetic data reviewed in Hedgecock et al. (1982), the "*G. cruentata*" and "*G. pulchra*" phenotypes described above for *G. pulchra* suggest the sharing of color pattern gene alleles between the two American species. An alternative explanation is that the color morphs are ecophenotypes resulting from environmentally dependent color pattern gene expression.

The overlap in color pattern between populations of *G. pulchra* from southern Ecuador and *G. cruentata* also extends to the west African *G. pelii. Goniopsis pelii* is characterized by "having small light spots on a purple background" (Manning & Holthuis 1981). The "*G. pulchra*" morphs are thus more similar in color pattern to *G. pelii* than to *G. cruentata.* The difference between *G. pelii* and *G. pulchra,* however, is the size of the carapace spots which are described as minute in the former (Manning & Holthuis 1981). Some juvenile "*G. pulchra*" morphs from Olón, nonetheless, have minute spots on a dark brown-purple carapace.

Manning & Holthuis (1981) mention a specimen of *G. cruentata* from Brazil with an atypical color pattern. While not describing the color pattern, this would suggest that Atlantic *Goniopsis* populations are also polymorphic for genes controlling color pattern. Rathbun (1918) does state that *G. pulchra* exhibits variability in terms of carapace blotching. Whether intermediate phenotypes constitute the "variability" Rathbun (1918) described is uncertain. It should be noted, however, that no intermediate color morphs were found in the alpheid shrimp sibling species-complex for which color pattern was used as a systematic indicator (Knowlton & Mills 1992).

With an increasing number of decapods being recognized as sibling and cryptic species (Knowlton 1986), it would be imprudent to argue for the conspecificity of *G. pulchra* and *G. cruentata* on color pattern polymorphism alone. A second possibility is that hybridization is taking place between *G. cruentata* and *G. pulchra.* With the exception of the broad "*G. pulchra*" frontal carapace, the color pattern of the specimen in Fig. 1B is identical to *G. cruentata* in almost every respect. Guayaquil is a large port city and *G. cruentata* larvae could have been transported from the Atlantic in ballast water. Should hybridization be taking place, the independent segregation of genes for color pattern and carapace width could well produce the color pattern combinations described here. However, the absence of distinct morphological differences between *G. pulchra* and *G. cruentata* prevents the unambiguous detection of hybrids on anatomical features alone.

A third, although less likely, possibility is that a *Goniopsis* species-complex exists in Ecuador. There is evidence that the *Goniopsis* color forms assortatively mate. At Olón and Valdivia, burrows of the land crab *Cardisoma crassum* were observed to contain pairs of crabs with one pair per burrow. A male and female will similarly share and protect a "burrow" (PVC pipe) in the laboratory. Hybridization between color morphs has nevertheless been observed under laboratory conditions.

There does appear to be geographic partitioning of the color morphs. The geographical partitioning may be the result of selection against brightly pigmented individuals in nonvegetated environments. Specimens from environments with vegetation (e.g., Monte Verde and Olón) were conspicuous in their coloration (brilliant red or yellow pigmentation) whereas crabs from nonvegetated sites were comparatively more drab. The "*G. cruentata*" morphs were predominant at sites with no vegetation where their coloration was similar to that of the substrate. Juveniles (cw less than 20 mm) from all collection localities were a drab brown and cryptic in coloration.

Color pattern is polymorphic in many decapod species and this had led to taxonomic confusion (e.g., mangrove crabs of the genus *Scylla*; Estampador 1949). The polymorphisms observed in *Goniopsis* color pattern, purportedly a taxonomically significant indicator for this genus, suggest that the systematics of *Goniopsis* be reexamined. Color pattern, at least for *G. pulchra* from Ecuador, does not appear to be species specific. Manning & Holthuis (1981), referring to the differences between *G. cruentata* and *G. pelii*, state that a "closer study based on much more material and taking also the West American *G. pulchra* into account may establish that the three shoud be considered subspecies of a single species." The data presented here would support such a taxonomic revision of *Goniopsis*.

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TWO NEW SPECIES AND ONE NEW COMBINATION OF FRESHWATER CRABS FROM MEXICO (CRUSTACEA: BRACHYURA: PSEUDOTHELPHUSIDAE)

Fernando Alvarez and José Luis Villalobos

Abstract.—*Pseudothelphusa guerreroensis* Rathbun, 1933, is referred to the genus *Tehuana* Rodríguez & Smalley, 1969, based on the morphology of the first gonopod, with a lobular marginal process partially fused to the mesial process, and the presence of a distinct superior frontal border of the carapace, both traits characteristic of *Tehuana.* Two new species, *Tehuana lamothei* and *Pseudothelphusa nayaritae,* are described from the Mexican States of Chiapas and Nayarit, respectively. *Tehuana lamothei* was collected 230 km southeast of the present southernmost limit of the genus. *Tehuana lamothei* is recognized by a gonopod with the most reduced mesial process of all of the species in the genus. *Pseudothelphusa nayaritae* belongs to a group of species from western Mexico which lacks a marginal process on the first gonopod.

Two specimens of *Pseudothelphusa guerreroensis* Rathbun, 1933, deposited in the Crustacean Collection, Instituto de Biología, Universidad Nacional Autónoma de México (IBUNAM EM-358), were compared with *Tehuana lamothei,* new species, described in this study. It was judged that the specimens of *P. guerreroensis* should be placed in the genus *Tehuana* Rodríguez & Smalley, 1969. Two key characters separate *Tehuana* from *Pseudothelphusa* de Saussure, 1857: the form of the marginal process of the gonopod, which is rounded and partially fused to the mesial process in the former, and absent or dentiform and completely fused to the mesial process in the latter; and the presence in *Tehuana,* and absence in *Pseudothelphusa,* of a defined superior frontal border of the carapace.

Tehuana lamothei, new species, is described from the mountains of northern Chiapas above 1000 m of altitude. The present work adds a sixth genus (*Tehuana*) to the pseudothelphusid crab fauna of Chiapas. The six genera, *Raddaus* Pretzmann, 1965; *Potamocarcinus* Milne Edwards, 1853; *Typhlopseudothelphusa* Rioja, 1952; *Odontothelphusa* Rodríguez, 1982; *Epithelphusa* Rodríguez & Smalley, 1969; and *Tehuana* Rodríguez & Smalley, 1969, are classified in three different tribes (Hypolobocerini, Potamocarcinini, and Pseudothelphusini). This high diversity is, in part, a reflection of the large number of rivers and the abrupt geography of this region. *Pseudothelphusa nayaritae,* new species, from the Mexican State of Nayarit, represents a modified form within the genus based on its gonopod morphology, since it has lost the characteristic marginal process. The absence of the marginal process is a character shared by five other species of *Pseudothelphusa* found in the western portion of the distribution of the genus. The presumed development of the marginal process (Rodríguez & Smalley, 1969) shows a sequence in which this process, starting from a caudal position (e.g., *Potamocarcinus*), first reaches the apex of the gonopod (e.g., *Spirothelphusa* Pretzmann, 1965), and then becomes recurved over the mesial crest as a conspicuous lobe (e.g., *Tehuana* and *Pseudothelphusa*). All the specimens discussed here are deposited in the Crustacean Collection, Instituto de Biología, Universidad Nacional Autónoma de México (IBUNAM). The gonopod terminology used is that proposed by Smalley (1964) and Smalley & Adkison (1984). Carapace width and carapace length are abbreviated as cw and cl; catalog numbers are preceded by the letters EM which denote an access code.

Tehuana Rodríguez & Smalley, 1969

Remarks.—The genus *Tehuana* was created to separate a subgroup of species of *Pseudothelphusa* with gonopods that exhibit a distinctly rounded marginal process only partially fused to the mesial process and a well marked superior frontal border of the carapace. The species are distributed west of the Isthmus of Tehuantepec (Rodríguez & Smalley 1969). The five species of *Tehuana* (*T. lamellifrons* Rathbun, 1893; *T. complanata* Rathbun, 1905; *T. veracruzana* Rodríguez & Smalley, 1969; *T. poglayenorum* Pretzmann, 1980; and *T. diabolis* Pretzmann, 1980) exhibit a progressive increase in size of the mesial process of the gonopod on a westward direction from Los Tuxtlas region, in the State of Veracruz.

Tehuana guerreroensis (Rathbun, 1933), new combination
Figs. 1, 4a–b

Pseudothelphusa guerreroensis Rathbun, 1933:360.—Pretzmann, 1965:10.—Smalley, 1970:105.

Pseudothelphusa (*Pseudothelphusa*) *guerreroensis* Rodríguez & Smalley, 1969:79, fig. 11, pl. 7.—Pretzmann, 1971: 22.—Pretzmann, 1972:104, figs. 640–642.

Pseudothelphusa guerreroensis Rodríguez, 1982:135, fig. 87.

Material examined.—1 male, cw 38.0 mm, cl 24.5 mm; Copanatoyac, Guerrero (17°27′N, 98°35′W), 26 Oct 1963, coll. M. Rosas; IBUNAM EM-358. 1 female, cw 55.3 mm, cl 35.0 mm; same locality, date, and collector as holotype; IBUNAM EM-358a.

Description.—Carapace slightly convex, surface smooth. Superior frontal border marked by irregular blunt tubercles. Front smooth, divided by median groove, slightly bilobed in dorsal view (Fig. 4a). Inferior frontal border prominent, composed of blunt tubercles, continuous with superior border of orbits. Median groove narrow and deep, dividing superior frontal border and front. Postfrontal lobes elevated, limited anteriorly by distinct groove. Cervical grooves arched, deep, wide, not reaching anterolateral margin. Gastric and branchial regions elevated. Branchial region divided by shallow depression. Anterolateral margin continuous, formed by blunt, irregular denticles. Ischium of third maxilliped trapezoidal, distal part wider than proximal part (Fig. 1d). Merus of third maxilliped broad, with external margin rounded, becoming straight distally; inner margin straight, with portion at base of carpus slightly arched. Ratio exopod/ischium of third maxilliped 0.71. Right chela missing. Left chela slender, surface smooth, with distinct large rounded tubercle at base of fixed finger (Figs. 1e, 4b). Fingers not gaping.

Gonopod curved in lateral view, straight in cephalic and caudal views (Fig. 1b, c). Apex with lateral process oval-shaped, with sharp triangular tooth oriented caudally (Fig. 1a). In lateral view, marginal and mesial processes oriented proximally. Mesial process reniform. In cephalic view, apex cavity exposed, terminal pore setae visible; marginal and mesial processes curved mesially. In caudal view, lateral and mesial crests of apex of same height, marginal and mesial processes completely separated, lateral process with large triangular tooth in central section.

Remarks.—The holotype of this species is a female deposited in the Berlin Zoology Museum. The type locality was reported erroneously in the original description by Rathbun (1933) to be "Malinaltepec, south of Teopa, Guerrero." The correct type locality is "Malinaltepec, south of Tlapa,

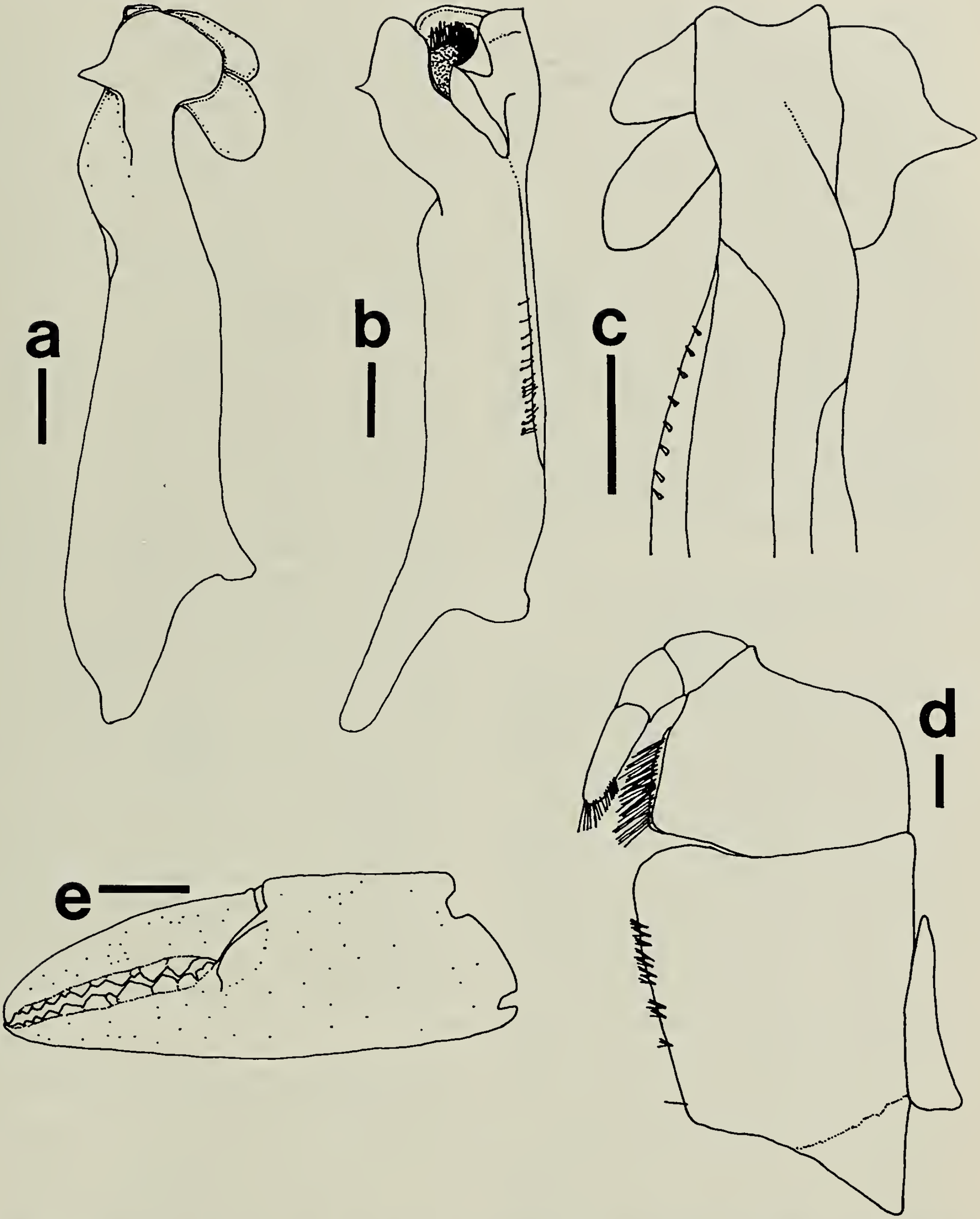

Fig. 1. *Tehuana guerreroensis,* new combination, a–c left gonopod: a, lateral view; b, cephalic view; c, caudal view; d, third maxilliped; e, left chela. Scale bars: a–d = 1 mm, e = 5 mm.

Guerrero," and cannot be located precisely since "Malinaltepec" is the name of a small mountain range, not of a town. Rodríguez & Smalley (1969) described the first male of the species from "Copanatoyac, 40 km southwest from the type locality," and also wrongly reported the type locality as "Malinaltepec south of Teapa, Guerrero." In spite of the fact that the male described by Rodríguez & Smalley (1969), and redescribed in this paper, cannot be a type specimen, its description has become the only reference to identify the species. We propose the assignment of *Pseudothelphusa guerreroensis* to the genus *Tehuana,* based on the presence of a distinct superior frontal border of the carapace and on the partially fused marginal and mesial processes in the male gonopod.

Tehuana lamothei, new species
Figs. 2, 4c

Holotype.—Male, cw 27.3 mm, cl 18.2 mm; Arroyo La Piedra, 1 km from Ixtacomitán, Chiapas (17°25′N, 93°05′W), 4 Apr 1986, colls. J. C. Nates, A. Cantú, D. Valle, and E. Lira; IBUNAM EM-5604.

Material examined.—2 males designated as paratypes, cw 33.7, 32.0 mm, cl 21.5, 20.8 mm; Tapilula, Chiapas (17°15′N, 93°01′W), 20 Apr 1981, coll. R. Lamothe, IBUNAM EM-8812. 4 males, cw 22.9, 22.5, 21.0, 17.3 mm, cl 15.4, 15.0, 14.0, 11.9 mm; 1 female, cw 34.8 mm, cl 22.2 mm; same locality and collectors as holotype; IBUNAM EM-5604a. 2 males, cw 37.4, 13.7 mm, cl 23.9, 9.2 mm; 1 female, cw 49.7 mm, cl 31.6 mm; same locality and collectors as paratypes; IBUNAM EM-8812a.

Description.—Dorsal surface of carapace slightly convex, smooth, covered with fine punctations. Superior frontal border straight, prominent, formed by small tubercles, divided by deep median notch, disappearing laterally behind orbit. In frontal view, inferior frontal border continuous, sinuous, thinner than superior one (Fig. 4c). Median groove narrow between postfrontal lobes; in dorsal view, deep and wide forming V-shaped notch in front. Postfrontal lobes limited anteriorly by shallow depressions. Cardiac region discernible. Cervical grooves deep, strongly curved, reaching anterolateral margin producing small notch. Anterolateral margin with 21–23 small denticles between cervical groove and epibranchial region. Merus of third maxilliped with distolateral margin rounded, distal and inner margins straight (Fig. 2e). Ratio exopod/ischium of third maxilliped 0.75. Major chela right, inner surface globose, fingers not gaping, and curved inwards distally (Fig. 2f). Propodus of fifth walking leg with distinct ridge bearing spines on ventral margin.

Gonopod curved in cephalic, lateral, and caudal views, straight in cephalic view (Figs. 2a–d). Apex bearing three distinct lobes or processes. In cephalic view, lateral process with superior margin describing a semicircle, with sharp triangular tooth oriented caudally, and small rounded tooth on cephalic margin. In lateral view, lateral process oriented caudally, marginal and mesial processes oriented anteriorly at 90° angle with respect to longitudinal axis of gonopod. Mesial process broadly rounded, partially fused to marginal process. Small blunt projection on mesial surface close to mesial crest, visible in cephalic and caudal views. Lateral crest of apex cavity rounded, higher than mesial crest. Field of terminal pore setae elongated on lateral portion of apical cavity.

Etymology.—This species is named after our colleague Rafael Lamothe, from Instituto de Biología at UNAM.

Remarks.—*Tehuana lamothei* exhibits the key characters that distinguish *Tehuana* from *Pseudothelphusa,* namely: the conspicuous superior border of the carapace and the gonopod's broadly rounded mesial process, partially fused to the also rounded marginal process. Relative to the other species of the genus, the gonopod morphology places *T. lamothei* at one end of the range of variation: it possesses the most reduced

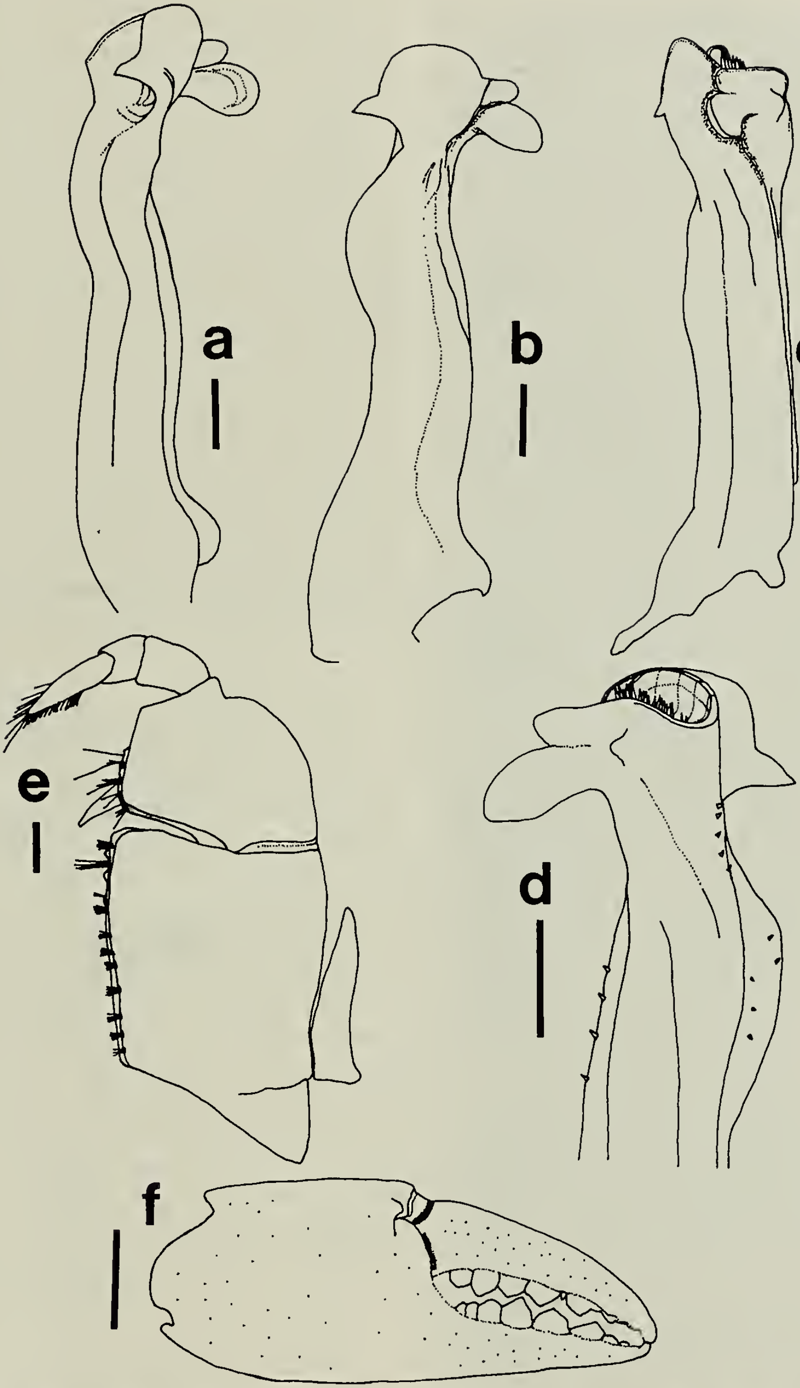

Fig. 2. *Tehuana lamothei,* new species, a–d left gonopod: a, lateral view; b, laterocephalic view; c, cephalic view; d, caudal view; e, third maxilliped; f, right chela. Scale bars: a–e = 1 mm, f = 5 mm.

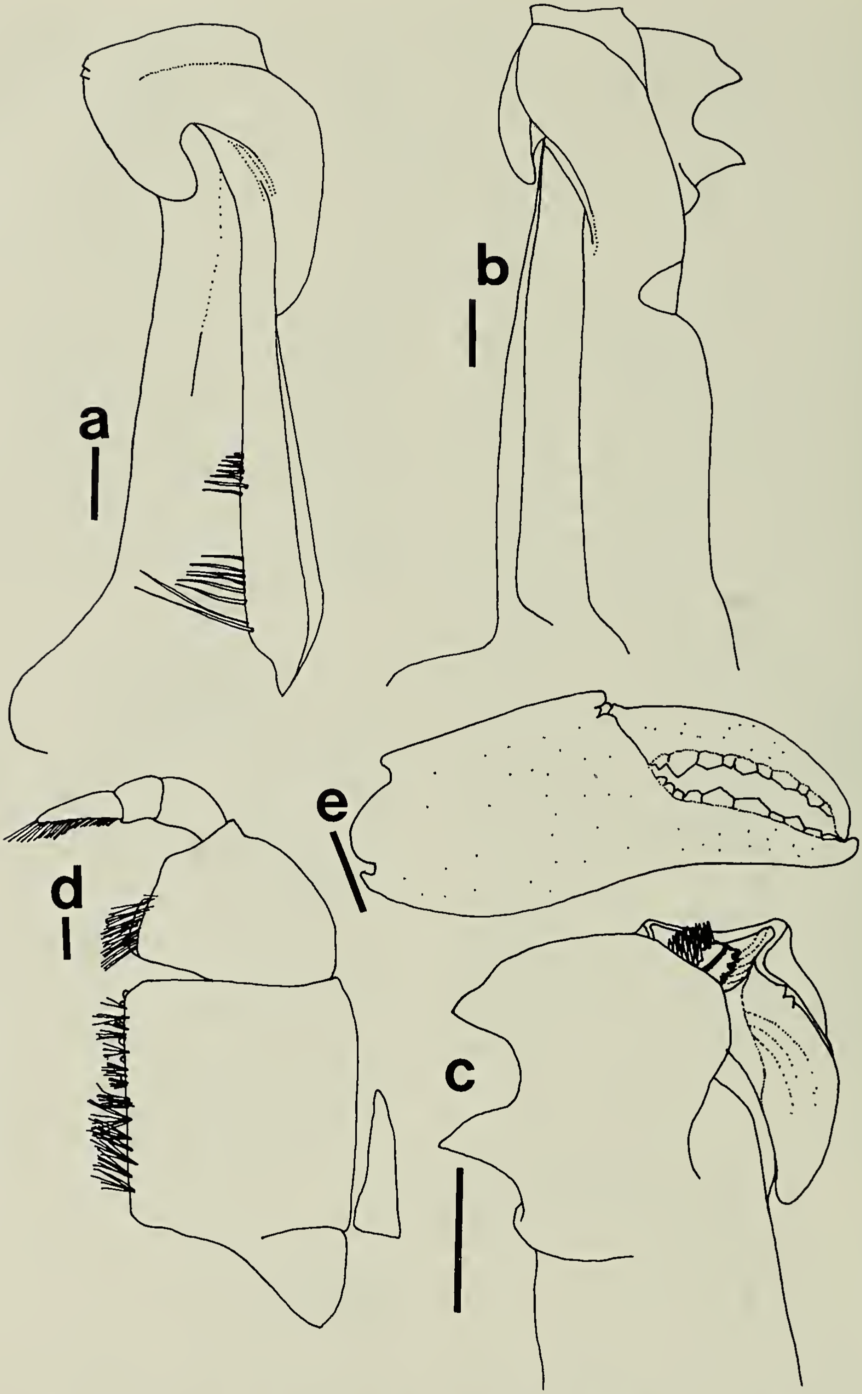

Fig. 3. *Pseudothelphusa nayaritae,* new species, a–c left gonopod: a, mesial view; b, caudal view; c, cephalic view; d, third maxilliped; e, right chela. Scale bars: a–d = 1 mm, e = 5 mm.

mesial process, that forms a 90° angle with respect to the longitudinal axis (i.e., oriented anteriorly); and its lateral process is the largest within the genus. In the other five species of *Tehuana,* the mesial process progressively increases in size, is oriented proximally, and the lateral process becomes very reduced. This sequence of gradual morphological change, which has been described for other pseudothelphusid crabs (Alvarez 1989; Alvarez & Villalobos 1991; Rodríguez 1982, 1987), also coincides in species of *Tehuana* with their geographical distribution. *Tehuana lamothei,* at one end of the spectrum, marks the southeastern limit of the range of the genus; *T. poglayenorum* and *T. diabolis,* with their intermediate morphology, occur in the central portion of the range; and *T. veracruzana* and *T. complanata,* occurring to the west, have the most enlarged mesial process.

Pseudothelphusa de Saussure, 1857

Remarks.—The genus *Pseudothelphusa* is distributed in Mexico from the 18°N parallel northwards, from the Gulf of Mexico, in Los Tuxtlas, Veracruz, across central Mexico to the Pacific slope. *Pseudothelphusa* is distinguished from the closely related *Tehuana* based on the marginal process of the gonopod which is completely fused to the mesial process, and in many species it appears as a sharp tooth (e.g., *P. parabelliana,* Alvarez, 1989). The marginal process can be reduced to a series of small denticles (e.g., *P. jouyi,* Rathbun, 1893) or be completely absent (e.g., *P. galloi,* Alvarez & Villalobos, 1990). The superior frontal border of the carapace is absent in most of the species of *Pseudothelphusa.*

Pseudothelphusa nayaritae, new species
Figs. 3, 4d

Holotype.—Male, cw 40.3 mm, cl 23.1 mm; Arroyo El Guayabito, Mecatán, Nayarit (21°30′N, 105°10′W), 5 Apr 1984, coll. R. Lamothe; IBUNAM EM-8820.

Fig. 4. *Tehuana guerreroensis,* new combination: a, front of carapace; b, right chela (cw 38.0 mm). *Tehuana lamothei,* new species: c, front of male holotype (cw 27.3 mm). *Pseudothelphusa nayaritae,* new species: d, front of male holotype (cw 40.3 mm).

Material examined.—1 female, cw 42.6 mm, cl 25.4 mm; same locality, date, and collector as holotype; IBUNAM EM-8820a.

Description.—Dorsal surface of carapace convex, smooth, covered with small papillae. Superior frontal border absent; front limited by a folding of the carapace. Inferior frontal border smooth, straight in frontal view; slightly biconvex in dorsal view, continuous with orbits (Fig. 4d). Region between front and postfrontal lobes sloping markedly towards front. Postfrontal lobes discernible. Median groove slightly marked between postfrontal lobes. Cervical grooves deep, straight anteriorly, curved towards gastric region posteriorly, not reaching anterolateral margin. Cardiac region indicated by conspicuous depressions. Posterior margin of carapace markedly biconvex in dorsal view. Anterolateral margins smooth, devoid of denticles. Ratio of exopod/ischium of third maxilliped 0.58. Major chela right, surface of palm smooth, fingers gaping and curving inwards distally (Fig. 3e).

Gonopod thick, strong. In mesial view (Fig. 3a), mesial process reniform, recurved proximally; marginal process reduced to 2 small triangular teeth situated on superior cephalic angle of mesial process. In cephalic view (Fig. 3b), gonopod decreasing in thickness distally; apex of gonopod with broad lateral process, rounded superior margin, laterally bearing 2 sharp triangular projections, forming wide U-shaped notch. In caudal view (Fig. 3c), sperm channel constricted at ⅔ of its length, curved mesially; sharp projections of lateral and mesial processes visible. Apex cavity elongated along a caudocephalic axis, mesial crest higher than lateral one, and field of terminal pore setae restricted to lateral portion of cavity.

Etymology.—The species name makes reference to the State of Nayarit, where the species was collected.

Remarks.—The description of *P. nayaritae* brings the number of species of *Pseudothelphusa* to 21, including *P. puntarenas* (Hobbs 1991) from Costa Rica, which is assigned to the genus *Pseudothelphusa* with caution due to its distribution and gonopod morphology. *Pseudothelphusa nayaritae* shares with *P. galloi, P. jouyi, P. lophophallus* Rodríguez & Smalley, 1969, *P. rechingeri* Pretzmann, 1965, and *P. sonorae* Rodríguez & Smalley, 1969, all distributed in western Mexico, the complete reduction of the marginal process of the gonopod. The vestiges of the marginal process are apparent only in *P. jouyi, P. lophophallus,* and *P. nayaritae,* in the form of a series of small teeth located on the superior cephalic angle of the mesial process of the gonopod. The lateral process of the gonopod in *P. nayaritae* is reminiscent of that of the *P. dilatata* Rathbun, 1898, species complex in central Mexico (Rodríguez 1982). *Pseudothelphusa nayaritae, P. peyotensis* (Rodríguez & Smalley 1969) and *P. leiophrys* (Rodríguez & Smalley 1969), are all found in the State of Nayarit. *Pseudothelphusa leiophrys* was originally described from the State of Colima (Rodríguez & Smalley 1969), and was recently collected in Nayarit, from El Durazno, 2 km north from Los Sabinos (IBUNAM EM-12294).

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A NEW SPECIES OF ANEMONE-CARRYING CRAB FROM NEW CALEDONIA (DECAPODA: BRACHYURA: XANTHIDAE: POLYDECTINAE)

Cheryl G. S. Tan and Peter K. L. Ng

Abstract.—A new species of polydectine crab, *Lybia tutelina,* from New Caledonia is described. It differs from other *Lybia* species in the structure of the male first gonopods, endopod of the first maxilliped, more rounded shape of the carapace, structure of the antennary fossae, and anterolateral margin of carapace. *L. tutelina* appears to be related to *L. hatagumoana* Sakai, 1961, from Japan, but the carapace, chelae and gonopods of the two species are substantially different.

Members of Polydectinae Dana, 1851, are generally recognized by their anemone-carrying behavior which presumably serves a protective function. The Polydectinae presently consists of only two genera: *Lybia* H. Milne Edwards, 1834, and *Polydectus* H. Milne Edwards, 1837. The genus *Lybia* consists of nine species: *L. australiensis* (Ward 1933), *L. caestifera* (Alcock 1896), *L. denticulata* Nobili, 1906, *L. edmondsoni* Takeda & Miyake, 1970, *L. hatagumoana* Sakai, 1961, *L. leptochelis* (Zehntner 1894), *L. plumosa* Barnard, 1947, *L. pugil* (Alcock 1896) and *L. tessellata* (Latreille 1812).

Partial revisions of the Polydectinae have been carried out by Guinot (1976) and Serène (1984). Both recognized three distinct groups within *Lybia*: the *L. tesellata* and *L. edmondsoni* group, the *L. plumosa* and *L. leptochelis* group, and *L. denticulata* by itself, this species being regarded as an intermediary between *Polydectus* and *Lybia.* This separation was based on characters such as structure of the carapace, the anterolateral border, the endopods of the first and third maxillipeds, the sternal plastrons, the chelipeds and the male first pleopod. Guinot (1976) did not, however, decide on the status of *L. australiensis, L. caestifera, L. hatagumoana* and *L. pugil* because she was unable to examine the type or other specimens of these species.

One species, *L. australiensis,* was originally placed in the genus *Prolybia* Ward, 1933. The species has not been reported since 1933. Serène (1968, 1984), Sakai (1967) and Guinot (1976) regarded *Prolybia* as a synonym of *Lybia.* The validity of the genus *Prolybia* can only be ascertained when its type species is re-examined.

In this paper, a new species of polydectine from New Caledonia, *Lybia tutelina,* is described. This species, with *L. hatagumoana,* appears to comprise yet another group within *Lybia.*

The abbreviations G1 and G2 are used for the male first and second pleopods respectively. Measurements (in millimeters) of the carapace are given as length times width. The acronym ORSTOM refers to Institut Francais de Recherche Scientifique pour le Développement en Coopération, Paris. The type specimen is deposited in the Muséum national d'Histoire naturelle (MNHN), Paris.

Family Xanthidae MacLeay, 1838
Subfamily Polydectinae Dana, 1851
Lybia tutelina, new species
Figs. 1, 2

Material examined.—Holotype male (MNHN-22773) 5.3 × 5.3 mm, New Caledonia, R/V *Alis,* Stn. DW 1174, coll. B.

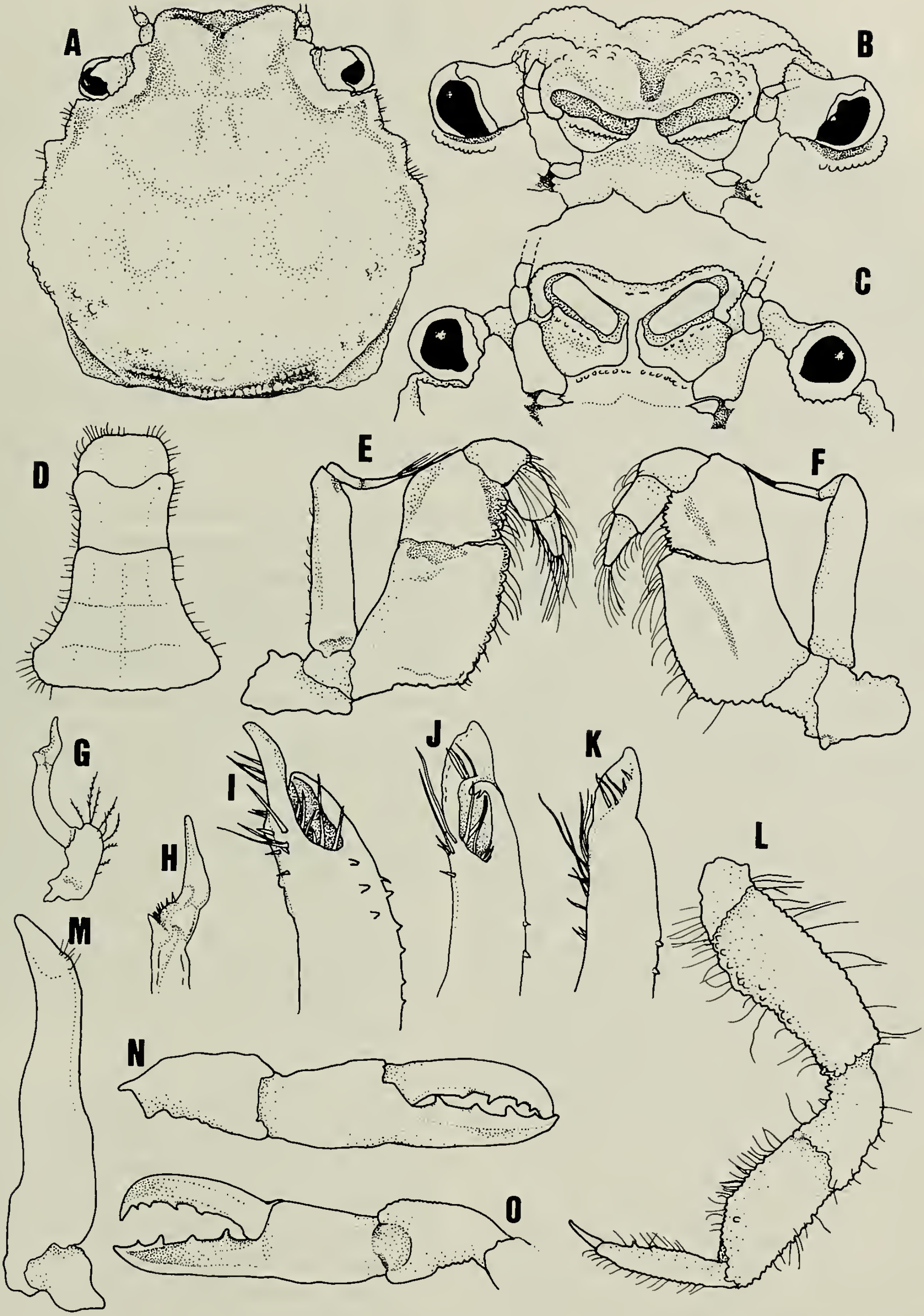

Fig. 1. *Lybia tutelina,* new species, holotype male (5.3 × 5.3 mm). A, carapace, dorsal surface; B, same frontal view; C, same front, ventral view; D, abdomen, excluding segments 1 and 2; E, left third maxilliped, inner surface; F, left third maxilliped, outer surface; G, right G2; H, tip of right G2; I–K, tip of right G1; L, right last leg, upper surface; M, right G1; N, right cheliped, outer surface; O, right cheliped, inner surface.

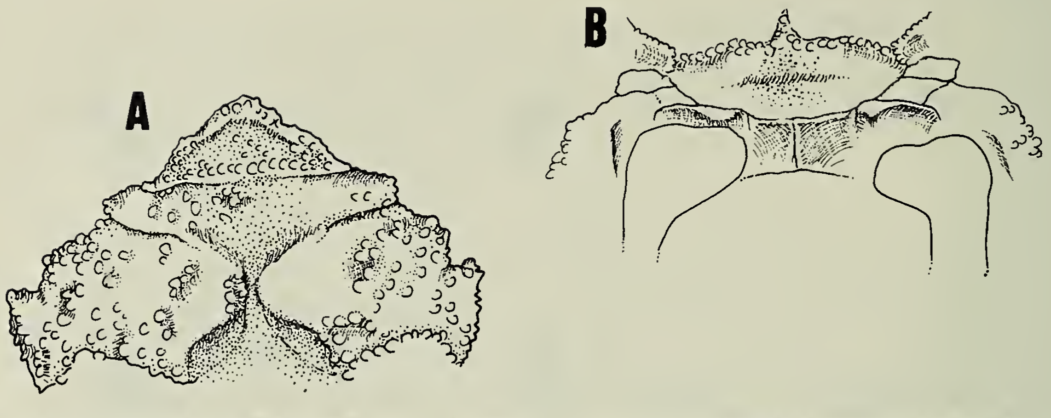

Fig. 2. *Lybia tutelina,* new species, holotype male (5.3 × 5.3 mm). A, anterior sternum; B, buccal region and endopods of first maxillipeds.

Richer de Forges, ORSTOM, 31 Oct 1989. Paratype female (MNHN-22774) 6.2 × 6.2 mm [ovigerous], New Caledonia, South Great Reef, Stn. 378bis, 74–76 m, 22°33′S–167°09′E, coll. B. Richer de Forges, ORSTOM, 21 Jan 1985.

Description of holotype male.—Carapace sub-globular, as long as broad, surface finely granular, sparsely pubescent, particularly at margins, anterior region between orbits raised to form 2 convexities posterior to front; anterolateral margin with 3 broad, triangular lobes (including external orbital angle), posterior-most being rather irregularly shaped, and lower than first two, each lobe bordered by fine granules; posterolateral margin rounded; posterior border with 2 rows of granules. Front squarish, slightly deflexed, with shallow median cleft. Margin of orbits lined with granules, supraorbital margin with cleft just behind cornea, infraorbital margin divided into 2 large pointed lobes. Posterior margin of carapace distinctly granulated. Antennal flagellum long, slender, basal segment large, elongate and rectangular, free, completely occupying orbital hiatus; antennular fossa oblique, basal segment large, free, anterior border with row of fine granules. Posterior margin of epistome with triangular central lobe. Inner margin of third maxillipeds with long setae; ischium 1.4 times longer than merus when measured along inner border, rectangular, inner margin coarsely granular, outer surface with weak, oblique, median sulcus; exopod slender, reaching to level of posterior half of merus; merus rounded along outer margin, inner margin with pointed granules, outer surface with short, weak, oblique median sulcus, palp 3-segmented, robust. Endopod of first maxilliped with straight anterior edge; inner angle rounded, inner margin curving gently outwards; outer angle sub-perpendicular, outer margin straight.

Anterior sternum coarsely granular, particularly around edges, sternite 4 demarcated from sternite 3 by shallow groove, sternites 3 and 2 separated by clear, moderately shallow groove, no suture between sternites 1 and 2.

Ambulatory legs short and thick, finely granular, inner edges appearing more coarsely granular than outer edges, edges sparsely pubescent. Chelipeds equal, symmetrical, slender, elongate; palm rectangular, fingers 1.4 times longer than palm, movable finger with hooked tip, cutting edge with 3 large, backward-pointing teeth and 1 denticle subdistally, immovable finger with 3 evenly spaced teeth and 1 denticle subdistally.

Abdomen sparsely hairy along borders,

Table 1.—Differences between *L. tutelina* and *L. hatagumoana*.[a]

	Lybia tutelina	*Lybia hatagumoana*
Carapace	As long as broad	Slightly longer than broad
Male abdomen	Segments 3–5 fused	All segments free[b]
G1	Short and stout, almost straight	Long, slender and sinuous
Dentition of fingers of cheliped	Movable and immovable fingers with 3 teeth and 1 subdistal denticle each	1 tooth on movable finger, 2 backward curving teeth on movable finger
Anterolateral margins of carapace	Trilobed (inclusive of external orbital angle) lobes obtuse, subequal	Trilobed (inclusive of external orbital angle) first epibranchial lobe large, with 2 small lobes on either side, lobes acute to subacute

[a] Based on Sakai (1961).

[b] Sakai (1961:144) described the male abdomen in *L. hatagumoana* as consisting of "seven free segments. . . ." Whether the segments are freely movable or fused but with visible sutures can only be ascertained when the type specimens are examined. In all other species of *Lybia*, including the new species, *L. tutelina*, segments 3–5 are fused.

with segments 3–5 fused, sutures faint; distal end of segment 6 bilobed; telson with truncated apex. G1 stout, 2.3 times longer than G2, distal portion sparsely covered with long setae and conical spines, apex bifurcated, with petaloid terminal process; G2 with pointed distal process, short spines subterminally.

Paratype female.—Female similar to male, except for margins of second and third anterolateral lobes more distinctly denticulated.

Etymology.—The Latin "tutelina" is a general term for any guardian deity, and is here used as a noun in apposition.

Discussion

There are certain difficulties in placing this new species in the existing species alliances suggested by Guinot (1976) and Serène (1984). From the figures given by Sakai (1961:142, figs. 2a–d; 1965:162, pl. 80, fig. 1; 1976:pl. 180, fig. 3), *L. hatagumoana* appears related to *L. tutelina*, in terms of the sub-globular carapace which is only slightly longer than broad, the fingers of the cheliped being slightly longer than the palm, and the dentition of the cheliped fingers. However, *L. tutelina* has a much stouter, straighter and shorter G1 relative to G2, whereas in *L. hatagumoana*, the G1 is longer, slender and sinuous. In this respect, *L. tutelina* resembles *L. plumosa* (see Guinot 1976:94, fig. 21A–C) and *L. leptochelis* (see Guinot 1976:94, fig. 21E, F). Differences between *L. tutelina* and *L. hatagumoana* are tabulated in Table 1.

L. hatagumoana appears to be a rare species, being originally recorded from Amaidaba, off the coast of Hayama, by Sakai (1961) and thereafter only from the Wakayama Prefecture, Japan, by Nagai (1990).

The male holotype of *L. tutelina* was carrying an anemone in each chela as is typical of crabs in this genus. The ovigerous paratype female carried only one anemone (in the left chela), the right chela was free.

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THREE NEW RARE *HETEROKROHNIA* SPECIES (CHAETOGNATHA) FROM DEEP BENTHIC SAMPLES IN THE NORTHEAST ATLANTIC

Jean-Paul Casanova

Abstract.—Three new rare chaetognath species of the genus *Heterokrohnia,* each represented by a single specimen, are described from deep benthic samples, two off northwest Africa (*H. angeli* and *H. discoveryi*) and one in the Bay of Biscay (*H. biscayensis*). They differ by many characters from hitherto known species, most important among these the number and shape of teeth. The diversity of the benthoplanktonic chaetognath fauna is probably as high as that of the planktonic one.

Chaetognath species of the family Heterokrohniidae are known to live in the water layer just above the sea bed (Casanova 1986a). Most of them have been described from the large R. V. *Discovery* collections: seven from deep near-bottom planktonic samples and another (*Heterokrohnia mirabiloides* Casanova & Chidgey, 1990) from benthic sledge samples. However, the gears used, trawls or sledges, are poorly adapted to catch these fragile animals, which thus are often more or less damaged. Nevertheless, even if slightly twisted, a single specimen may be described as a new species if its characteristics are so particular as to avoid any confusion with previous known species. This is the case for the three new species described below.

Heterokrohnia angeli, new species
Figs. 1a, 2a, 3a–d

Material examined.—*Discovery* St. 8976, BN2-4, 5 Aug 1976, 32°54.4′N, 11°38.5′W, 3610–3646 m, holotype (Natural History Museum, London, 1994. 2095).

Description.—The specimen is 6 mm in body length without tail fin. Tail constitutes 40% of this length. Body stumpy (Fig. 1a) and opaque.

Head triangular with a small apical gland cell complex. Anterior teeth, 8/9, short and conical (Figs. 2a, 3a, d). Posterior teeth, 13/14, slightly longer (Figs. 2a, 3b, c). All teeth with apical part differentiated (Figs. 2a, 3c, d). Hooks not numerous, 9 on each side. Vestibular organs oval, thin and smooth (Figs. 2a, 3c). Eyes absent. Corona ciliata and glandular neck canals not observed. Neither collarette (very probably stripped off), nor gut diverticula present. Transverse musculature very thin and difficult to observe (for this purpose the body has been cleared with lactic acid and stained with methylene blue); it extends from neck to slightly beyond the large ventral ganglion in trunk and in about the first sixth of tail.

Lateral fins begin beyond the ventral ganglion, at a distance less than half the ganglion length. Tail fin damaged. All fins with numerous rays. Ovaries not developed. Seminal vesicles large, opening posterolaterally, in contact with both lateral and tail fins.

Comparisons with other species.—The shape of teeth immediately differentiate *H. angeli* from all known *Heterokrohnia* species but one, *H. bathybia* Marumo & Kitou, 1966 from southern Japan. Indeed the latter has both anterior and posterior teeth described as "thick and short", but their extremity is not differentiated and they are less

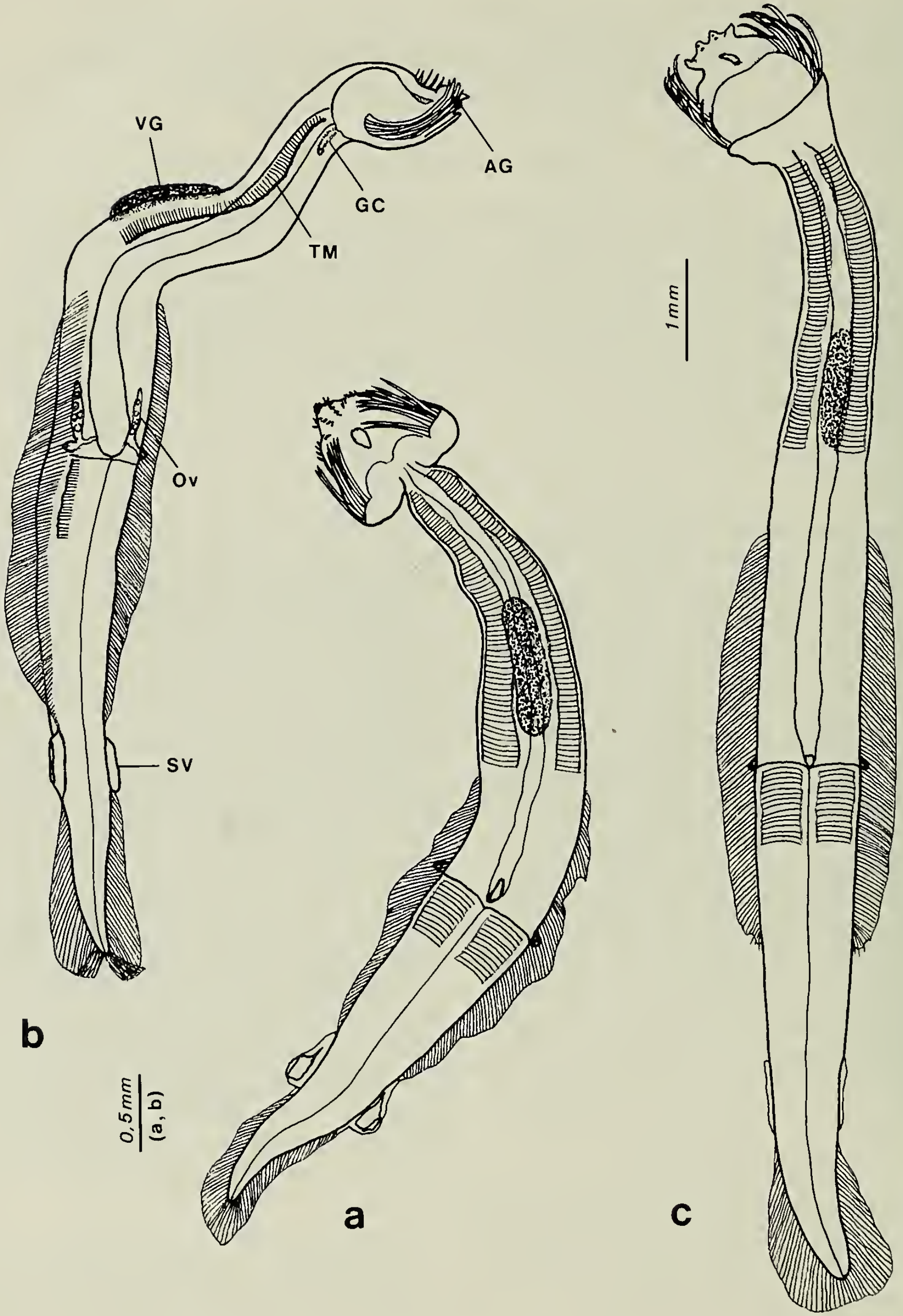

Fig. 1. a, *Heterokrohnia angeli,* new species in ventral view; b, *Heterokrohnia discoveryi,* new species in dorsolateral view; c, *Heterokrohnia biscayensis,* new species in ventral view. AG = apical gland cell complex, GC = glandular canals, Ov = ovaries, SV = seminal vesicles, TM = transverse musculature, VG = ventral ganglion.

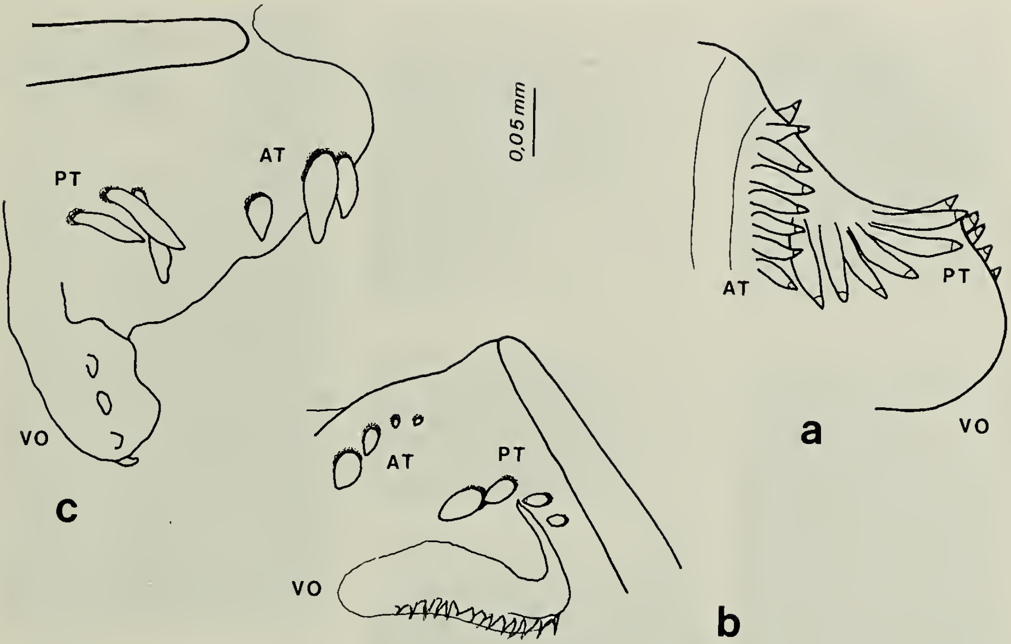

Fig. 2. Teeth and vestibular organs of the three new *Heterokrohnia* species: a, *H. angeli* in ventral view; b, *H. discoveryi* in ventrolateral view; c, *H. biscayensis* in lateral view. AT = anterior teeth, PT = posterior teeth, VO = vestibular organs.

numerous at comparable size: respectively 1–2 and 0–4. Other characters distinguish the Japanese species from *H. angeli,* for instance its notched vestibular organs or its very short ventral ganglion. But it must be noted that the presence of a collarette in *H. bathybia* cannot be regarded as a specific difference since this fragile tissue is often lost during sampling.

Etymology.—This species is named after Dr. Martin V. Angel who gave me this specimen.

Heterokrohnia discoveryi, new species
Figs. 1b, 2b, 3e–g

Material examined.—*Discovery* St. 10141 N° 1, SBN, 3 Oct 1979, 24°34.8′N, 19°40.7′W, 3460–3470 m, holotype (Natural History Museum, London, 1994. 2096).

Description.—Another small species: length 7.1 mm without tail fin. Tail represents 42.2% of body length. Body stumpy (Fig. 1b), with the four longitudinal muscle masses well separated.

Head with a small apical gland cell complex. Anterior teeth, 4/5, short, regularly increasing in size, the two innermost being the stoutest and the outermost hardly visible (Figs. 2b, 3e, g). Posterior teeth, 4 on each side, slightly longer and stout, distant from each other (Figs. 2b, 3f, g), the outermost being reduced. Hooks, 14 on each side, gently curved. Vestibular organs bracket-shaped (Figs. 2b, 3g), narrow and posteriorly festooned. Eyes absent. Corona ciliata abraded away. Remnants of collarette tissue (small vacuolar cells) on neck. Short glandular canals visible laterally on neck (Fig. 1b), embedded in collarette. Gut without diverticula. Transverse musculature thick, extending from neck to end of ventral ganglion in trunk and in the first sixth of tail.

Lateral fins originate posterior to the ventral ganglion. Tail fin sheathing deeply the

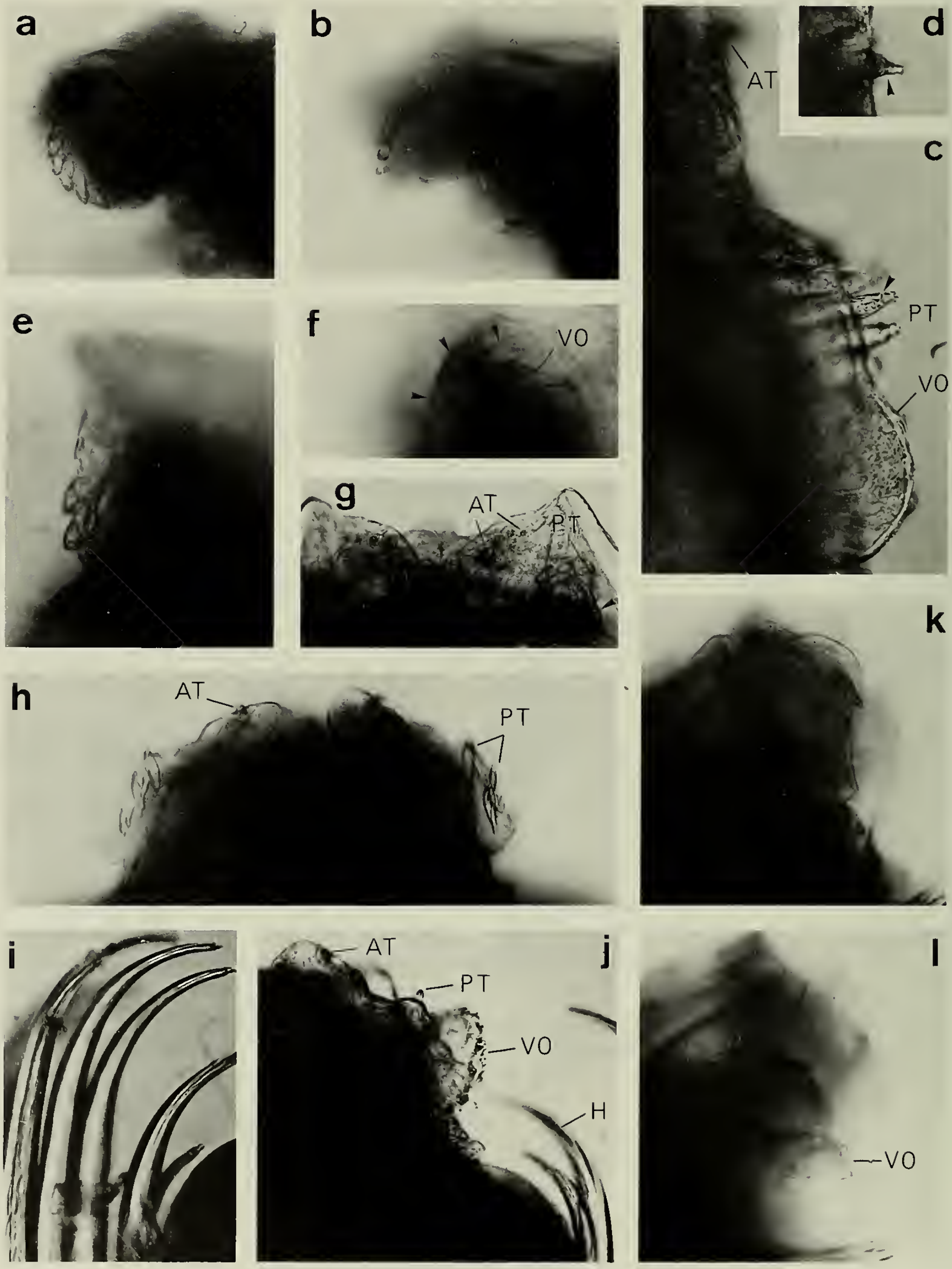

Fig. 3. *Heterokrohnia angeli,* new species (a–d): a, Left anterior teeth in lateral view; b, Left posterior teeth in lateral view; c, Dorsal view of right vestibular organ and teeth; d, Detail of the anterior tooth shown in c (in c and d, arrowheads indicate the differentiated apical part of teeth). *Heterokrohnia discoveryi,* new species (e–g): e, Left anterior teeth in lateral view; f, Left posterior teeth (indicated by arrowheads) in lateral view; g, Ventral view of anterior part of head (the left vestibular organ is indicated by an arrowhead). *Heterokrohnia biscayensis,*

tail extremity. All fins rayed throughout. Ovaries slightly developed. Seminal vesicles empty, elongated, laterally open, in contact with both lateral and tail fins.

Comparisons with other species.—The shape and number of teeth set *H. discoveryi* apart from the 13 *Heterokrohnia* species described hitherto. But the shape of vestibular organs as well as the outermost anterior teeth very reduced in size may indicate that this species is related to *H. furnestinae* Casanova & Chidgey, 1987 in which the anterior teeth are all reduced or absent. The latter is easily recognizable by its acute needle-like posterior teeth. Further specimens are needed to confirm this claim of relationship.

Etymology.—This species is named after the R. V. *Discovery* on board of which the specimen was caught.

Heterokrohnia biscayensis, new species

Figs. 1c, 2c, 3h–l

Material examined.—St TS03 (Cruise ECOFER IV), suprabenthic sledge, 10 May 1991, 44°43.254′N, 2°19.509′W, 2410 m, holotype (Muséum national d'Histoire Naturelle, Paris, UD 271).

Description.—Body length 12.4 mm without tail fin. Tail is 40.7% of this length. Body transparent and relatively rigid.

Head without apical gland cells (Fig. 1c). All teeth short and more or less conical, 3/3 anterior and 3/4 posterior (Figs. 2c, 3h, j–l). Hooks, 12 on each side, very curved distally (Fig. 3i). Vestibular organs prominent and papillated on their edge (Figs. 2c, 3j, l). Eyes absent. Corona ciliata, collarette and glandular canals on neck not observed. Gut diverticula absent. Transverse musculature thin, from neck to end of ventral ganglion in trunk and in less than the first sixth of tail.

Lateral fins begin beyond the ventral ganglion, at a distance equal to the ganglion length. Dense rays on both lateral and tail fins. Ovaries not developed. Seminal vesicles empty, oval, laterally open, well separated from lateral fins and slightly apart from tail fin.

Comparisons with other species.—In this case also, teeth easily differentiate *H. biscayensis* from all its congener except *H. bathybia* of which part of the head armature has been described above. But the two species cannot be confused, the latter being recognizable at first sight by its more developed transverse musculature that extends far beyond the ventral ganglion in the trunk and almost into the anterior quarter of the tail.

Etymology.—The name of this species recalls that it was caught in the Bay of Biscay.

Diversity of the deep bottom chaetognath fauna

The benthoplanktonic habitat of heterokrohniids explains why *Heterokrohnia mirabilis* Ritter-Záhony, 1911, which is the least linked with the bottom, remained for so long the sole known species of this family. It was 55 years before the second representative, *H. bathybia,* was described. When Dawson (1968) found a few specimens of *H. mirabilis* in bottom trawls and not in plankton hauls above, he suspected that it lives "at or very close to the bottom." I was able to confirm this view when I studied the chaetognaths sampled by the R. V. *Discovery* on St. 9541 off Mauretania, between the surface and 4000 m (i.e., ≠ within 10 m of the sea bed): in the few metres above the

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←

new species (h–l): h, Dorsal view of anterior part of head; i, Distal part of hooks; j, Ventral view of left anterior part of head; k, Right anterior teeth in lateral view; l, Right posterior teeth in lateral view. AT = anterior teeth, H = hooks, PT = posterior teeth, VO = vestibular organs. Magnification: ×110 (a, b, g–l) and ×270 (c–f).

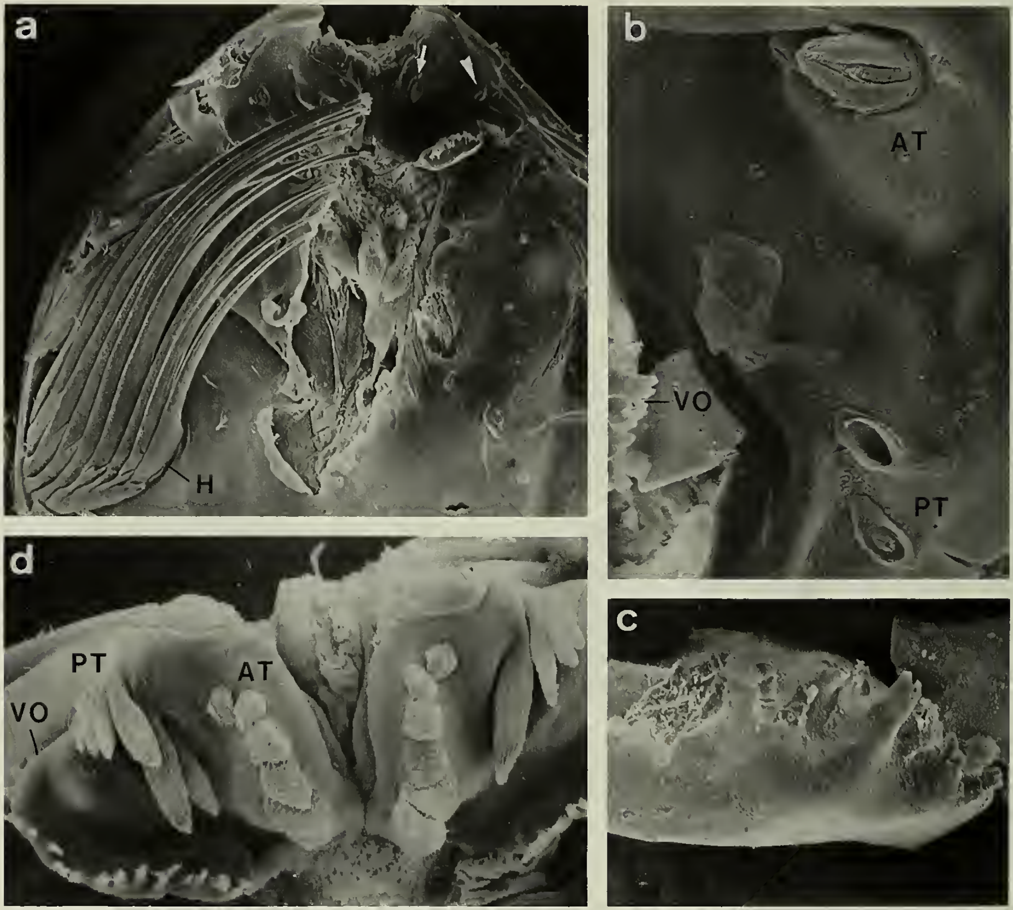

Fig. 4. SEM photographs of head armature. *Heterokrohnia* sp. 1 from SW of Ireland (a–c): a, Ventral view of head (the left anterior tooth is indicated by an arrow and the place of the posterior ones by an arrowhead) (×75); b, Area of teeth (×350); c, Detail of the left vestibular organ (×430). *Heterokrohnia* sp. 2 from the Bay of Biscay (×225); d, Anteroventral view of head. AT = anterior teeth, H = hooks, PT = posterior teeth or place of them, VO = vestibular organs.

bottom (mab) were four new *Heterokrohnia* and one species belonging to a new genus *Archeterokrohnia* (Casanova 1986a, 1986b). Since then, further species have been described until today 20 species of this family are known: 16 *Heterokrohnia,* 3 *Archeterokrohnia* and the curious *Xenokrohnia sorbei* Casanova, 1993.

All but two of these species, *Heterokrohnia involucrum* Dawson, 1968 and *H. mirabilis,* which may be found around 1500 mab, never occur >500 mab. Even the three Antarctic species *H. longidentata* and *H. fragilis* Kapp & Hagen, 1985 and *Archeterokrohnia longicaudata* (Hagen & Kapp, 1986), said to be planktonic when caught with plankton nets, are more likely benthoplanktonic since hauls started in every case between 16 and 77 mab.

Heterokrohniids are said to be very deep-living organisms. This is only partly true. In fact, two species have been caught at depths less than 1000 m: 800–815 m for *H. wishnerae* Casanova, 1992 in the Pacific off Mexico (Casanova 1991 as *Heterokrohnia* sp.) and 677–738 m for *Xenokrohnia sorbei* in the Bay of Biscay (Casanova 1993).

Thus, it appears that the specific diversity (richness) of benthoplanktonic chaetognaths is high in deep water, probably comparable with that of the planktonic species. In almost every near-bottom sample deeper than 700 m, new species are discovered in newly investigated areas. Even in the northeast Atlantic, at present the best studied region, rare new species are wanting to be described, e.g., two incomplete specimens from benthic hauls: one (*Heterokrohnia* sp. 1) off southwest Ireland (*Discovery* st. 9779, 49°20′N, 12°49.5′W, 1404–1398 m), with small delicate bulb-like teeth and short sausage-shaped vestibular organs (Fig. 4a–c); another (*Heterokrohnia* sp. 2) from the Bay of Biscay (same station as *H. biscayensis*), which seems to be related to the species of the *longidentata* group (Casanova 1992) because of its arrangement and shape of teeth (Fig. 4d). They cannot be named today, since they may have relatives with the same type of head armature but differing by other features.

Further research on deep living benthoplanktonic chaetognaths is needed to enlarge our knowledge of these interesting species whose body organization is more variable than those strictly planktonic ones. First, we need a faunistic survey and numerical data. Note that in addition to the new species described or reported above, one genus and two other species are also known from single specimens only: *Bathyspadella edentata* Tokioka, 1939, *Krohnittella tokiokai* Bieri, 1974 and *Archeterokrohnia longicaudata*. Sometimes, this scarcity may be due to the small number of samples realized in an area. But this may be also a reality, since there are abundant and rare benthoplanktonic species as for the planktonic ones. In spite of the maladjustment of gears used to catch these organisms, it is obvious that the number of specimens collected is different according to the species. For instance, in the numerous *Discovery* samples in the northeast Atlantic that I observed (both near bottom and epibenthic samples), there were nearly two hundred *Heterokrohnia heterodonta* Casanova, 1986, about ten *H. curvichaeta* Casanova, 1986 and only one *H. angeli* and *H. discoveryi*. Second we need to describe more fully the structure and function of interesting organs such as the archaic genital apparatus of the heterokrohniids and the curious ventral secretory gland (probably digestive) of *Xenokrohnia sorbei*. The discovery of other archaic features in other deep benthoplanktonic chaetognaths might also be revealed and throw further light on this curious phylum.

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ANATOMICAL OBSERVATIONS OF THE SAND DOLLAR *MELLITA QUINQUIESPERFORATA* (LESKE, 1778) (ECHINODERMATA: ECHINOIDEA) AND THE DESIGNATION OF A NEOTYPE

Rich Mooi and Antony S. Harold

Abstract.—A neotype for the sand dollar *Mellita quinquiesperforata* (Leske, 1778) is designated and described. Quantitative and qualitative data are given for the test, spines, and pedicellariae of the neotype. Figures of plate and food groove patterns are also given for non-type specimens.

The genus *Mellita* L. Agassiz, 1841 comprises seven living species. Four occur only on the Pacific side of the Isthmus of Panama, and three on the Atlantic side (Harold & Telford 1990). *Mellita quinquiesperforata* (Leske, 1778), one of the Atlantic species, is the type species and most widely distributed member of the genus. In spite of its widespread occurrence, and its prominence in both appropriate habitats and shell shops, *M. quinquiesperforata* has a taxonomic history described as "strange" by Harold & Telford (1990:999). In their recent revision of the genus, Harold & Telford (1990) described this history, synonymizing *Mellita lata* Clark, 1940 and *Mellita latiambulacra* Clark, 1940 with *M. quinquiesperforata,* but raising *M. quinquiesperforata tenuis* Clark, 1940 to the status of species. For the *Mellita* occurring along the eastern coast of the United States, they named a new species, *Mellita isometra* Harold & Telford, 1990. These actions restricted the name *M. quinquiesperforata* to mainland populations occurring west of the Mississippi delta along the Central and South American coasts to southern Brazil, and to populations from some Caribbean Islands in association with terrigenous sand substrates.

The only reference to the deposition of the specimens in Klein's (1734) figures of *Mellita testudinata* (as pre-Linnean, this name is unavailable), upon which Leske's description of "*Echinodiscus quinquies perforatus*" is based, is "Hospitatur in museo Trieriano" (Leske 1778:198). At the time, the practice of designating type specimens was not well established, and it is even conceivable that Leske did not have the actual material in hand. Apparently, none of the earlier monographers of the genus (L. Agassiz 1841, Clark 1940, Mortensen 1948) made attempts to locate and examine Klein's specimens. Although Harold & Telford (1990:998) did make such attempts, they were "unable to ascertain whether or not these specimens still exist." There are currently no museums with natural history collections in Trier, Germany. Correspondence with the other museums that do exist there has failed to uncover the specimens. The importance of this species to studies in systematics, biogeography, ecology, and physiology compels us to designate a neotype. The name *Mellita quinquiesperforata* has been applied to a wide variety of taxa and used in many different senses. In particular, the eastern U.S. fossil *Mellita ampla* Ravenel, 1848 was placed in synonymy with *M. quinquiesperforata* by Harold & Telford (1990), but our preliminary examination suggests that *M. ampla* should be maintained as a separate taxon. Therefore, it is imperative that comparisons be made with types of both *M. quinquiesperforata* and *M. isometra.* Before these analyses can be done, the name *M. quinquiesperforata* must be stabilized by designating and describing in detail a neotype.

Most aspects of the anatomy of *M. quinquiesperforata* remain poorly or not at all figured. This is particularly true for external appendages such as spines and pedicellariae, which are notably variable within and between species of clypeasteroids (Mooi 1989). Although presented under the name *Mellita quinquiesperforata,* the majority of previous figures are actually of *M. isometra,* the species most commonly encountered in marine laboratories of the eastern seaboard (for example, see Mooi [1986] and Telford et al. [1985] for spination and podia of *M. isometra*). Louis Agassiz (1841) recognized two species that are together synonymous with *M. quinquiesperforata.* He was the only one to figure spines of any kind from *M. quinquiesperforata,* in the sense of Harold & Telford (1990). Under the name of *M. testudinata,* Agassiz showed a single spine from the aboral margin of one of the lunules (L. Agassiz 1841: plate 4a, fig. 7a), although he does not indicate which one. Under the name *M. quinquefora,* he showed a poorly drawn club-shaped spine (L. Agassiz 1841: plate 3, fig. 11a) from the aboral surface, and three views of spines (L. Agassiz 1841: plate 3, figs. 11l, c, d) from the aboral margins of unspecified lunules. He described these spines as resembling elongated spoons, an observation that is not consistent with our own. Clark (1914: plate 125, figs. 16–21) figured several spines and pedicellariae from what he calls *M. quinquiesperforata,* but without knowing the locality of the specimen, or its appearance, it is impossible to know if this is indeed *M. quinquiesperforata,* or (as we suspect) *M. isometra.* In addition, Clark's figures are not especially accurate, and the figure of the "miliary spine" (Clark 1914: plate 125, fig. 16) seems to be a geniculate spine. A single bidentate pedicellaria from "*Mellita 5-perforata lata* H.L. Clark" was figured by Mortensen (1948), but it lacks detail in the tooth structure of the valves. No figures of biphyllous pedicellariae exist in the literature.

The plate pattern of the oral surface of *M. quinquiesperforata* from the "Gulf of Mexico" was figured by Durham (1955: fig. 17A). He also shows the basicoronal plate system (Durham 1955: fig. 16B). Unfortunately, there are errors in the positions and numbers of plate sutures associated with the anal lunule in Durham's drawing of *M. quinquiesperforata* (similar errors appear in his figure of *Leodia sexiesperforata* [Leske, 1778]). No figures of the plate pattern from the aboral surface exist in the literature, although some details can be made out in L. Agassiz's figure of *M. quinquefora* (L. Agassiz 1841: plate 3, fig. 1) and *M. testudinata* (L. Agassiz 1841, plate 4a, fig. 10). We could locate only 2 figures that unambiguously show the internal structure of *M. quinquiesperforata*: those in Mortensen (1948: plate 62, fig. 3) and Harold & Telford (1990: fig. 7). Only in the latter is the Aristotle's lantern visible.

Alexander Agassiz (1872) noted that *M. quinquiesperforata* "has a wide geographical range, and is liable to great variations." In the past, and in conjunction with taxonomic confusion stemming from these variations, it has been difficult to determine an unequivocal suite of characters for *M. quinquiesperforata.* For example, D. Pawson of the National Museum of Natural History, Washington, D.C. recently brought to our attention some difficulties in the use of Harold & Telford's (1990) key, particularly with respect to spine morphology, posterior paired lunule angle, and petaloid size. The present state of knowledge regarding the variation within the species suggests that the populations occurring in the northwestern Gulf of Mexico, including the type locality of Veracruz, Mexico, unequivocally belong to a single taxon. Harold & Telford (1990) pointed out that there was some distinctiveness of populations, particularly those from islands in the Caribbean and from the southern parts of the range, but they preferred to recognize them only as geographic or ecophenotypic variants of *M. quinquiesperforata.* Some of these variants could turn out to be separate species, making it especially important to associate a specimen with the name *M. quinquiesperforata.* It is clear that a full description, especially of the spines, pedicellariae, and features of *M. quinquiesperforata*'s test architecture are necessary for adequate comparisons with types and other specimens of the rest of the species in *Mellita.*

Methods

Terminology of external appendages and test features is that of Mooi (1989), and the plate columns are labeled according to Lovén (1892). We provide an abbreviated synonymy, including all names that have been applied to *M. quinquiesperforata.* For references to more literature on this species, see Mortensen (1948) and Harold & Telford (1990). For a description, summary of intraspecific variation, and diagnosis of the species as a whole, see Harold & Telford (1990). Unless indicated otherwise, measurements are made directly from the neotype using dial calipers, with the value given in parentheses after each measurement representing percent test length. Additional comments are intended to cover anatomical aspects not emphasized by Harold & Telford (1990). Lunule angle is the number of degrees subtended by axes drawn through the lunules in ambulacra I and V. Spines and pedicellariae were removed from the test of the neotype and placed in droplets of approximately 5% sodium hypochlorite (Clorox). Fully cleaned spines were drawn using a camera lucida mounted on a compound microscope. Ten each of miliary spines (from aboral interambulacrum 2), aboral club-shaped spines (from aboral interambulacrum 2), geniculate spines (from oral ambulacrum I), locomotory spines (from oral interambulacrum 2), and anal lunule fringe spines (from the aboral edge at the mid-point of the lunule) were measured to the nearest μm using a calibrated eye-piece micrometer. To avoid damaging the neotype, specimens of similar size to, and collected with the neotype were prepared or dissected as follows. Plate patterns were made visible by polishing the specimen with a graded series of water-proof sand papers, and then painting the specimen with a light coat of a solution of equal parts glycerol and 95% ethanol. The plate patterns of both surfaces were drawn with the aid of a camera lucida mounted on a binocular dissecting microscope. The Aristotle's lantern was exposed through dissection of the aboral surface of another specimen and measured.

Order Clypeasteroida L. Agassiz, 1835
Family Mellitidae Stefanini, 1911
Genus *Mellita* L. Agassiz, 1841
Mellita quinquiesperforata (Leske, 1778)
Figs. 1–3

Echinodiscus quinquies perforatus Leske, 1778:197, pl. 21C, D.

Echinus pentaporus.—Gmelin, 1788:3189.

Clypeaster pentaporus.—Lamarck, 1801: 349.

Scutella quinquefora.—Lamarck, 1816:9.

Scutella pentapora.—Blainville, 1830:223.

Mellita quinquefora.—L. Agassiz, 1841:36, pl. 3 (plate is erroneously labelled "*Encope pentapora*").

Mellita testudinata.—L. Agassiz, 1841:40, pl. 4a, figs. 7–9.

Mellita nummularia.—L. Agassiz & Desor, 1847:139.

Mellita testudinea.—Gray, 1855:22.

Mellita pentapora.—Lütken, 1864:107.

Mellita quinquiesperforata.—H. L. Clark, 1911:599.

Mellita quinquiesperforatus.—H. L. Clark, 1925:174.

Mellita lata.—H. L. Clark, 1940:437, pl. 60, fig. 1, pl. 61, fig. 1, pl. 62, figs. 1, 2.
Mellita latiambulacra.—H. L. Clark, 1940: 439, pl. 62, figs. 3–6.
Mellita quinquisperforata var. *latiambulacra.*—Penchaszadeh & Layrisse, 1985: 393.

Neotype.—California Academy of Sciences, Invertebrate Zoology (CASIZ) 096152, 44.2 mm test length, beach 2 mi south of Veracruz, Mexico, A. G. Smith, March 1954 (collected with CASIZ 087802, geology accession number 34684, 11 specimens in lot not counting neotype, ranging from 26.6 mm to 44.6 mm test length).

Description of neotype.—Test dimensions (Fig. 1): Length 44.2 mm; maximum width 48.0 mm (108.6%); distance from ambitus at ambulacrum III to anterior edge of madreporic plate 19.4 mm (43.9%); test thickness at center of madreporic plate 5.6 mm (12.7%); test thickest anterior to madreporic plate, thickness at highest point 5.9 mm (13.3%); distance from ambitus at ambulacrum III to highest point of test 13.2 mm (29.9%); distance from ambitus at ambulacrum III to anterior edge of peristome 13.0 mm (29.4%); mouth diameter 2.0 mm (4.5%); distance from anterior edge of peristome to anterior edge of periproct 4.0 mm (9.0%); periproct indenting basicoronal, in depression leading to anterior edge of anal lunule, length 1.9 mm (4.3%).

Petaloids (Fig. 1A): Only a single trailing podium in each of petaloids Ib, IIb, IIIa, IVa and Va (see also Fig. 3). Following measurements represent length of indicated petaloid pore pair column in ambulacra: Ib 11.2 mm (25.3%); IIb 10.00 mm (22.6%); IIIa 11.3 mm (25.6%); IVa 11.0 (24.9%); Va 11.7 mm (26.5%). Following measurements represent greatest width of petaloid in ambulacra: I 5.4 mm (12.2%); II 5.2 mm (11.8%); III 5.0 mm (11.3%); IV 5.1 mm (11.5%); V 5.5 mm (12.4%).

Food grooves: Primary grooves bifurcate on, or just distal to ambulacral basicoronal plates; two main branches in each ambulacrum restricted to ambulacral plates; distal, secondary branches extend onto interambulacral plates (see also Fig. 3). Following measurements represent greatest distance (orthogonal to lunule axis) between main branches of food grooves in ambulacra: I 9.5 mm (21.5%); II 10.1 mm (22.9%); III 6.3 mm (14.3%); IV 10.0 mm (22.6%); V 9.3 mm (21.0%).

Lunules (Fig. 1): Lunules closed. Following measurements represent lengths and widths respectively of lunules in ambulacra: I 8.4 mm (19.0%) and 1.7 mm (3.8%); II 8.6 mm (19.5%) and 1.7 mm (3.8%); IV 7.7 mm (17.4%) and 1.8 mm (4.1%); V 8.4 mm (19.0%) and V 1.7 mm (3.8%); lunule angle 73.5°; distance from anterior edge of madreporic plate to anterior edge of anal lunule 6.6 mm (14.9%); length and width of anal lunule 11.8 mm (26.7%), 2.5 mm (5.7%).

Spines (Fig. 2): Measurements given here are mean spine lengths, followed by (in parentheses) range and standard deviation. Aboral miliary spines (Fig. 2A) slender, bent at base so that whole spine leans "down-slope" from apical system, distal end with typical sac-bearing tip architecture (see Mooi 1986), length 508.2 μm (486–528, 11.8). Aboral club-shaped spines (Fig. 2B, C) fairly stout, with thick shaft bent at base so that whole spine leans "down-slope" in manner similar to aboral miliaries, tip moderately expanded and club-shaped, length 642 μm (605–658, 15.0). Geniculate spines (Fig. 2D) of oral surface slender and sharply bent just distal to point half way up shaft, length 572 μm (546–598, 18.5). Locomotory spines (Fig. 2E) of oral surface long, slender, sharply bent proximal to base, moderately pointed, length 2397 μm (2073–2611, 153.0). Anal lunule fringe spines (Fig. 2F) from aboral edge of lunule paddle-shaped, but broadest and most greatly flattened at lunule's mid-point, shaft proximal to base slightly bent in same plane as flattening, tip

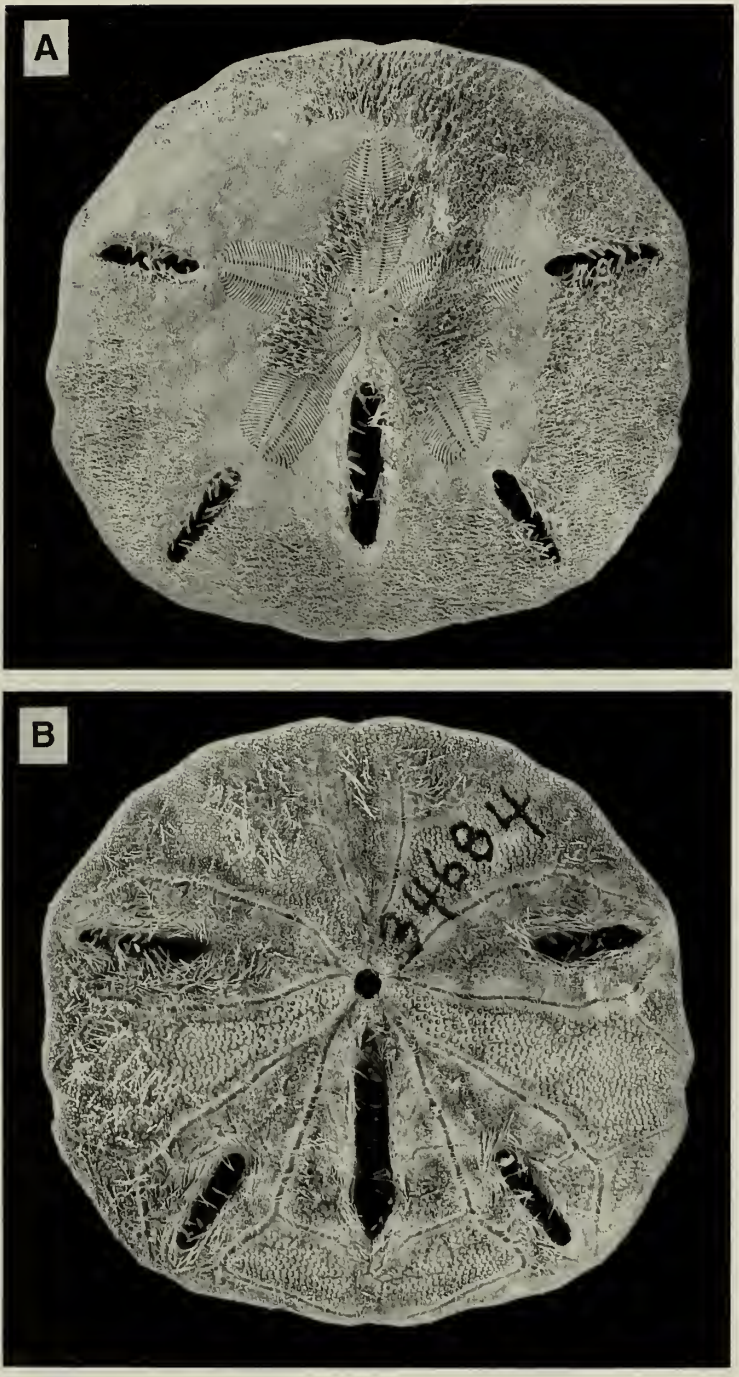

Fig. 1. *Mellita quinquiesperforata,* neotype (CASIZ 096152, 44.2 mm test length). A. Photograph of aboral surface; B. Photograph of oral surface.

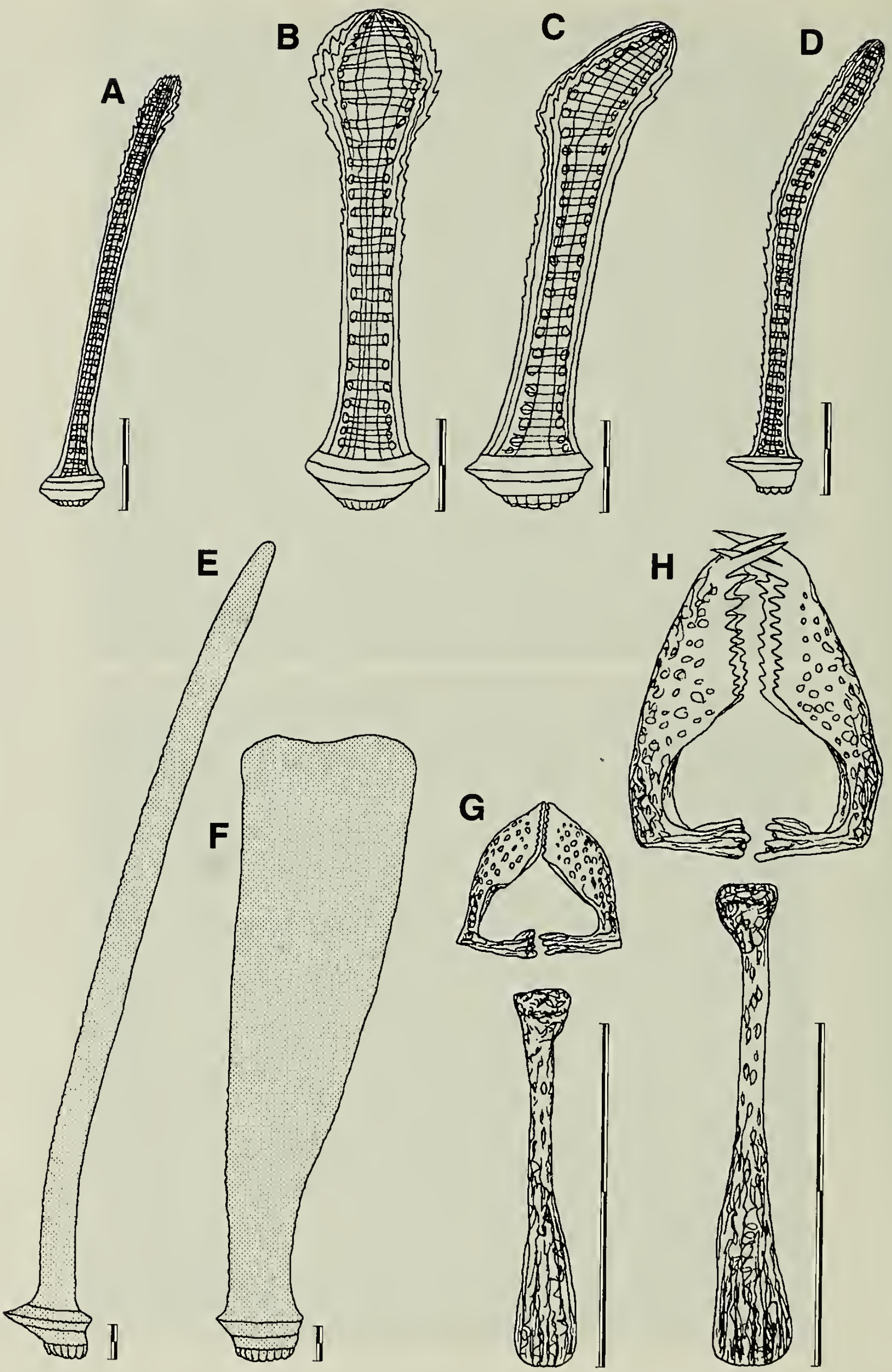

Fig. 2. *Mellita quinquiesperforata,* neotype (CASIZ 096152), skeletal elements of external appendages. A. Miliary spine from interambulacrum on aboral surface, apex left; B. Club-shaped spine from interambulacrum on aboral surface; C. Club-shaped spine from interambulacrum on aboral surface, view orthogonal to that in B, apex left; D. Geniculate spine from ambulacrum on oral surface; E. Locomotory spine from interambulacrum on oral surface, details of stereom structure omitted; F. Anal lunule fringe spine from aboral edge at mid-point

chisel-like and square, length 1610 μm (1370–1772, 115.8).

Pedicellariae (Fig. 2): Pedicellariae of two types, both with two valves forming a "jaw" attached to stem by long, flexible neck of almost same length as stem. Valves of biphyllous pedicellariae (Fig. 2G) with minute teeth all of similar size, valve length approximately 45 μm. Stem slender, tapering distally but ending in slight swelling, stem length approximately 110 μm. Valves of bidentate pedicellariae (Fig. 2H) with variably sized teeth, 2 or 3 long, distal "canine" teeth on a valve interlocking with those of opposing valve, valve length approximately 95 μm. Stem slender, same general shape as for biphyllous, stem length approximately 140 μm.

Plate pattern (Fig. 3), Aristotle's lantern of non-types.—Aboral plating around ambulacral lunules festooned except in ambulacrum III, which lacks lunule. Aborally, narrowest point of interambulacrum 5 posterior to anal lunule. At ambitus, interambulacra and ambulacra approximately same width. Orally, interambulacra discontinuous by single ambulacral plate except for interambulacrum 5, which is continuous. During ontogeny, last post-basicoronal plates to become disjunct from their corresponding basicoronals are those in interambulacra 1b, 2a, 3b and 4a. Four interambulacral plates form perimeter of anal lunule on oral surface, two circumferential sutures close to posterior end of lunule. Interambulacral basicoronal plates longer than ambulacral basicoronals. Interambulacral basicoronal 5 deeply indented by periproct. In specimen 42.5 mm long, Aristotle's lantern 8.8 mm long (20.7% test length).

Remarks.—Klein (1734) described and figured specimens of this species from Veracruz and Leske (1778), the first post-Linnaean writer to describe *M. quinquiesperforata* (as *Echinodiscus quinquies perforatus*) referred specifically to Klein's figures (Harold & Telford 1990). Accordingly, we have chosen a specimen from a lot from Veracruz as the neotype. The neotype does not differ significantly from the material examined by Harold & Telford (1990). How-

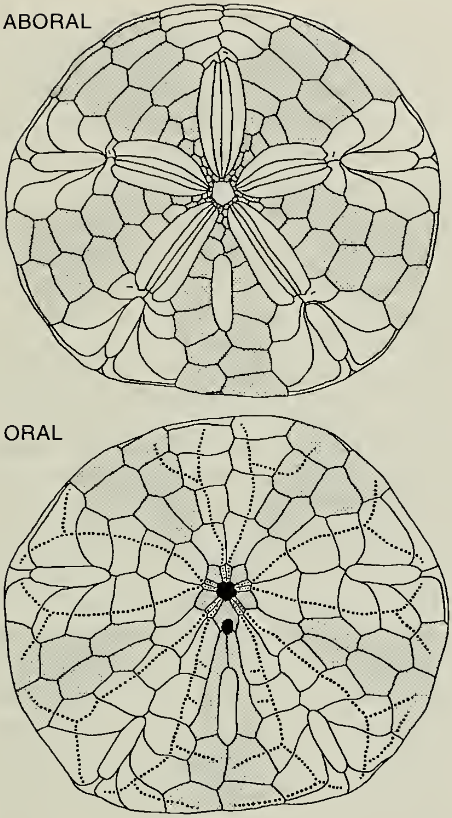

Fig. 3. *Mellita quinquiesperforata* (CASIZ 087802, 44.6 mm test length, collected with neotype), plate and food groove patterns. Food grooves represented by dotted lines, details of plating in petaloids omitted. Mouth and periproct in solid black, interambulacral plates shaded.

←

of anal lunule, details of stereom structure omitted; G. Valves (upper) and stem (lower) of biphyllous pedicellaria; H. Valves (upper) and stem (lower) of bidentate pedicellaria. All scale bars 100 μm long.

ever, as noted by Harold & Telford (1990), there is substantial variation within *M. quinquiesperforata,* particularly in width to length ratio, profile, and spine dimensions. In spite of previous attempts to do so (for example, see Clark 1940), Harold & Telford (1990) could find no basis upon which to partition this variation into species. We concur based on the characters examined by previous authors as well as on new observations (D. Pawson, A. S. Harold, & R. Mooi, unpublished observations). The neotype here designated not only comes from the type locality, it also exhibits the sharply inclined anterior profile, anteriorly placed site of maximum thickness, very broad test, and spatulate spines bordering the lunules listed in Harold & Telford's (1990) diagnosis. Although pedicellarial types can be diagnostic of certain clypeasteroid clades (Mortensen 1948, Mooi 1989), the pedicellariae of the neotype illustrated here (Fig. 2) are typical not only of *Mellita quinquiesperforata,* but of the genus as a whole, and do not offer additional taxonomic information.

The neotype typifies the apomorphies shared by *M. quinquiesperforata* and other *Mellita.* Phylogenetic revision of fossil *Mellita* (R. Mooi & A. S. Harold, unpublished observations) indicates that *Leodia sexiesperforata* is a member of the clade encompassing both fossil and extant *Mellita* species. Taking this into account, the apomorphies of *Mellita* include a single trailing podium at the end of each petaloid, and the periproct indenting the basicoronal plate. Harold & Telford (1990) added the loss of the lunule in ambulacrum III to this list. However, this character is actually applicable only to a smaller clade of largely extant *Mellita,* and not to the genus as a whole (R. Mooi & A. S. Harold, unpublished observations). Our examination of the neotype and associated material also affords an opportunity to rectify Durham's (1955) error in interpretation of the plate patterns around the anal lunule (compare our Fig. 3 with Durham 1955: fig. 17A).

A survey of spine morphometrics within the Mellitidae (D. Pawson, A. S. Harold & R. Mooi, unpublished observations) reveals unexpected divergences from the characters given in the key by Harold & Telford (1990). They use the relative lengths of anal lunule fringe spines and locomotory spines in their first couplet: in *M. tenuis* and *M. isometra,* the anal lunule fringe spines are supposed to be "substantially longer" than the locomotories. In all other *Mellita,* the reverse is the case. The anal lunule fringe spines are shorter than the locomotories in the neotype and other examples of *M. quinquiesperforata* and is therefore in accord with Harold & Telford's key. However, with the recognition that some populations of *M. isometra,* and perhaps of *M. tenuis,* have longer locomotories than anal lunule fringe spines, more comprehensive study of intraspecific variation (including all available types) is essential to assess the systematic, environmental, and ontogenetic significance of previously unrecognized variation in relative spine lengths.

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DESCRIPTION OF *MASTIGLANIS ASOPOS*, A NEW PIMELODID CATFISH FROM NORTHERN BRAZIL, WITH COMMENTS ON PHYLOGENETIC RELATIONSHIPS INSIDE THE SUBFAMILY RHAMDIINAE (SILURIFORMES: PIMELODIDAE)

Flávio A. Bockmann

Abstract.—Mastiglanis asopos, a new genus and species of the neotropical catfish family Pimelodidae, is described from the Amazon basin, and rio Capim and its adjacencies, in northern Brazil. Its monophyly is supported by various autapomorphies in external and internal morphology, such as the first dorsal- and pectoral-fin elements filamentous distally, and the presence of a remarkable osseous process at the anterior portion of the premaxilla. *Mastiglanis* shares unambiguously all diagnostic features proposed for the subfamily Rhamdiinae, and also those that delimit a subset called the *Nemuroglanis* sub-clade. Eleven new synapomorphies are proposed to corroborate the monophyly of the latter group. Additional character evidence supports a hypothesis placing *Mastiglanis* as the sister group of the remainder of the *Nemuroglanis* sub-clade.

Resumo.—Mastiglanis asopos, um novo gênero e espécie da família Pimelodidae é descrito para a região norte brasileira (bacia Amazônica e rio Capim e arredores). Seu monofiletismo é indicado por vários caracteres apomórficos observáveis na morfologia externa e interna, dentre os quais destacam-se: os primeiros elementos ("espinhos") das nadadeiras dorsal e peitoral extremamente alongados e a presença de um notável processo ósseo na região anterior da premaxila. *Mastiglanis* compartilha todos os caracteres diagnósticos da subfamília Rhamdiinae, assim como, todos aqueles que definem um subgrupo mais restrito chamado "*Nemuroglanis* sub-clade." O monofiletismo deste último é corroborado por onze novas sinapomorfias. *Mastiglanis* é provisoriamente posicionado como grupo-irmão de todos os outros componentes do "*Nemuroglanis* sub-clade."

The most recent account on the situation of the systematics of South American freshwater fishes is that of Böhlke et al. (1978), who estimated that a large portion of that fish fauna, especially that from the Amazon basin, remains undescribed and even unknown. In spite of the considerable progress made since the publication of Böhlke et al.'s paper, only recently have catfishes from the Amazon basin been dealt within a phylogenetic context (e.g., Stewart 1986a, 1986b; Ferraris & Mago-Leccia 1989; Pinna 1989).

The fish herein studied is an illustrative example of the above-mentioned situation, for it remained unknown until now in spite of its distinctive external features and wide distribution throughout the Amazonian basin. This paper describes this pimelodid catfish as a new genus and species, and discusses its relationships within a recently provided synapomorphy scheme of the Rhamdiinae (Lundberg et al. 1991a). Additional new corroboration is given to a formerly suggested rhamdiine subset (Ferraris 1988) as well as a discussion about the arrangement of the genera therein included.

Material and Methods

Morphometric values were taken with calipers and expressed to the nearest 0.1 mm. All measurements are made point-to-point on the specimens' left side whenever possible. Morphometric data are expressed as proportions of standard length (SL), or head length (HL; all subunits of the cephalic region, excepting the barbels which were expressed in proportions of SL). Each proportion is provided with its arithmetic mean, followed by the range and standard deviation. The number of specimens tallied in counts is presented enclosed in parentheses. When meristics vary, the count for the holotype is indicated by an asterisk (*). Methodology and terminology for measurements followed Lundberg & McDade (1986), with the following measurements added: prepelvic length, preadipose length, dorsal-fin base length (taken as the gap between the insertion point of the first and the last elements), maxillary-barbel length, outer- and inner-mental barbel length, head depth (taken at the vertical through the posterior margin of the fleshy opercular flap), head width (taken at its maximum width), fleshy interorbital distance (the space between the fleshy upper orbital rims), preorbital length (measured from snout tip to anterior orbital rim), anterior internarial space, and length of first and second branched rays of the dorsal and pectoral fins.

Some paratypes of *Mastiglanis asopos* and additional comparative material of Pimelodidae were cleared and counterstained employing the Taylor & Van Dyke (1985) technique, which provides a differential staining of the skeletal system elements. Vertebral counts included the first five vertebrae transformed in the Weberian apparatus, and the compound caudal centrum (PU1+U1) was counted as one. Principal caudal-fin ray counts included all branched rays plus one unbranched ray in each lobe, following Hubbs & Lagler (1958). Counts for each lobe, upper first, are separated by a plus sign. Pterygiophores, vertebrae, gill rakers, ribs, and branchiostegal rays were counted on cleared and stained specimens only. Anatomical illustrations were sketched using a Zeiss stereomicroscope with a camera lucida attachment. In the drawings, bone is represented by stipple and cartilage by open circles.

Institutional abbreviations are: California Academy of Sciences, San Francisco (CAS); Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP); Museu Nacional do Rio de Janeiro, Rio de Janeiro (MNRJ); Universidade Federal do Rio de Janeiro, Rio de Janeiro (UFRJ); Departamento de Biologia Animal e Vegetal da Universidade do Estado de Rio de Janeiro, Rio de Janeiro (DBAV-UERJ), National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Comparative material examined (CS-cleared and stained preparations).—Acentronichthys leptos, UFRJ 289 (1 ex., CS), UFRJ 505 (1 ex., CS); *Brachyglanis* sp., MZUSP 45895 (1 ex., CS); *Brachyplatystoma filamentosa,* MZUSP 45896 (1 ex., CS); *Brachyrhamdia meesi,* UFRJ 397 (2 ex., CS); *Calophysus macropterus,* MZUSP 26415 (1 ex., CS), MZUSP 45904 (1 ex., CS); *Cetopsorhamdia iheringi,* UFRJ 689 (2 ex., CS); *Cetopsorhamdia picklei,* USNM 121218 (2 ex., paratypes, CS); *Chasmocranus longior,* MZUSP 45909 (2 ex., CS); *Chasmocranus truncatorostris,* UFRJ 322 (1 ex., CS), UFRJ 504 (1 ex., CS); *Cheirocerus goeldi,* MZUSP 45905 (2 ex., CS); *Gladioglanis conquistador,* MZUSP 45906 (2 ex., CS); *Goeldiella leques,* MZUSP 45907 (1 ex., CS); *Heptapterus mustelinus,* UFRJ 291 (1 ex., CS); *Hypophthalmus edentatus,* MZUSP 43304 (1 ex., CS); *Iheringichthys labrosus,* UFRJ 690 (1 ex., CS), DBAV-UERJ 146 (1 ex.); *Imparales mariai,* USNM 121251 (1 ex., holotype); *Imparales panamensis,* USNM 293454 (1 ex., CS); *Imparfinis minutus,* MZUSP 39990 (1 ex., CS), UFRJ 320 (4 ex.); *I. mirini,* MZUSP 45899 (1 ex., CS); *I. nemacheir,* USNM 121163 (2 ex., CS); *I.*

piperatus, CAS 63636 (1 ex., holotype); *I. schubarti,* MZUSP 45897 (1 ex., CS); *Imparfinis* sp. 1, MZUSP 45900 (1 ex., CS); *Imparfinis* sp. 2, MZUSP 45898 (1 ex., CS); *Imparfinis* sp. 3, UFRJ 393 (1 ex., CS); *Lophiosilurus alexandri,* UFRJ 042 (1 ex., CS); *Megalonema platanus,* MZUSP 45902 (1 ex., CS); *Megalonema* sp., DBAV-UERJ 122 (1 ex., CS); *Microglanis parahybae,* UFRJ 693 (2 ex., CS); *Nannoglanis bifasciatus,* MZUSP 45903 (2 ex., CS); *Nannorhamdia stictonotus,* UFRJ 292 (3 ex., CS); *Nemuroglanis* sp., MZUSP 45908 (1 ex., CS); *Parapimelodus valenciennis,* DBAV-UERJ 230 (1 ex., CS); *Phenacorhamdia boliviana,* MZUSP 42296 (2 ex., CS); *Phenacorhamdia* sp., MZUSP 45901 (1 ex., CS); *Pimelodella lateristriga,* UFRJ 503 (2 ex., CS); *Pimelodella* sp., UFRJ 502 (2 ex., CS); *Pimelodus maculatus,* UFRJ 691 (2 ex., CS); *P. ornatus,* DBAV-UERJ 934 (1 ex., CS); *Pseudopimelodus* sp., DBAV-UERJ 118 (1 ex., CS); *Rhamdia* sp., UFRJ 321 (3 ex., CS); *Rhamdiopsis* sp., UFRJ 708 (1 ex., CS).

Mastiglanis, new genus

Diagnosis.—A small pimelodid catfish displaying the suite of apomorphic characters ascribed to the subfamily Rhamdiinae (Lundberg, 1991a). It also exhibits all attributes that characterize a more restricted monophyletic unit called "*Nemuroglanis* sub-clade" (Ferraris 1988; see also Phylogenetic Relationships section below). *Mastiglanis* is distinguishable from all other rhamdiines by the following putatively autapomorphic traits: 1—integument pigmentation very reduced; 2—anteriormost element of the dorsal fin (homologous to dorsal-fin spine) prolonged as a long filament; 3—first pectoral-fin element (homologous to pectoral-fin spine) prolonged as a long filament; 4—anterior internarial width greater than the posterior one; 5—frontals narrow at supraorbital portion; 6—an anterodorsal oriented shelf-like process at the symphysial region of premaxilla; 7—anterior cornua of mesethmoid abruptly assuming a reversed direction at their mid-length; 8—an elongated metapterygoid; 9—a lamina at the anterodorsal margin of the opercle; 10—rear portion of opercular bone tapered and curved ventrally. Other characters considered plesiomorphic or of unknown polarity but still useful for identification include: eyes large; long maxillary barbels extending beyond adipose-fin origin; mouth ventral; bones of cranial roof thin, lacking ornamentation and connected via lap junctions (dentate sutures absent); well-developed supraoccipital process; and triangular pectoral fins.

Type species.—*Mastiglanis asopos,* new species.

Etymology.—From the Greek mastix (mastigo, in latinized form) meaning whip, in allusion to the filamentous elements of pectoral and dorsal fins; and glanis, the name of the Greek catfish of Aristotle, a common denomination for fishes of the order Siluriformes. The last two letters of the word mastigo were suppressed for the sake of euphony. Gender masculine.

Mastiglanis asopos, new species
Figs. 1, 2, Table 1

Diagnosis.—As for the genus.

Holotype.—MNRJ 12227, SL 65.9 mm, Brazil, Pará, Igarapé Saracazinho, tributary of rio Trombetas, near Porto Trombetas, coll. É. P. Caramaschi & D. F. Moraes Jr., 14 Dec 1990.

Paratypes.—MNRJ 12228, 10 ex., SL 42.5–53.1 mm, taken with holotype; MNRJ 12229, 1 ex. cleared and stained, SL 48.8 mm, taken with holotype; MZUSP 7446, 2 ex., SL 44.8–51.5 mm, Brazil, Amazonas, município de Silves, rio Sanabani, coll. EPA, 7–8 Dec 1967; MZUSP 23299, 2 ex., SL 37.0–39.1 mm, Brazil, Amazonas, rio Jauaperi, beach 30 km upstream from the river mouth, coll. T. Roberts, 19 Nov 1968; MZUSP 23533, 1 ex., SL 39.6 mm, Brazil, Amazonas, left margin of the rio Içá, Cuiauá, Igarapé da Cachoeira, coll. EPA, 18 Oct 1968; MZUSP 23541, 10 ex., SL 30.8–58.2 mm, Brazil, Amazonas, left margin of the rio Içá, upstream from Cuiauá, Igarapé Boa Vista, coll. EPA, 19 Oct 1968; MZUSP 23549, 1 ex., SL 43.0 mm, Brazil, Amazonas, left margin of the rio Solimões, 7 km downstream from the Santo Antonio do Içá, Igarapé Içá, coll. EPA, 20 Oct 1968; MZUSP 23875, 1 ex., SL 35.8 mm, Brazil, Pará, rio Capim, Caranandéua beach, coll. EPA, 17 Aug 1970; MZUSP 24282, 2 ex., SL 28.3–34.7 mm, Brazil, Pará, município de São Luis, rio Tapajós, coll. EPA, 5 Nov 1970; MZUSP 25635, 1 ex., SL 27.4 mm, Brazil, Pará, pov. Pimental, right margin of the rio Tapajós, mouth of the Igarapé Pimental, coll. J. C. de Oliveira, 15–31 Jul 1979; MZUSP 30617, 84 ex., SL 16.5–40.0 mm, Brazil, Amazonas, rio Negro, 2 hours upstream from Barcelos, Urumari beach, coll. M. Goulding, 6 Oct 1979, 0000 h; MZUSP 30618, 11 ex., SL 19.6–41.8 mm, Brazil, Amazonas, beach at the Tamaquaré island, coll. M. Goulding, 10 Oct 1979, 2100 h; MZUSP 30633, 2 ex., SL 32.9–33.8 mm, Brazil, Amazonas, Massarabi, rio Negro, coll. M. Goulding, 18 Oct 1979; 2000 h; MZUSP 30635, 1 ex., SL 35.5 mm, Brazil, Amazonas, beach at Paraná do Jacaré, coll. M. Goulding, 7 Oct 1979, 2100 h; MZUSP 30636, 2 ex., SL 30.7–34.7 mm, Brazil, Amazonas, beach near mouth of rio Ararará (tributary of rio Negro), coll. M. Goulding, 6 Oct 1979, 2100 h; MZUSP 34953, 6 ex., SL 39.0–49.4 mm, Brazil, Amazonas, rio Daraá (tributary of rio Negro), Cachoeira do Aracu, coll. M. Goulding, 10 Feb 1980; MZUSP 34954, 17 ex., SL 26.4–38.1 mm, Brazil, Amazonas, near mouth of rio Marauiá (tributary of rio Negro), coll. M. Goulding, 13 Oct 1979; MZUSP 34955, 6 ex., SL 29.6–33.2 mm, Brazil, Amazonas, confluence of rio Arirará with rio Negro, coll. M. Goulding, Oct 1979; MZUSP 44215, 1 ex. cleared and stained, SL 52.0 mm, taken with MZUSP 34953; UFRJ 381, 2 ex., SL 35.7–38.6 mm, Brazil, Pará, muni-

Fig. 1. *Mastiglanis asopos*, n. gen. and sp. Lateral view of holotype, MNRJ 12227, 65.9 mm SL. Scale bar: 10 mm.

Table 1.—Morphometric data of *Mastiglanis asopos* taken from holotype (MNRJ 12227) and 10 paratypes (MNRJ 12228). Morphometric data 1–23 are expressed as percentage of standard length and 24–33 as percentage of head length. H: holotype; *SD*: standard deviation.

	H	$\bar{X}$	Range	*SD*
Standard length (mm)	65.9		42.5–65.9	
1. Predorsal length	35.4	34.9	33.6–35.8	0.75
2. Preanal length	69.2	69.6	68.0–71.2	1.06
3. Prepelvic length	43.7	42.6	40.1–43.7	1.09
4. Preadipose length	64.5	64.2	61.7–66.9	1.45
5. Caudal-peduncle length	20.0	20.8	18.8–22.5	1.28
6. Caudal-peduncle depth	5.9	5.9	5.6–6.3	0.24
7. Adipose-fin length	22.2	23.0	20.5–26.0	1.66
8. Dorsal fin to adipose fin	17.3	17.7	16.2–19.5	0.84
9. Anal-fin base	10.3	11.2	10.3–12.0	0.65
10. Dorsal-fin spine length	44.3	38.4	35.0–44.3	3.17
11. Length of first branched dorsal-fin ray	23.2	24.6	23.1–26.7	1.19
12. Length of second branched dorsal-fin ray	19.6	21.0	19.1–22.9	1.14
13. Dorsal-fin base	12.7	13.2	12.6–13.8	0.36
14. Pelvic-fin length	17.5	17.8	17.4–18.5	0.37
15. Pectoral-fin spine length	64.0	55.7	49.7–64.0	4.54
16. Length of first branched pectoral-fin ray	21.9	20.9	19.7–21.9	0.75
17. Length of second branched pectoral-fin ray	17.0	16.8	16.2–17.2	0.39
18. Body depth	14.6	13.6	12.2–14.6	0.90
19. Body width	17.3	16.2	15.1–17.3	0.72
20. Maxillary-barbel length	75.1	69.8	63.0–77.7	4.49
21. Outer mental-barbel length	40.7	35.2	26.1–42.7	5.03
22. Inner mental-barbel length	17.9	16.7	14.7–20.3	1.89
23. Head length	23.4	24.3	23.4–25.7	0.66
24. Head depth	50.6	47.7	44.4–53.0	2.58
25. Head width	72.1	69.9	67.2–72.7	1.90
26. Bony interorbital	10.3	10.0	8.7–11.3	0.82
27. Fleshy interorbital	22.1	22.7	21.7–24.6	0.94
28. Eye diameter	20.1	20.1	18.9–21.8	0.77
29. Preorbital length	42.9	41.6	39.2–43.5	1.74
30. Snout length	27.9	29.5	23.4–33.6	2.94
31. Internarial length	16.2	17.8	16.2–19.2	0.98
32. Anterior internarial width	13.6	14.1	13.3–15.0	0.57
33. Posterior internarial width	9.7	9.1	8.2–9.7	0.54

cípio de Castanhal, coll. H. Cunha, Oct 1990; UFRJ 382, 1 ex. cleared and stained, SL 38.0 mm, taken with UFRJ 381.

Description.—Morphometric data are given in Table 1. Refer to Fig. 1 for general appearance. A small rhamdiine catfish (largest specimen 65.9 mm SL). Dorsal profile slightly ascendent toward dorsal-fin origin, nearly straight to adipose-fin origin and from there slightly concave caudally. Ventral profile straight to anal-fin origin, gently concave to caudal peduncle. Body relatively elongated, elliptical in cross-section at dorsal-fin origin, gradually more compressed toward caudal peduncle. A conspicuous axillary organ present on each side of trunk, immediately above pectoral fins, composed of globular corpuscles covered by translucent skin. Lateral line complete. In preserved specimens, myomeres conspicuous along body, totaling around 32.

Head depressed, dorsally covered by a thin skin, cheek filled with muscular mass of adductor mandibulae. Snout long and pointed, conical in dorsal view. Posterior nostrils surrounded anterolaterally by skin flaps, well separated from anterior tubular nostrils (internarial length about twice the distance between posterior nostrils). Eyes large, lying close together, with orbital rim subtly invaginated anterodorsally. Mouth ventral, with crescentic aspect, with fleshy rictal fold at corner. Upper jaw markedly longer than lower. Premaxilla bearing approximately 30 tiny viliform teeth arranged in 4 irregular rows, its posterior corner gently curved posteriorly. Lower jaw with similar dentition disposed in 3 rows. Palatine and vomer edentulous. Barbels nearly ovoid in cross section. Maxillary barbels long, extending posteriorly beyond origin of anal fin. Outer and inner mental barbels long, extending posteriorly beyond pelvic- and pectoral-fin origins, respectively. Mental barbels supported by large and morphologically complex cartilaginous plates not fused mesially. Branchiostegal membranes medially overlapping, joined to isthmus region only at its anteriormost portion. Seven branchiostegal rays (5 on anterior ceratohyal, 1 on posterior ceratohyal, 1 on cartilage in between). Ten long gill rakers on first ceratobranchial plus 1 on the angle formed with first epibranchial. Fontanel reaching base of supraoccipital process, interrupted by epiphyseal bridge just behind eyes. Anterior portion of cranial fontanel narrow. Supraoccipital process well developed, wide, with lateral edges parallel and distal tip concave. Bones of cranial roof thin, with smooth texture (devoid of ornamentation). Frontals, sphenotics, pterotics, and supraoccipital joined via overlapping joints. Nasal bones elongate. Infraorbital series poorly ossified and comprised of five elements: lacrimal, a tiny canal transversely fused to lacrimal, and three tubular ossicles.

Dorsal fin well developed, triangular in overall shape with posterior margin gently concave, with i+6 rays. First dorsal-fin element (homologous to dorsal-fin spine) segmented, rigid at its proximal portion (a region as long as the first branched element), and with distal portion produced into a long and flexible filament reaching beyond adipose-fin origin when fin is adpressed to trunk. First and second branched dorsal-fin elements also rather developed. Locking element (spinelet) absent. Seven dorsal-fin pterygiophores articulating with bifid neural spines of vertebrae 6 through 12–13. First proximal radial enlarged. Two anteriormost proximal radials closely approximated for their entire lengths, and suturally connected at their proximal thirds, almost forming a single structure.

Pectoral fin scythe-shaped with i+8 (3), i+9 (10*). First element unfused, segmented, unserrated posteriorly, with basal portion (equivalent to length of first branched element) rigid and distal portion filamentous (Figs. 1, 2), the tip of which extends beyond anal-fin origin when pectoral fin is adpressed to trunk. Postcleithral process reduced, slightly curved dorsally.

Pelvic fin large, with i+5 rays, its origin vertically below fifth branched ray of dorsal fin.

Anal-fin rays ii+7 (7), iii+6 (4), iii+7 (2*) (plus 1 rudimentary anterior ray); anal fin with rounded margin in lateral profile, and originating at myomere 20–21. Nine blade-like pterygiophores between hemal spines of vertebrae 22 through 27–28.

Adipose fin long, barely triangular in shape, moderately high, its origin slightly in advance of origin of anal fin, nearly above the centra of vertebrae 16 or 17.

Caudal fin deeply forked, its lobes equal in length. Principal caudal rays i+7–i+8, procurrent caudal rays xiv (1), xv (2), xvi (7*), xvii (3) above; xiv (3), xv (7), xvi (2*), xvii (1) below. Hypural 1, hypural 1 and 2, and 3, 4, and 5 fused. Parahypural separate.

Six or seven pairs of ribs associated with parapophyses of vertebrae 6 to 11–12. First complete haemal spine on vertebrae 13 or 14. Distal extremities of pleural ribs strongly flattened dorsoventrally, presenting a scythe-like aspect. Total vertebrae 38. Swim

Fig. 2. Dorsal view of *Mastiglanis asopos,* paratype, MNRJ 12228, 42.5 mm SL.

bladder reduced, bilobed, transversely aligned, restricted to anterior body cavity.

Pigmentation in alcohol.—Overall body color pale yellowish (transparent when alive and white immediately after fixation). Dorsal half of trunk with almost indistinct disperse punctuation, ventral half devoid of pigment. Dorsal portion of body with seven conspicuous areas of concentrated dark chromatophores: one between head and dorsal fin (just behind nape), one in front of dorsal-fin origin, one at the level of last three branched dorsal-fin rays, one between dorsal and adipose fin, one just behind the adipose-fin origin, one on the posterior point of adipose-fin base, and one on caudal peduncle. Laterally, there are chromatophores concentrated along the horizontal septum, posteriorly to caudal-fin base, forming a poorly defined stripe. Some scattered melanophores present on top of head region, along path of infraorbital canals and over cheek. Dispersed melanophores at the humeral region, just above pectoral fins. Dorsal part of maxillary barbels darkly pigmented. Adipose fin with few irregularly distributed melanophores. Dorsal-, pectoral-, and caudal-fin rays lightly pigmented. Interradial membranes hyaline. Pigmentation intensity increases with size.

Etymology.—The specific name is derived from the Greek river-God Asopos, given in reference to the widespread distribution of this fish throughout Amazonian drainages.

Distribution.—Known to occur in the

Fig. 3. Distribution of *Mastiglanis asopos.* Asterisk indicates the locality where holotype was collected.

Amazon basin and the rio Capim, northern Brazil (Fig. 3).

Autapomorphies of *Mastiglanis*

Mees (1974) attempted to rediagnose the pimelodid genus *Imparfinis* on the basis of presence of free orbital rim and dorsal- and pectoral-fin spines, and as a consequence considered *Nannorhamdia* as its junior synonym. More recently, Mees & Cala (1989) tentatively gave a new definition to *Imparfinis* (also including *Nannorhamdia*). However, no derived character supporting the monophyly of *Imparfinis* was presented, making the genus a taxonomic waste-basket that encompasses medium- and small-sized rhamdiines not ascribed to other known genera. Because *Mastiglanis* does not have any evident derived characters shared with any other single rhamdiine genus, it would certainly fall into *Imparfinis* by traditional generic diagnoses. However, ongoing studies indicate that *Imparfinis piperatus,* the type species of its genus, plus some species, but not all, currently assigned to *Imparfinis* and *Nannorhamdia* compose a monophyletic group. This group is herein called *Imparfinis* sensu stricto. This group includes, at least, the following nominal species: *Chasmocranus peruanus, Imparfinis mirini, Imparfinis hasemani, Imparfinis piperatus, Nannorhamdia benedettii, Nannorhamdia guttatus, Nannorhamdia lineata, Nanno-*

rhamdia nemacheir, Nannorhamdia schubarti, Pimelodella cochabambae, Pimelodus longicauda, and *Rhamdia minuta.* At the moment, it is not possible to unambiguously assess the monophyly of *Nannorhamdia,* mainly because of uncertainties regarding *Nannorhamdia spurrellii,* the type species of the genus. Therefore, the synonymy between *Imparfinis* and *Nannorhamdia* is still doubtful. In any case, the specific composition of *Imparfinis* proposed by Mees & Cala (1989) makes the genus a non-monophyletic unit because the characters herein presented (see below) indicate that *Imparfinis* sensu stricto appears to be more closely related to a restricted group including the majority of the *Nemuroglanis* subclade (e.g., *Acentronichthys, Cetopsorhamdia, Chasmocranus,* and *Heptapterus,* none synonymized into *Imparfinis*), than to *Mastiglanis, Nemuroglanis, Rhamdiopsis,* and at least one species currently in *Nannorhamdia, Nannorhamdia stictonotus* Fowler (and probably *Imparfinis pseudonemacheir* Mees & Cala, a closely related species). Given the situation depicted above, *Mastiglanis* cannot be placed in *Imparfinis.* Also, *Mastiglanis* does not share any exclusive character with *Nemuroglanis, Rhamdiopsis* or *Nannorhamdia strictonotus,* justifying its generic rank. These attributes plus autapomorphies for the new genus are described and discussed below.

The integument pigmentation of *Mastiglanis* is limited to faint maculae on the dorsal region of trunk and head, a faint band of melanophores along the lateral line, and scattered melanophores on fin rays and maxillary barbels. Similar reductive pigmentation is encountered among cave dwelling pimelodids such as the monotypic genera *Caecorhamdella* Borodin, *Caecorhamdia* Norman, and *Typhlobagrus* Ribeiro, often accompanied by eye degeneration. However, *Mastiglanis* does not inhabit caves (it has diurnal activity, swimming in rock pools with sandy bottom covered with leaf litter deposition; É. P. Caramaschi, pers. comm.) and has very well-developed eyes. Irrespective of their habitats, the troglobitic pimelodids are related to relatively plesiomorphous unresolved rhamdiine assemblages (Ferraris, 1988; Lundberg et al., 1991a). Due to the large phylogenetic distance between them, the reduction in pigment is interpreted as an independent event, thus an autapomorphy for *Mastiglanis.*

The first elements of the pectoral and dorsal fins in *Mastiglanis* are prolonged into long and flexible filaments. The pectoral-fin filament is about 2.5 times as long as the first branched pectoral-fin element, and the dorsal filament is 1.5 times as long as the first branched dorsal-fin element, rare situations within Pimelodidae (Figs. 1, 2). Some species of *Pimelodella,* such as *P. figueroai* Dall, *P. griffini* Eigenmann, *P. insignis* Schubart, *P. martinezi* Fernández-Yépez, and *P. taenioptera* Ribeiro, show very similar filamentous conditions in the dorsal spine, but no other character is congruent with a hypothesis of close relationships between them and *Mastiglanis,* hence this trait is considered homoplastic. The most similar condition is present in the pectoral spine of *Nannorhamdia nemacheir* Eigenmann & Fisher, but various differences maintain it isolated from *Mastiglanis* [e.g., different body appearance, dark coloration, number of vertebrae (39–40 vs. 38 in *Mastiglanis*)]. Regardless of its distinctive traits, *Nannorhamdia nemacheir* certainly pertains to the genus *Imparfinis* sensu stricto, which is sufficient reason to consider the filamentous condition of the pectoral spine as not-homologous in this species and *Mastiglanis* (see Phylogenetic Relationships section below).

Usually in rhamdiines, the distance between the posterior nostrils is approximately equal to the distance between the anterior ones. A different situation occurs in *Mastiglanis,* where the anterior nostrils are nearly 1.5 times further apart than the posterior ones. Therefore, this situation is interpreted as an autapomorphy of *Mastiglanis.*

The eyes of *Mastiglanis* are set relatively close to one another (Bony Interorbital Distance about 10.0% of HL), while in other rhamdiines the eyes are separated by a considerably larger gap (Bony Interorbital Distance at least to 18.0% of HL). Therefore, the close placement of eyes of *Mastiglanis* is considered derived. This feature is seen osteologically by the narrowness of the orbitosphenoid and the frontals in the supraorbital region (Figs. 4, 5).

Perhaps the most striking autapomorphy of *Mastiglanis* is a prominent plate-like process at the anteroproximal portion of the premaxilla (Figs. 4, 5). This process, unique within rhamdiines, is edentulous and gently directed dorsally, and is related to the pointed snout of this fish.

Another autapomorphy identified at the anterior cranial region is the modified anterior mesethmoid cornua. Plesiomorphically, the catfish mesethmoid cornua have arms that diverge anterolaterally gradually. In *Mastiglanis,* the arms reverse abruptly at mid length, assuming a posterolateral orientation—a situation unique within Rhamdiinae (Fig. 5).

Among rhamdiine catfishes the common metapterygoid configuration is that illustrated by Lundberg & McDade (1986) for *Brachyrhamdia,* where the bone is roughly quadrangular and approximately as long as deep. The metapterygoid in *Mastiglanis,* contrastingly, is longitudinally elongate, rectangular in shape (Fig. 6).

Finally, two other uniquely derived characters of *Mastiglanis* may be observed in its opercle. A sloping osseous flange is present on the dorsal border of the opercle, lying in the same plane of the bone. This lamina is raised just posterior to the site of articulation of the preopercle and decreases gradually towards the posterior extremity of the bone, reaching to its mid length (Fig. 6). A dorsal lamina is also present in the opercle of other rhamdiines, but it is medially reflected, originated at its mid length, and increases towards the posterior extremity of the bone. Although both structures can still be considered homologous, the state in *Mastiglanis* is hypothesized as derived since it is a condition unknown within rhamdiines. Also, the distal extremity of the opercle of *Mastiglanis* is exclusively tapered and directed ventrally (Fig. 6), a difference which can be taken as additional evidence for its monophyly.

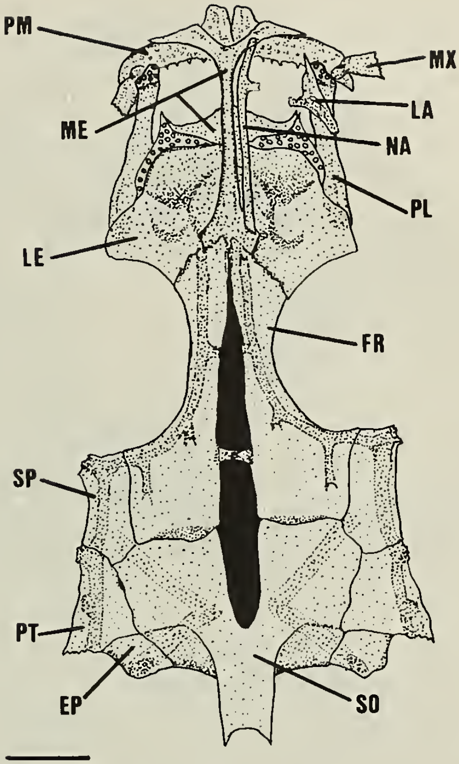

Fig. 4. Dorsal view of cranial skeleton of *Mastiglanis asopos,* paratype, UFRJ 382, 38.0 mm SL. Scale bar: 1 mm. Abbreviations: EP—Epioccipital; FR—Frontal; LA—Lacrimal; LE—Lateral ethmoid; ME—Mesethmoid; MX—Maxilla; NA—Nasal; PL—Palatine; PM—Premaxilla; PT—Pterotic; SO—Supraoccipital; SP—Sphenotic. Extrascapula and infraorbitals not represented.

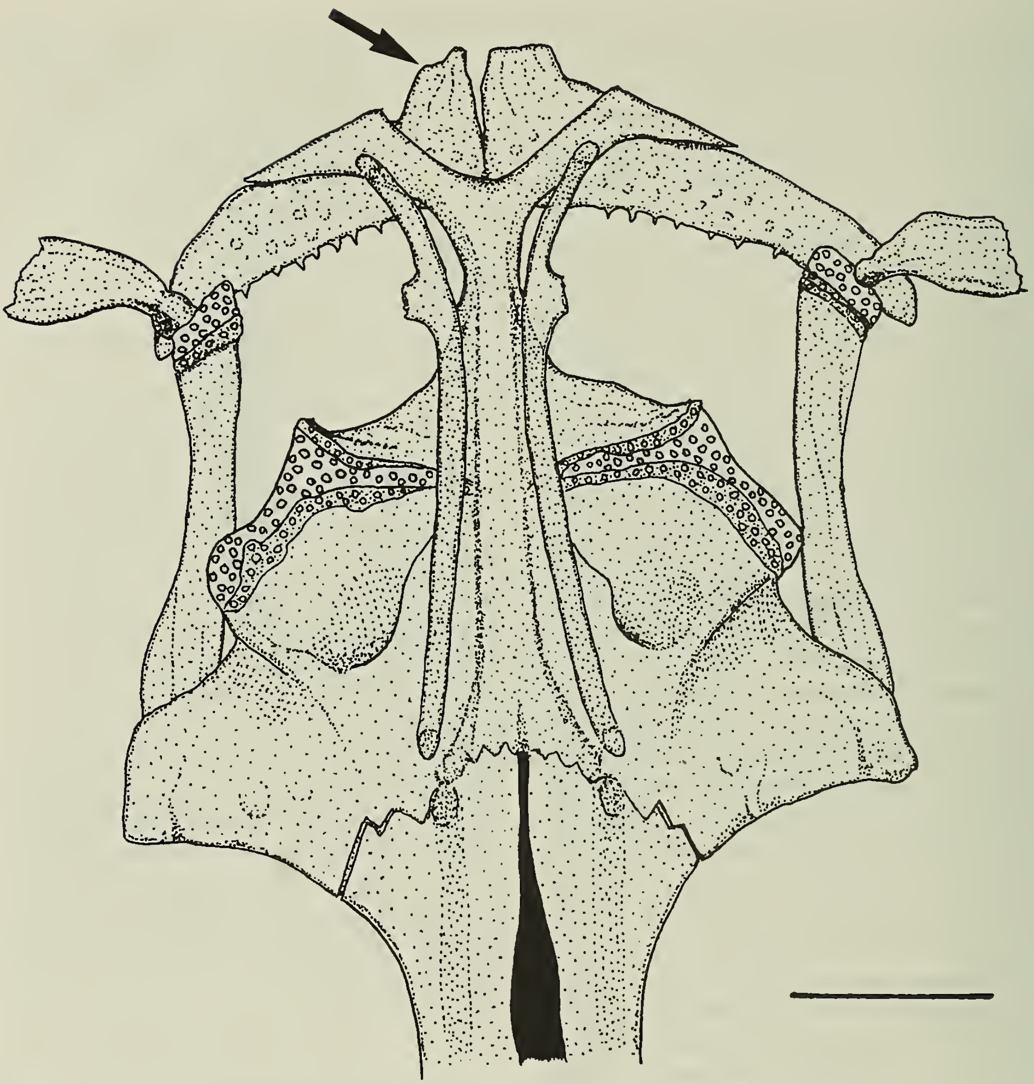

Fig. 5. Anterior portion of the cranial skeleton of *Mastiglanis asopos*, paratype, MZUSP 44215, 52.0 mm SL. Arrow points to the anterior process of premaxilla. Scale bar: 1 mm.

Phylogenetic Relationships of *Mastiglanis*

The family Pimelodidae has recently received a cladistic treatment, and large monophyletic subsets have been identified, a first step towards the elucidation of phylogenetic relationships in this still much confused assemblage (Lundberg & McDade 1986; Stewart 1986a, Ferraris 1988, Lundberg et al. 1988, Lundberg et al. 1991a, 1991b). Lundberg & McDade (1986) and Lundberg et al. (1991a) provided evidence for a monophyletic group within Pimelodidae composed of the following genera: *Acentronichthys, Brachyglanis, Brachyrhamdia, Caecorhamdella, Caecorhamdia, Cetopsorhamdia, Chasmocranus, Gladioglanis, Goeldiella, Heptapterus, Horiomyzon, Imparales, Imparfinis, Leptorhamdia, Medemichthys, Myoglanis, Nannorhamdia,*

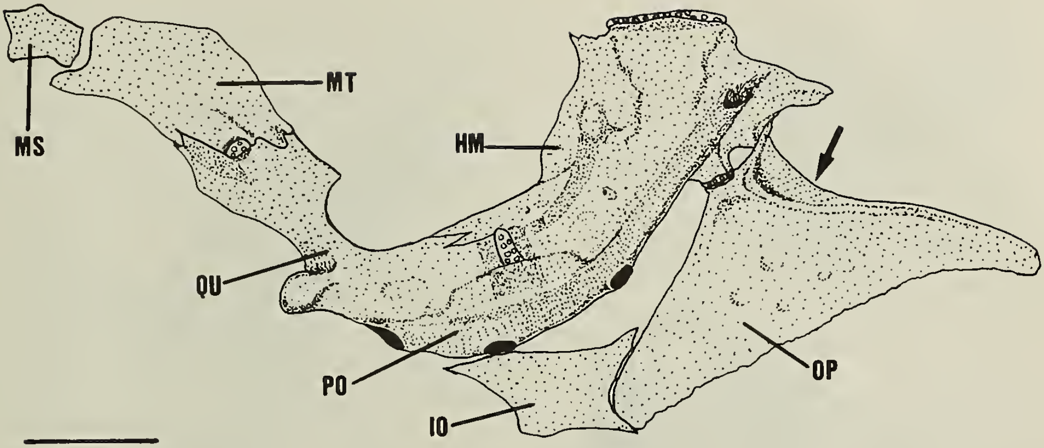

Fig. 6. Lateral view of the left suspensorium and opercular series of *Mastiglanis asopos*, paratype, MZUSP 44215, 52.0 mm SL. Arrow shows the osseous lamina running on dorsal edge of opercle. Scale bar: 1 mm. Abbreviations: HM—Hyomandibula; IO—Interopercle; MS—Mesopterygoid; MT—Metapterygoid; OP—Opercle; PO—Preopercle; QU—Quadrate.

Nemuroglanis, Pariolius, Phenacorhamdia, Phreatobius, Pimelodella, Rhamdella, Rhamdia, Rhamdiopsis, and *Typhlobagrus.* Two other nominal genera, *Nannoglanis* and *Rhamdioglanis,* can be added to this list. Lundberg et al. (1991a) ranked the above monophyletic group as the subfamily Rhamdiinae. The following synapomorphies for the Rhamdiinae are compiled from Lundberg et al. (1991a): 1) posterior limb of fourth tranverse process laterally expanded above swim bladder and notched once to several times; 2) neural spines of Weberian complex centrum joined by a straight-edged, horizontal or sometimes sloping bony lamina; 3) process for insertion of levator operculi muscle on posterodorsal corner of hyomandibula greatly expanded; 4) quadrate with a free dorsal margin and bifid shape, its posterior and anterior limbs articulate separately with hyomandibula and metapterygoid; 5) presence of an anteriorly recurved process drawn out from ventrolateral corner of mesethmoid. *Mastiglanis* presents all of the above characters, supporting its inclusion in Rhamdiinae. Further, it has the following derived traits shared exclusively by a rhamdiine subgroup called *Nemuroglanis* subclade (Ferraris 1988): the laminar portion of complex centrum transverse process, posterior to branched segment, is triangular and extends nearly to the lateral tip of the fifth vertebral transverse process; the first dorsal-fin basal pterygiophore is inserted behind the Weberian complex, usually above vertebrae 7 to 10; the "dorsal-fin spine" is thin and flexible and the dorsal-fin lock is absent; the "pectoral-fin spine" is thin and flexible for its distal half. This subset is composed of the following genera: *Acentronichthys, Cetopsorhamdia, Chasmocranus, Heptapterus, Horiomyzon, Imparales, Imparfinis, Medemichthys, Nannoglanis, Nannorhamdia, Nemuroglanis, Pariolius, Phenacorhamdia, Phreatobius, Rhamdioglanis, Rhamdiopsis,* and now also *Mastiglanis.* In addition to those characters, new traits supporting an hypothesis of monophyly of the *Nemurglanis* sub-clade are proposed below.

Various modifications of the pectoral girdle and associated parts are related to the reduction of the pectoral-fin spine men-

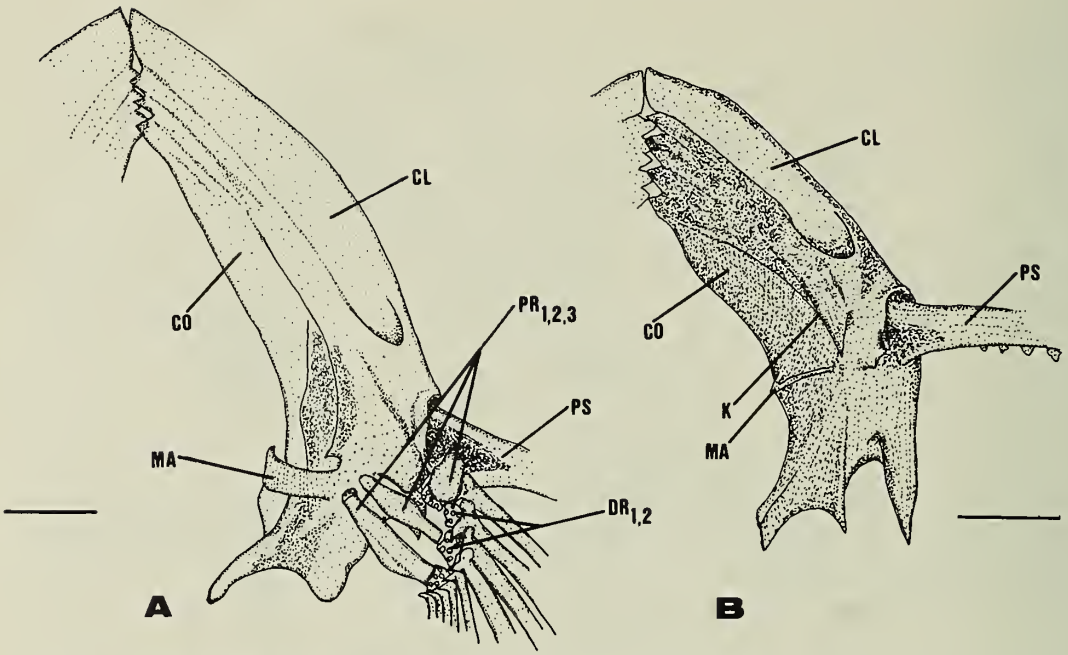

Fig. 7. Ventral view of the pectoral girdle of: A. *Mastiglanis asopos,* paratype, MZUSP 44215, 52.0 mm SL, Scale bar: 1 mm; B. *Brachyrhamdia meesi,* UFRJ 397, 42.8 mm SL, Scale bar: 2 mm SL. Abbreviations: CL—Cleithrum; CO—Coracoid; DR 1, 2—Distal radials 1 and 2; K—Coracoid keel; MA—Mesocoracoid arch; PR 1, 2, 3—Proximal radials 1, 2, and 3; PS—Pectoral spine.

tioned above. Plesiomorphically, the mesocoracoid arch is a slender and delicate ring (Fig. 7B, Arratia 1987, Grande 1989, Grande & Lundberg 1988). Within Rhamdiinae, this structure differs markedly in the *Nemuroglanis* sub-clade, where it is modified into a wide band (Fig. 7A). Also, the two posterior proximal radials are apomorphically enlarged and flattened in the *Nemuroglanis* sub-clade (Fig. 7A). In most pimelodids, in contrast, the pectoral radials are plesiomorphically thin.

Two other characters of the pectoral-fin girdle offer further support for the monophyly of the *Nemuroglanis* sub-clade, including *Mastiglanis.* Usually the ventral portion of the catfish pectoral girdle is formed by a horizontal bridge composed of the two cleithra ligamentously united to each other and by the scapulo-coracoid (hypocoracoid of Regan 1911) tightly joined to its bilateral counterpart via an interdigitating suture (Regan 1911). The interlocking symphysis of the scapulo-coracoid is absent in Diplomystidae (Regan 1911, Arratia 1987), but widely distributed among almost all other siluriforms, including the basal genus *Hypsidoris,* being probably the plesiomorphic condition at the level of non-diplomystid catfishes. *Hypsidoris* has the scapulo-coracoids interdigitated with six sutural dentations (Grande 1987). Seven dentations are present in the fossil ictalurid *Astephus* (Grande & Lundberg 1988). The same situation occurs among the majority of Pimelodidae, Pseudopimelodidae, and Rhamdiinae exclusive of the *Nemuroglanis* sub-clade, where all have at least four scapulo-coracoid dentations (Fig. 7B). In contrast, the *Nemuroglanis* sub-clade have a delicate pectoral girdle with a short mesial contact line comprising only three weakly joined scapulo-coracoid dentations. The contact surface between the cleithra is also reduced (Fig. 7A). Therefore, the extreme reduction of the sutural extension between the scapulo-coracoids is interpreted as apomorphic. Within pimelodids, a similar condition is developed homoplastically in the *Calophysus* group (Stewart 1986a) and *Megalonema.*

Another feature postulated as autapomorphic for the *Nemuroglanis* sub-clade is the absence of a pointed process projected posteroventrally from the coracoid keel. Although such a process has not been noted in Diplomystidae or Hypsidoridae, the hypothesized consecutive sister-groups of all other extant siluriforms (Fink & Fink 1981, Arratia 1987, Grande 1987), it is present in the majority of pimelodids, including all rhamdiines outside of the *Nemuroglanis* sub-clade (Fig. 7B), and in various other catfish families (e.g., Ariidae, Bagridae, Auchenipteridae, Mochockidae). Consequently, its absence is interpreted as a synapomorphy for the genera in the *Nemuroglanis* subclade (Fig. 7A).

The gas bladder composed of one anterior and two posterior chambers is the hypothesized generalized display for siluriforms (Regan 1911; Chardon 1968). The posterior chambers in members of the *Nemuroglanis* sub-clade are atrophied. The gas bladder in these catfishes is represented only by a bilobed transversely aligned structure, covered anterodorsally by the anterior limbs of the transverse process of the complex vertebra.

Among the members of the *Nemuroglanis* sub-clade, the nasal bone is comparatively longer and less ossified than in remaining rhamdiines (Figs. 4, 5). The morphology of this bone in basal rhamdiines is similar to that in other catfishes (e.g., *Hypsidoris*), i.e., a short and robust structure. Hence, the elongation and reduced ossification of the nasal is interpreted as a synapormorphy for the *Nemuroglanis* sub-clade.

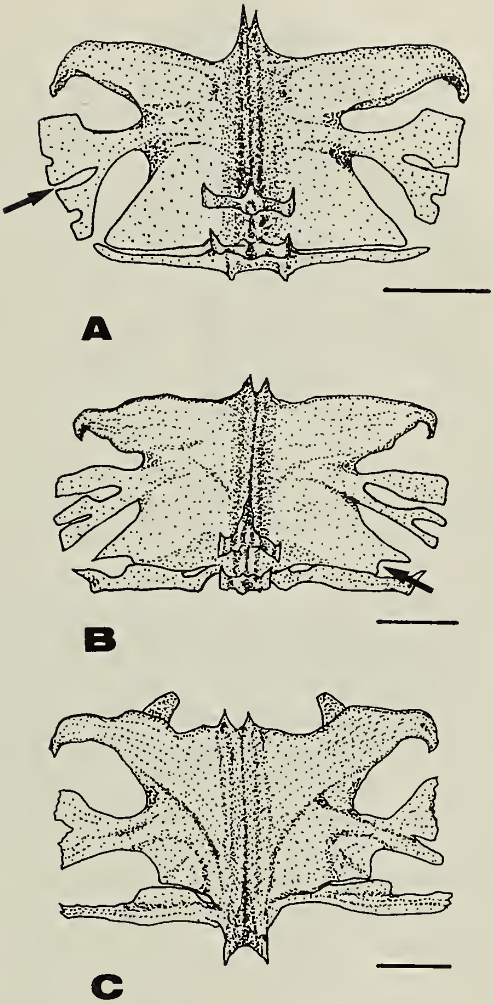

Fig. 8. Dorsal view of the complex vertebrae of: A. *Mastiglanis asopos*, paratype, UFRJ 382, 38.0 mm (arrow indicates the medial notch); B. *Imparfinis minutus*, UFRJ 320, 48.0 mm (arrow indicates the notch at angle of the triangular posterior lamina); C. *Rhamdia* sp., UFRJ 321, 44.0 mm.

Plesiomorphically among catfishes, the neural arch of the fourth vertebra is sloped posteriorly, and gives rise to two divergent ridges that reach the anterior limbs of the transverse process of the fourth vertebra (see fig. 9 in Arratia 1987). This situation is seen in the basal ictalurid *Astephus* (fig. 12A–B in Grande & Lundberg 1988), and also in many Rhamdiinae (Fig. 8C), but not in the

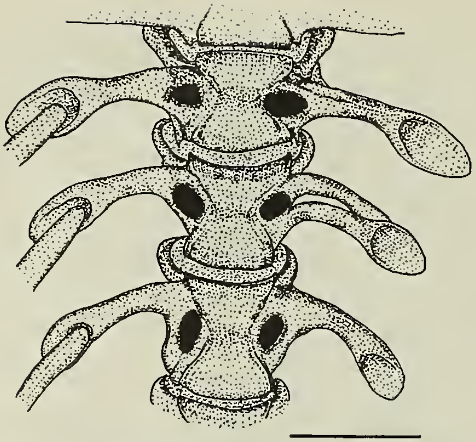

Fig. 9. Ventral view of the unmodified anterior vertebrae of *Cetopsorhamdia iheringi,* UFRJ 689, 53.0 mm SL. Scale bar: 1 mm.

Nemuroglanis sub-clade, where the ridges are apomorphically absent (Fig. 8A–B).

In the *Nemuroglanis* sub-clade, the transverse process of the fourth vertebra branches three times. The anterior division separates the principal anterior and posterior limbs, as in the hypothesized primitive condition (Grande & Lundberg 1988). Additional ramifications of the posterior limb is an apomorphic character of Rhamdiinae (Lundberg & McDade 1986). Uniquely among the members of *Nemuroglanis* sub-clade, however, there is an exclusive deep posterior notch that delimits a posterior triangular lamina (Ferraris 1988). In addition, *Mastiglanis* and all other members of the *Nemuroglanis* sub-clade exclusively possess a distinct deep medial notch that divides the posterior limb of the fourth transverse process into two divergent, approximately symmetrical, long arms (compare Fig. 8A–B and Fig. 8C; for other examples see fig. 4C in Lundberg & McDade 1986 and fig. 3 in Ferraris 1988). These arms may secondarily branch and coalesce distally.

Another point of evidence for the monophyly of the *Nemuroglanis* sub-clade is the unmodified anterior free vertebrae. In taxa belonging to that clade, the proximal extremities of the pleural ribs fit under the distally expanded and concave tips of the parapophyses (Fig. 9). In the majority of pimelodids (and other catfishes), contrastingly, the ribs are associated ventrally with the parapophyses without well-defined alveolar sites for articulation. A very similar condition, postulated as independent, is observed in the pimelodines *Calophysus* and *Megalonema.*

Mastiglanis and all other members of the *Nemuroglanis* sub-clade have the hemal and neural spines of the caudal vertebrae oriented at about 35° to the column axis (Fig. 10A–B). In contrast, a more open angle (greater or equal to 45°, modally 55°) is largely diffused among other pimelodids, including remaining rhamdiines (Fig. 10C). Due to a more restricted distribution, the former situation (an oblique angle) is considered an apomorphic transformation from the latter one (an open angle), corroborating the *Nemuroglanis* sub-clade monophyly. Also, the components of this sub-clade share derived robust hemal and neural spines of the last free precaudal vertebrae, differing from the plesiomorphic state (hemal and neural spines uniformly thin along their lengths) observed in other rhamdiines (compare Fig. 10A–B and Fig. 10C).

However, *Mastiglanis, Nannorhamdia stictonotus, Nemuroglanis,* and *Rhamdiopsis* present the plesiomorphic state of one character that occurs apomorphically among all other taxa related to the *Nemuroglanis* sub-clade (Fig. 10A–C). *Acentronichthys,*

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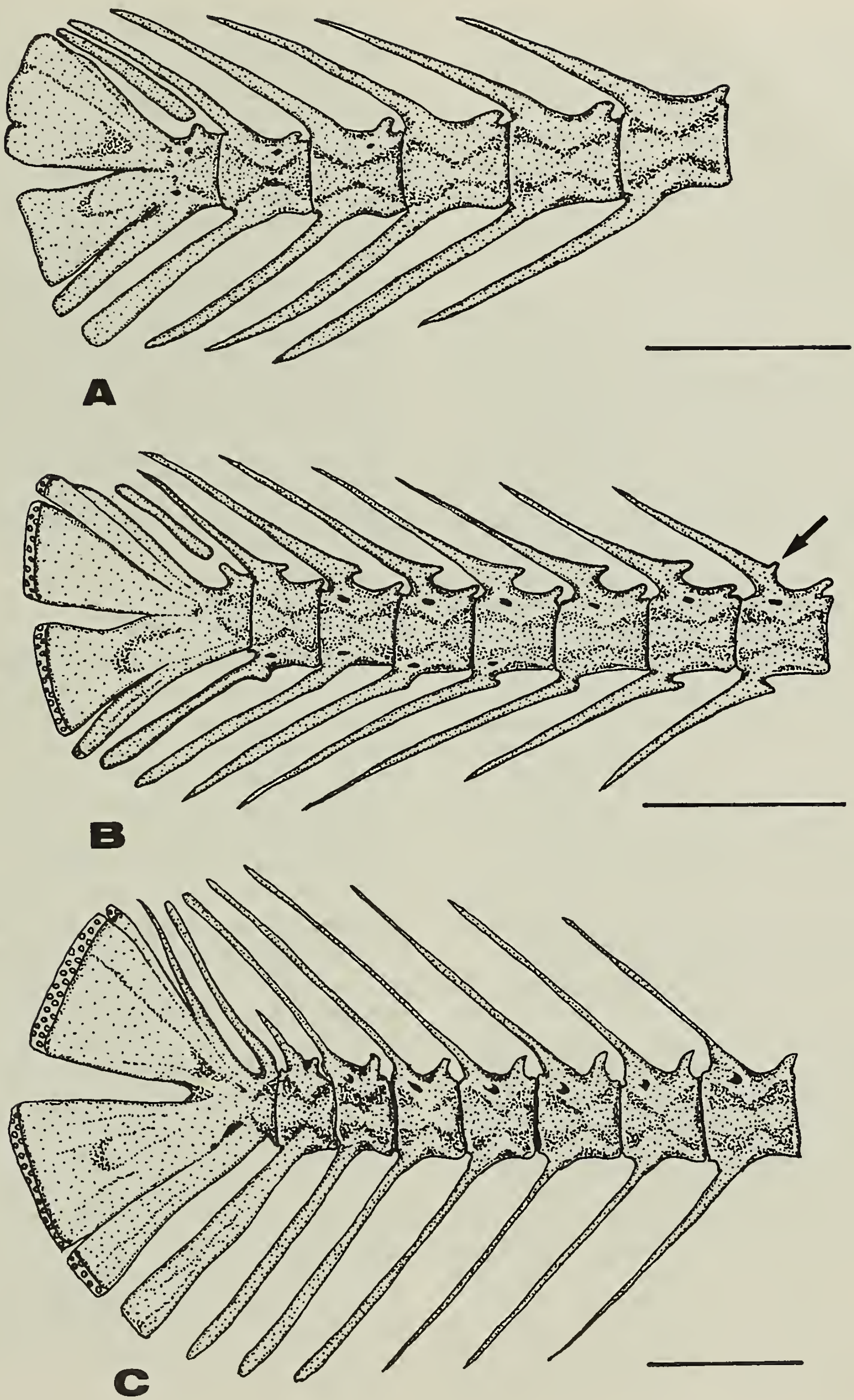
Fig. 10. Posterior caudal vertebrae of: A. *Mastiglanis asopos,* paratype, MZUSP 34953, 52.0 mm SL; B. *Imparfinis minutus,* UFRJ 320, 48.0 mm SL (arrow points to the neural process); C. *Goeldiella eques,* MZUSP 45907, 77.6 mm SL.


A
B
C

Cetopsorhamdia, Chasmocranus, Heptapterus, Imparales, Imparfinis, Phenacorhamdia, and probably the remaining genera of the *Nemuroglanis* sub-clade, exhibit a median anterior process nearly parallel to the vertebral column axis at the base of spines, at least, of the last five vertebrae (Fig. 10B, see arrow). This derived trait constitutes evidence for the monophyly of a group including these genera.

An additional derived character provides putative evidence for a more inclusive monophyletic group within the *Nemuroglanis* sub-clade. In *Acentronichthys, Cetopsorhamdia, Chasmocranus, Heptapterus, Imparales, Imparfinis, Phenacorhamdia,* and also *Nannorhamdia stictonotus* and *Rhamdiopsis* (and probably *Pariolius, Medemichthys, Nannoglanis,* and *Rhamdioglanis*), the triangular posterior lamina of the complex centrum transverse process has at its distal angle an additional notch (Fig. 8B, arrow). This configuration is not present in *Nemuroglanis* and *Mastiglanis* (Fig. 8A), where the posterior margin of the triangular posterior lamina is fully straight. The former condition is considered apomorphic and defines a subset including all genera of the *Nemuroglanis* sub-clade except *Nemuroglanis* and *Mastiglanis.* Consequently, *Nemuroglanis* and *Mastiglanis* are candidates for the position of sister group to the other *Nemuroglanis* sub-clade members.

Furthermore, the medial notch separating two symmetrical arms of the posterior limb of complex vertebrae is more attenuated in *Mastiglanis* than in other members of the *Nemuroglanis* sub-clade, including *Nemuroglanis* (compare Fig. 8A and Fig. 8B). This may be an indication that *Mastiglanis* is the sister-group of all other members of the *Nemuroglanis* sub-clade. Although I acknowledge that it is a weak evidence, it is the only one available at present. Two other characters might be used as further evidence for that hypothesis. Almost all members of the *Nemuroglanis* sub-clade share a pectoral fin with a rounded contour, an unquestionable derived trait, as opposed to triangular (the widespread siluriform configuration) as seen in *Mastiglanis.* Also, *Mastiglanis* presents a seemingly plesiomorphic well-developed supraoccipital process (vs. a reduced condition seen in all other *Nemuroglanis* subclade members). However, both derived states are also found at some level in some species of *Brachyglanis, Myoglanis, Leptorhamdia,* and *Gladioglanis,* that were pointed as potentially related to the *Nemuroglanis* sub-clade by Lundberg et al. (1991a). As the distribution of these features is still poorly known, their value as indicators of relationships is not decisive at present. More conclusive proposals with respect to the position of *Mastiglanis* must await a detailed phylogenetic analysis of Rhamdiinae (Bockmann, in prep.).

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Applications published in the *Bulletin of Zoological Nomenclature*

The following Applications were published on 30 September 1994 in Vol. 51, Part 3 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.
2904 *Nesopupa* Pilsbry, 1900 (Mollusca, Gastropoda): proposed conservation.
2902 *Acanthoteuthis* Wagner in Münster, 1839 and *Kelaeno* Münster, 1842 (Mollusca, Cephalopoda): proposed conservation of usage.
2915 *Lironeca* Leach, 1818 (Crustacea, Isopoda): proposed conservation as the correct original spelling.
2844 *Oniscus asellus* Linnaeus, 1758 (Crustacea, Isopoda): proposed designation of a neotype.
2638 *Apis terrestris* Linnaeus, 1758, *A. muscorum* Linnaeus, 1758 and *A. lucorum* Linnaeus, 1761 (currently *Bombus terrestris, B. muscorum* and *B. lucorum*) and *Bombus humilis* Illiger, 1806 (Insecta, Hymenoptera): proposed conservation of usage of the specific names.
2866 MEGALODONTIDAE Morris & Lycett, 1853 (Mollusca, Bivalvia) and MEGALODONTIDAE Konow, 1897 (Insecta, Hymenoptera): proposed removal of homonymy.
2936 CAECILIIDAE Rafinesque-Schmaltz, 1814 (Amphibia, Gymnophiona) and CAECILIIDAE Kolbe, 1880 (Insecta, Psocoptera): proposed removal of the homonymy by the revocation of Opinion 1462 and the adoption of the spelling CAECILIUSIDAE for the psocopteran family name.
2362 PHRYNOBATRACHINAE Laurent, 1941 (Amphibia, Anura): proposed conservation.
2895 *Plesiosaurus rugosus* Owen, 1840 (currently *Eretmosaurus rugosus*; Reptilia, Plesiosauria): proposed designation of a neotype.
2875 *Coluber poecilogyrus* Wied-Neuwied, [1824] (currently *Liophis poecilogyrus*) (Reptilia, Serpentes): proposed conservation of the specific name.
2856 *Psittacus banksii* Latham, 1790 and *P. lathami* Temminck, 1807 (currently *Calyptorhynchus banksii* and *C. lathami*; Aves, Psittaciformes): proposed conservation of the specific names.

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 30 September 1994 in Vol. 51, Part 3 of the *Bulletin of Zoological Nomenclature.* Copies of these Opinions can be obtained free of charge from the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Opinion No.

1778 *Acineta* Ehrenberg, [1834] and *Tokophrya* Bütschli, 1889 (Ciliophora, Suctoria): conserved, and *Acineta tuberosa* Ehrenberg, [1834] and *Podophrya quadripartita* Claparède & Lachmann, 1859 (currently *Tokophrya quadripartita*): specific names conserved.

1779 *Potamolithus* Pilsbry & Rush, 1896 (Mollusca, Gastropoda): placed on the Official List with *Paludina lapidum* d'Orbigny, 1835 as the type species.

1780 *Turbo politus* Linnaeus, 1758 (currently *Melanella polita*; Mollusca, Gastropoda): usage of the specific name conserved, so conserving the specific name of *Buccinum acicula* Müller, 1774 (currently *Cecilioides acicula*).

1781 *Termes lacteus* Froggatt, 1898 (currently *Coptotermes lacteus*; Insecta, Isoptera): specific name conserved.

1782 *Corisa nigrolineata* Fieber, 1848 (currently *Sigara* (*Pseudovermicorixa*) *nigrolineata*; Insecta, Heteroptera): specific name conserved.

1783 *Aradus caucasicus* Kolenati, 1857 (Insecta, Heteroptera): syntype replaced by a neotype, so conserving the usage of the specific name and that of *A. hieroglyphicus* Sahlberg, 1878.

1784 *Buprestis* Linnaeus, 1758 and *Chrysobothris* Eschscholtz, 1829 (Insecta, Coleoptera): conserved by the designation of *Buprestis octoguttata* Linnaeus, 1758 as the type species of *Buprestis,* and *Chrysobothris* and *Dicerca* Eschscholtz, 1829: conserved as the correct original spellings.

1785 *Dytiscus biguttatus* Olivier, 1795 (currently *Agabus biguttatus*; Insecta, Coleoptera): specific name conserved.

1786 *Ascopora* Trautschold, 1876 (Bryozoa, Cryptostomata): *Ceriopora nodosa* Fischer von Waldheim, 1837 designated as the type species.

1787 *Mugil curema* and *M. liza* Valenciennes in Cuvier & Valenciennes, 1836 (Osteichthyes, Perciformes): specific names conserved.

1788 *Scelidosaurus harrisonii* Owen, 1861 (Reptilia, Ornithischia): lectotype replaced.

1789 *Pseudoxyrhopus* Günther, 1881 (Reptilia, Serpentes): conserved.

1790 *Lagomeryx* Roger, 1904 (Mammalia, Artiodactyla): *Lagomeryx ruetimeyeri* Thenius, 1948 designated as the type species.

1791 *Procervulus* Gaudry, 1877 (Mammalia, Artiodactyla): *Antilope dichotoma* Gervais, 1849 designated as the type species.

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.

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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.

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